SECOND EDITION

A NEW ECOLOGY
SYSTEMS PERSPECTIVE

Søren Nors Nielsen, Brian D. Fath

Simone Bastianoni, João Carlos Marques,
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Sven E. Jørgensen and Enzo Tiezzi

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Dedication

Starting around the first Ecological Summit back in 1996 in Copenhagen, a small group of researchers initiated a project to understand nature's functional thermodynamic and information-based principles aimed to improve environmental management. This project has pulsed along during the ensuing decades, on the way adding new members, but also losing others. This volume is dedicated to those we have lost in gratitude for the scientific inheritance we received from them. Although missing in body, their spirit is still with us in the ideas they expressed and in the many discussions, papers, and books they contributed. For this we are very grateful, and have continued the work in memory of Giuseppe Bendoricchio, Sven Erik Jørgensen, James J. Kay, Ramon Margalef, Howard T. Odum, Milan Straškraba, and Yuri Svirezhev.

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Preface to the Second Edition

The first edition of *A New Ecology* emanated out of a brainstorming workshop that Sven Jørgensen organized in June 2005 on the Danish Island, Møn. Out of those sessions emerged the ideas that shaped that book which was published in 2007. The field of ecology is rapidly changing, and we notice there is movement toward systems ideas and holistic thinking. Perhaps there is some impact of the ideas in *A New Ecology*, but there is much more to do to mainstream this approach and witness its penetration into standard ecology and biology textbooks. A stronger integration of physical sciences (physics, chemistry, engineering, etc.) with the biological sciences would help realize a holistic science as envisioned here. Even further work is needed then to incorporate the social sciences and policy choices that are needed to find pathways that promote sustainable development.

During the ensuing period between editions, we unfortunately lost two critical members of our research group, Tiezzi (2010) and Jørgensen (2016). In fact, it was Sven's initiative to have a second edition. He made the arrangements and initial outlines for the new book. The book has the same main elements of the first edition but with the addition of one chapter on hierarchy (Chapter 5) and another on the application of the principles to policy and management (Chapter 11). Other chapters have been updated and expanded. Due to a close collaboration of the authors, the book is truly a team effort in which all authors are free to comment and contribute to each chapter. In preparing the second edition, the "team" was able to meet on two occasions for brainstorming, first in Montpelier, France, during the EcoSummit 2016 (Fig. 1). The second meeting occurred at the International Institute for Applied Systems Analysis in Laxenburg, Austria, in January 2017 (Fig. 2). In addition to the meetings, numerous emails, "ping-pongs" as Sven

FIGURE 1 Breakout meeting during lunch of the Ecosummit 2016 in Montpelier, France (Simone, João, Søren, Larry, Felix, and Brian).

FIGURE 2 Selfie taken in January 2017 in the Elisabeth Room of Schloss Laxenburg, current home of the International Institute for Applied Systems Analysis, Laxenburg, Austria (João, Brian, Simone, Søren, and Larry).

referred to them, have produced this volume. The book also would not have been possible without the patient persistence of the Elsevier publisher, Emily Thomson. We hope that the reader has as much fun reading the book as we did in discussing, learning, and constructing the ideas that have shaped our research agenda in systems ecology.

Søren Nors Nielsen
Copenhagen, June 2019

Brian D. Fath
Laxenburg, June 2019

CHAPTER

1

Introduction: A New Ecology Is Needed

1.1 ENVIRONMENTAL MANAGEMENT HAS CHANGED

The political agenda imposed on ecologists and environmental managers has changed since the early 1990s. Since the Rio Declaration and Agenda 21 in 1992, the focus has been on sustainability, which inevitably has made ecosystem functioning a core issue. Sustainable Development is, according to the Rio Declaration, defined as follows: "development that meets the needs of the present without compromising the ability of future generations to meet their own needs." And, the contrasting parties are invited to "act in a way that is economically profitable, socially acceptable, and environmentally compatible." Already the Rio Declaration emphasized the importance of ecosystems in **Principle 7: States shall cooperate in a spirit of global partnership to conserve, protect and restore the health and integrity of the Earth's ecosystems**.

In view of the different contributions to global environmental degradation, states have common but differentiated responsibilities. The developed countries acknowledge the responsibility that they bear in the international pursuit of sustainable development in view of the pressures their societies place on the global environment and of the technologies and financial resources they command.

The changing climate represents one of the largest threats to ecosystems of the Earth, which poses a threat to stable life conditions of all species including humans all over the world. Considering globalization, there is no region where human population can ignore this and consider themselves not to be affected by any of the scenarios presented in an increasing number of reports. We are already seeing the impacts today in increased hurricane strength and activity, heat waves, flooding, and temperature anomalies that are beyond the "normal" historical trends. Since 1995, the United Nations has been responsible for a series of conferences on climate change known as Conference of Parties (COPs), of which the third led to an important milestone with the Kyoto Protocol in 1997, COP 3, which was ratified by 191 states. Unfortunately, the strategies proposed were not sufficient to mitigate the emission of greenhouse gases. However, it did demonstrate the need to come together as a global community to address the topic and change the dialogue toward emission reduction pathways. Already, before it ended, there was discussion of post-Kyoto (it sunsetted in 2012) and a new agreement that would more aggressively address the issue. The financial crisis of the late 2000s made countries less collaborative; even though the economic collapse resulted in lowering emissions, the efforts of most countries was to turn that around as soon as possible, without new regulations that the business community felt would be hamstringing. After some gaps and compromise, a more bottom-up approach (nationally determined contributions (NDCs)) emerged at the COP21 meeting in Paris in 2015. The Paris Agreement came into force in early November 2016. The adopting countries have agreed to implement reduction measures from 2020. A recent, fall 2018, IPPC report indicates that warming will reach a critical 1.5°C threshold by 2030 unless substantial and urgent actions are taken in the near term. While the science is clear, are humans capable of managing such a massive, international, multidimensional issue? Can we use our knowledge of ecological systems and practices—how they balance biogeochemical cycles? Can a new ecology help point the way?

Another major international effort at cooperation for the environment was the Convention on Biological Diversity (CBD), adopted in 2000. The CBD, with 12 principles, explicitly called for an Ecosystem Approach—that placed the ecosystem concept centrally into environmental management considerations. It is particularly clear from the last 10 of the 12 principles:

1) The objectives of management of land, water, and living resources are a matter of societal choice.
2) Management should be decentralized to the lowest appropriate level.

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3) Ecosystem managers should consider the effects (actual or potential) of their activities on adjacent and other ecosystems.
4) Recognizing potential gains from management, there is usually a need to understand and manage the ecosystem in an economic context. Any such ecosystem management program should:
   a. reduce those market distortions that adversely affect biological diversity;
   b. align incentives to promote biodiversity conservation and sustainable use;
   c. internalize costs and benefits in the given ecosystem to the extent feasible.
5) Conservation of ecosystem structure and functioning, in order to maintain ecosystem services, should be a priority target of the ecosystem approach.
6) Ecosystems must be managed within the limits of their functioning.
7) The ecosystem approach should be undertaken at the appropriate spatial and temporal scales.
8) Recognizing the varying temporal scales and lag effects that characterize ecosystem processes, objectives for ecosystem management should be set for the long term.
9) Management must recognize that change is inevitable.
10) The ecosystem approach should seek the appropriate balance between, and integration of, conservation and use of biological diversity.
11) The ecosystem approach should consider all forms of relevant information, including scientific and indigenous and local knowledge, innovations and practices.
12) The ecosystem approach should involve all relevant sectors of society and scientific disciplines.

In addition, in the book *Ecosystems and Human Well-being, a Report of the Conceptual Framework Working Group of the Millennium Ecosystem Assessment* from 2003, ecosystems are the core topic. In Chapter 2 of the book, it is emphasized that an assessment of the ecosystem condition, the provision of services, and their relation to human well-being requires an integrated approach. This enables a decision process to determine which service or set of services is valued most highly and how to develop approaches to maintain services by managing the system sustainably. Ecosystem services are the benefits people obtain from nature. These include provisioning services such as food and water; regulating services such as flood and disease control; cultural services such as spiritual, recreational, and educational benefits; and supporting services such as nutrient cycling that maintain the conditions for life on Earth.

Today, environmental managers have realized that maintenance of ecosystem structure and functioning (see Principle 5 above) by an integrated approach is a prerequisite for a successful environmental management strategy, which is able to optimize the ecosystem services for the benefit of humans and nature. Another question is whether we have sufficient knowledge in ecology and systems ecology to give adequate and appropriate information about ecosystem structure, function, and response to disturbance to pursue the presented environmental management strategy and ecosystem sustainability with a scientific basis. In any way, the political demands provide a daunting challenge for ecosystem ecology.

This development in turn has been accentuated by the adoption of the Sustainable Development Goals (SDGs) by 194 countries. The SDGs describe 17 issues that need to be addressed and considered for humanity to achieve a sustainable state of our societies and eventually the whole Earth. Although, only three of the goals (13, 14, 15) are directly or very closely linked to the environment, clearly our societies are embedded in and therefore dependent on the state of the ecosystems adjacent to us in our everyday life. The goals are addressed in 169 targets believed to assist in reaching the goals, the SDGs. The targets share some concerns with the previously mentioned report from the Rio Summit in 1992, which also included some indication of possible actions to be taken. Actions and targets are not enough if they do not clearly indicate what priorities to give or in which direction to go. This book carries the idea that such lessons may be learned from nature and that true sustainability may only be achieved from increasing our understanding of nature's function and learning to work with rather than at odds with nature.

Recently, a new important player has entered the scene—the Catholic church—with the Vatican's release of the Papal ecclesial named "Laudate Si" (2015), which clearly addresses the connection between poverty and environmental quality and the fact that there is a strong bias between developed and developing countries. Developed countries' industries are continuously searching for and exploiting resources from the rest of the world, with increasing impact on the viability of local populations but also their activities play an important role in the decrease of global diversity. Sustainable development is a social justice issue as well. All the more, a reason to take the courage and action to address the issue.

1.2 ECOLOGY IS CHANGING

As a consequence of the changing paradigm direction of environmental management, we need to focus on ecosystem ecology. An ecosystem according to the Millennium Report (2003) is defined as "a dynamic complex of plants, animals, and microorganism communities and the nonliving environment, interacting as a functional unit. Humans are an integral part of ecosystems."

A well-defined ecosystem has strong interactions among its components and weak interactions across its boundaries. A useful ecosystem boundary is the place where a number of discontinuities coincide, for instance, in the distribution of organism, soil type, drainage basin, or depth in a water body. At a larger scale, regional and even globally distributed ecosystems can be evaluated based on a commonality of basic structural units. Three questions are fundamental to pursue for ecosystem-based environmental management:

I: What are the underlying ecosystem properties that can explain their response to perturbations and human interventions?

II: Are we able to formulate at least building blocks of an ecosystem theory in the form of useful propositions about processes and properties? We prefer the word "propositions" and not laws because ecosystem dynamics are so complex that universal laws give way to contextual propensities. The propositions capture these general tendencies of ecosystem properties and processes that can be applied to understand the very nature of ecosystems, including their response to human impacts.

III: Is the ecosystem theory sufficiently developed to be able to explain ecological observations with practical application for environmental management?

The scope of this book is an attempt to answer these questions to the extent that is currently possible. The authors of this book have realized that an ecosystem theory is a prerequisite for wider application of ecological sciences in environmental management because theory provides a strong guide for environmental management and resource conservation.

1.3 A NEW ECOLOGY

Over the years, the authors of this book along with other colleagues, collaborators, and researchers have proposed new ways of looking at ecology primarily from principles of thermodynamics, self-organization, complexity, dynamics (evolution), information, and interrelations (networks), among other foundational aspects. In particular, Jorgensen and Fath (2004b) presented 10 thermodynamic principles in ecology, and Jorgensen et al. (2015) expanded that list to 14 properties of ecosystems. Upon further reflection, refinement, and consideration, our team took the task to revisit the principles, remove redundancies, and derivative concepts (e.g., saying ecosystems are open implies that they need continued energy to survive). The result, although likely not the final word as science is always learning and changing based on new evidence, is what we believe to be a tight set of nine core ecosystem principles (Table 1.1). These are subdivided into three categories, the material constraints, the ontological properties, and phenomenological properties.

The material constraints refer to the laws of thermodynamics and the periodic table (how chemicals react and interact). The ontological properties consider both the fact that ecosystems are self-organizing systems in response to physical flows of energy—this is the physically driven biological aspect, and ecosystems are dynamic and changing due to evolutionary processes and pressure—this is the biologically driven biological aspect. Lastly, the phenomenological properties include observed features such as diversity, hierarchies, networks, and information. These principles are described in detail in the book in a series of statements about ecosystems and how those apply to both the broader field of ecology and to environmental management.

1.4 BOOK OUTLINE

Chapters 2—8 present the fundamental properties that explain typical ecosystem processes under "normal" growth and development and their responses to disturbance. These are followed by 3 chapters of that show their

TABLE 1.1 Ecosystem Principles.

MATERIAL CONSTRAINTS
1) Ecosystems conserve matter and energy—first law **2)** All processes are dissipative—second law **3)** All life uses largely the same biochemical constituents and processes
ONTOLOGICAL PROPERTIES
4) An ecosystem uses surplus energy to move further away from thermodynamic equilibrium (physically driven biological aspect)—centripetality **5)** Ecosystems coevolve and adapt to prevailing conditions (biologically driven biological aspect)
PHENOMENOLOGICAL PROPERTIES
6) Ecosystems have diversity of structure and function **7)** Ecosystems are emergent hierarchically **8)** Ecosystems work together in networks that improve the resource flow utilization **9)** Ecosystems have an enormous amount of genetic, biochemical, and process information

explanatory power in ecology and application to ecology and environmental management. The book is laid out as follows:

1) Chapter 1 is the introduction you are reading now.
2) *Ecosystems are open systems*—open to energy, mass, and information. Openness is an absolute necessity because the maintenance of ecosystems far from thermodynamic equilibrium requires an input of energy (Chapter 2).
3) *Ecosystems are ontically open*, meaning that—in addition to the physical openness of Chapter 2—due to their enormous complexity, it is impossible to predict accurately all possible outcomes in advance regarding ecosystem behavior. The implications are that it is more appropriate to discuss the propensity of ecosystems to show a certain pattern or to discuss the direction of responses (Chapter 3).
4) *Ecosystems have network connectivity*, which gives them new and emergent properties. Ecosystem networks have synergistic properties, which are able to explain the cooperative integration of ecosystem components, which can at least sometimes yield unexpected system relations (Chapter 4).
5) *Ecosystems are organized hierarchically* in the sense that we can understand one level only by understanding interactions with the levels below and above the scale of focus. This property gives an interplay of top-down and bottom-up control within the system (Chapter 5).
6) *Ecosystems have directed development*, meaning they change progressively to increase, in particular feedback and autocatalysis (Chapter 6).
7) *Ecosystems grow and develop*; they gain biomass and structure, enlarge their networks, and increase their information content. We can follow this growth and development using holistic metrics such as power and eco-exergy, respectively (Chapter 7).
8) *Ecosystems have complex response to disturbance and decay*, but when we understand properties of ecosystems such as adaptation, biodiversity, resistance, and resilience, to mention a few of the most important properties covered in the book, we can explain and sometimes predict the responses of ecosystems to disturbances (Chapter 8).
9) *Ecosystem principles have broad explanatory power in ecology* as we show that the principles provide explanations for many textbook concepts in ecology (Chapter 9).
10) *Ecosystem principles have ecological applications* (Chapter 10).
11) *Ecosystem principles have environmental management and policy applications* and need therefore in the future to be taken much more into account when taking management initiatives, be it prevention/mitigation or remediation of existing and recognized environmental problems (Chapter 11).
12) Conclusions (Chapter 12).

Chapters 2—8 are directed to answer the first question. The second question is addressed in Chapter 9 and summarized in Chapter 12. The last question regarding the applicability of the presented theory to explain ecological observations and to be applied in environmental management is addressed in Chapters 10 and 11. The application of the theory in environmental management has been mostly limited to the use of ecological indicators for ecosystem health assessment as described in Chapter 9. The theory has much wider applicability, but the use of ecological indicators has a direct link to ecosystem theory that facilitates testing the theory. Tests of the theory according to its applicability in practical environmental management and to explain ecological observations is crucial for the general acceptance of the ecosystem theory, but it does not exclude that it cannot be improved significantly. On the contrary, it is expected that the theory will be considerably improved by persistent and ongoing application because the weaknesses in the present theory will inevitably be uncovered as the number of case studies increases. Discovery of theoretical weaknesses will inspire improvements. Therefore, it is less important that the theory has flaws and lacks important elements than that it is sufficiently developed to be directly applied. We, the authors, are of the opinion that we have an ecosystem theory that is ready to be applied but which also inevitably will be developed significantly during the next one to two decades due to (hopefully) its wider application. In fact, this second edition exemplifies the learning that has taken since the first edition was released a decade ago.

An ecosystem theory as the one presented in this book may be compared with geographical maps. Basics maps were available already 2000 years ago that could provide an overview of where you would find towns, mountains, forests, etc. These maps were considerably improved over time as technologies improved, and the geographical maps used in the 17th and 18th centuries were much more accurate and detailed, which themselves are not comparable with the satellite-based and interactive maps of today. Our ecosystem theory as presented here may be comparable with the geographical maps of the 18th century. They are very useful, but they can be improved considerably when new methods, information, and observations are available. It may take 20 or 50 years before we have the quality of an ecosystem theory comparable with today's geographical maps, but the present level of our ecosystem theory is nevertheless suitable for immediate application. Only through this application will we discover new methods and demand for improvements, both theoretical and practical for science and management, ultimately leading to a more complete and accurate ecosystem theory.

CHAPTER

2

Ecosystems Have Thermodynamic Openness

Without the Sun, everything on Earth dies! ***From the plaintive Ukrainian folksong*, "**Я бачив як вітер ...**".**

2.1 WHY MUST ECOSYSTEMS BE OPEN?

The many 1 m trees that we planted more than 30 years ago in our gardens, which were open fields at the time, are more than 30 m tall today. The trees have increased their biomass in the form of trunks, stems, leaves, and roots. The structures of the gardens have also changed. Today, biodiversity is much higher—not so much due to different plants, but the tall trees and the voluminous bushes with berries attract many insects and birds. The garden today is a much more complex ecosystem. The biomass has increased, the biodiversity has increased, and the number of ecological interactions among the abundant species has increased.

When you follow the development of an ecosystem over a longer period or even during a couple of spring months, you are witness to one of the many wonders in nature: an inconceivably complex system is developing in front of you. What makes this development of complex (and beautiful) systems in nature possible?

In accordance with classic thermodynamics, all *isolated systems* will move toward thermodynamic equilibrium, a state of equal distribution of components and maximum probability. This means that all the gradients have been eliminated, i.e., there are no differences in any energy potentials such as concentration of chemicals or temperature differences, and structures in the system will have ceased to exist: a homogenous dead system will be the result. This is expressed thermodynamically as follows: entropy will always increase in an isolated system. As work capacity is a result of gradients in certain intensive variables such as temperature, pressure, and chemical potential, etc. (see Table 2.1), a system at *thermodynamic equilibrium* can do no work. But our gardens are moving away from thermodynamic equilibrium with a seemingly faster and faster rate every year, at least in the early stages of growth and development. This means that our gardens cannot be isolated. They must be at least nonisolated (in established terminology this usually refers to the system being either closed, i.e., may exchange only energy with the surroundings, or open, which may exchange both matter and energy with the surroundings); but birds, insects, squirrels, and an occasional fox enter from outside the garden—from the environment of the garden, maybe from a forest 1000 m away. In fact, the garden as all other ecosystems must be open (see also Table 2.2, where the thermodynamic definitions of isolated, closed, and open systems are presented). Gardens are open to energy inputs from the solar radiation, which is absolutely necessary to avoid the system moving toward thermodynamic equilibrium. Without solar radiation the system would die. The energy contained in the solar radiation provides the energy needed for maintenance of the plants and animals, measured by the respiration. When the demand for maintenance energy is covered, additional energy is used to move the system further away from thermodynamic equilibrium. The thermodynamic openness of ecosystems explains why ecosystems are able to move away from thermodynamic equilibrium: to grow and to build structures and gradients. It should be noted that the use of the term "thermodynamic equilibrium" in the above context does not refer to true thermodynamic equilibrium, i.e., a system with absolutely no gradients, a disintegrated system at 0 K. Rather, it refers to a system that has no gradients with respect to its environment that may be at other conditions of equilibrium like the biosphere, an Oparinian sea, and similar environments.

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TABLE 2.1 Different Forms of Energy and Their Intensive and Extensive Variables.

Energy Form	Extensive Variable	Intensive Variable
Heat	Entropy (J/K)	Temperature (K)
Expansion	Volume (m^3)	Pressure ($Pa = kg/s^2\ m$)
Chemical	Moles (M)	Chemical potential (J/moles)
Electrical	Charge (Ampere sec)	Voltage (Volt)
Potential	Mass (kg)	(Gravity) (height) (m^2/s^2)
Kinetic	Mass (kg)	$0.5(\text{Velocity})^2$ (m^2/s^2)

Potential and kinetic energy is denoted mechanical energy.

TABLE 2.2 Definitions of Various Thermodynamic Systems.

System Type	Definition
Isolated	No exchange of energy, mass, and information with the environment
Nonisolated	Exchange of energy and information, but no mass with the environment
Closed	Exchange of energy and information, but no mass with the environment
Open	Exchange of energy, mass, and information with the environment

Ecosystem openness is, in most cases, only a necessary condition. For example, a balanced aquarium and also our planet are more nonisolated than open; openness is only incidental. One wonders what would be the elements of sufficient conditions to create an ecosystem from solar radiation? Openness is obviously not a sufficient condition for ecosystems because all open systems are not ecosystems. If a necessary condition is removed, however, the process or system in question cannot proceed. So, openness (or nonisolation) as a necessary condition makes this a pivotal property of ecosystems, one to examine very closely for far-reaching consequences. And, if these are to be expressed in thermodynamic terms, ecologists need to be aware that aspects of thermodynamics—particularly entropy and the second law—have for several decades been under some serious challenges in physics, and no longer enjoy the solid standing in science they once held (Capek and Sheehan, 2005). Like a garden, science is open too—ever exploring, changing, and improving. In this chapter, we will not take these modern challenges too into account.

2.2 AN ISOLATED SYSTEM WOULD DIE (MAXIMUM ENTROPY)

The spontaneous tendency of energy to degrade and be dissipated in the environment is evident in the phenomena of everyday life. A ball bouncing tends to make smaller and smaller bounces and dissipation of heat. A jug that falls to the ground breaks (dissipation) into many pieces and the inverse process, which could be seen running a film of the fall backwards, never happens in nature. Except, of course, the jug did come into existence by the same kind of nonspontaneous processes that make the garden grow. It is instructive to ponder how openness or nonisolation operates here, as necessary conditions. Perfume leaves a bottle and dissipates into the room; we never see an empty bottle spontaneously fill, although the laws of probability do allow for this possibility. There is thus a tendency for energy to disperse and turn into the heat form—a process called dissipation. The process of dissipation also relates to the irreversible spread of matter illustrated in the above examples. The thermodynamic function known as *entropy* (S) is the extensive variable for heat and measures the extent to which work has been degraded to heat. Strictly speaking, the entropy concept only applies to isolated systems close to equilibrium, but it is often used in a metaphorical sense in connection with everyday far-from-equilibrium systems. We will follow this practice here as a useful way to consider ecosystems; revisions can come later when thermodynamic ecology is much better understood from theory and greater rigor is possible. Transformations tend to occur spontaneously in the direction of increasing entropy or maximum dissipation. The idea of the passage of time, of the direction of the transformation, is inherent in the concept of entropy. The term was coined by Clausius from τροπη (transformation) and εντροπη (evolution, mutation, or even confusion).

Clausius used the concept of entropy and reworded the first and second thermodynamic laws in 1865 (Clausius, 1865) in a wider and more universal framework: Die Energie der Welt ist Konstant (the energy of the world is constant) and Die Entropy der Welt strebt einem Maximum zu (the entropy of the world tends toward a maximum). Maximum entropy, which corresponds to the equilibrium state of a system, is a state in which the energy is completely degraded and can no longer produce work. Well, maybe not literally "completely degraded" but rather, let us say, only "degradiented," meaning brought to a point of equilibrium where there is no gradient with its surroundings, therefore no possibility to do work. Energy at 300 K at the Earth's surface is unusable but can perform work after it passes to outer space where the temperature is 3 K and a thermal gradient is reestablished. Again, it is common practice to use the term "degraded" in the sense we have, and "completely" for emphasis; for continuity in communication these practices will be followed here.

Entropy is, therefore, a concept that shows us the direction of events. "Time's Arrow," as Harold Blum (1951) has called it. Barry Commoner (1971) notes that sandcastles (order) do not appear spontaneously but can only disappear (disorder); a wooden hut in time becomes a pile of beams and boards: the inverse processes do not occur. The spontaneous direction of an isolated system is thus from order to disorder and entropy, as metaphor, indicates this inexorable process, the process which has the maximum probability of occurring. In this way, the concepts of disorder and probability are linked in the concept of entropy. Entropy is in fact a measure of disorder and probability even though for systems like a garden it cannot be measured. Entropy generation can be calculated approximately, however, for reasonably complex systems, and for this one should consult the publications of Aoki (1987, 1988, 1989).

War is a disordering activity, but from such can often arise other levels and kinds of order. For example, a South Seas chieftain once warred on his neighbors and collected their ornately carved wooden thrones as part of the spoils and symbols of their defeat; they came to signify his superiority over his enemies and this enabled him to govern for many years as leader of a well-organized society. This social order, of course, came out of the original disordering activity of warfare, and it was sustained. The captured thrones were stored in a grand thatched building for display on special holidays, a shrine that came to symbolize the chieftain's power and authority over his subjects. One year, a typhoon hit the island and swept the structure and its thrones away in the night. The disordering of the storm went far beyond the scattering of matter, for the social order that had emerged from disorder quickly unraveled also and was swept away with the storm. The remnant society was forced in its recovery to face a hard lesson of the region—"People who live in grass houses shouldn't stow thrones!" In order to understand this order−disorder relationship better, it is useful to describe a model experiment: the mixing of gases.

Suppose we have two gases, one red and one yellow, in two containers separated by a wall. If we remove the wall, then we see that the two gases mix until there is a uniform distribution: an orange mixture. Well, a uniformly *mixed* distribution, anyway; in a statistical sense the distribution is actually random. If they were originally mixed, then they would not be expected to spontaneously separate into red and yellow. The "orange" state is that of maximum disorder, the situation of greatest entropy because it was reached spontaneously from a situation of initial order—the maximum of which, by the way, is the uniform distribution. Random, uniform; one must take care in choice of wording. Entropy is a measure of the degree of disorder of the system (notice that the scientific literature presents several definitions of the concept of entropy). The disordered state occurred because it had the highest statistical probability. The law of increasing entropy expresses therefore also a law of probability, of statistical tendency toward disorder. The most likely state is realized, namely the state of greatest entropy or disorder. When the gases mix, the most probable phenomenon occurs: degeneration into disorder—randomness. Nobel Laureate in Physics, Richard Feynman (1994), comments that irreversibility is caused by the general accidents of life. It is not against the laws of physics that the red and yellow gases could separate; it is simply improbable and would not happen in a million years. Things are irreversible only in the sense that going toward randomness is probable whereas going toward order, while it is possible and in agreement with the laws of physics, would almost never happen in the case of simple particulars such as gases. Yet, we see the complex, ordered garden grow before us.

So, it is also in the case of our South Sea islanders. Two populations kept separate by distance over evolutionary time could be expected to develop different traits. Let one such set be considered "red" traits, and the other "yellow." Over time, without mixing, the red traits would get redder and the yellow traits yellower—the populations would diverge. If a disordering event like a storm or war caused the islanders to disperse and eventually encounter one another and mix reproductively, then their distinctive traits would, over a long period of time, merge and converge toward "orange." A chieftain governing such a population would not be able to muster the power to reverse the trend by spontaneous means. A tyrant might resort to genocide to develop a genetically pure race of people. Without entropy such an extreme measure, which has over human history caused much misery, would never be needed. Spontaneous dehomogenization could occur, reestablishing the kind of thermodynamic gradient (red vs. yellow) that would again make possible the further ordering work of disordering war. No entropy, no work or war—necessary or sufficient condition?

The principle of increasing entropy is now clearer in orange molecules and people: high-entropy states are favored because they are more probable, and this fact can be expressed by a particular relation as shown by Boltzmann (1905): $S = -k \log p$, where S is entropy, k Boltzmann's constant, and p the probability of an event occurring. The logarithmic dependence makes the probability of zero entropy equal to one. The universality of the law of entropy increase (we speak metaphorically) was stressed by Clausius in the sense that energy is degraded ("degradiented") from one end of the universe to the other and that it becomes less and less available in time, until "Wärmetode", or the "thermal death" of the universe. Evolution toward this thermal death is the subject of much discussion. Jørgensen et al. (1995) showed that the expansion of the universe implies that the thermodynamic equilibrium is moving farther and farther away. In order to extend the theory from the planetary to the cosmic context it is necessary to introduce unknown effects such as gravitation. Current astrophysics suggests an expanding universe that originated in a great primordial explosion (big bang) from a low-entropy state, but the limits of theoretical thermodynamic models do not allow confirmation or provide evidence.

The study of entropy continues: this fundamental concept has been applied to diverse fields such as linguistics, the codification of language, and to music and information theory, unfortunately leading to a confusing use of concepts which must be taken into account when reading literature in the area. Thermodynamics has taught us many fascinating lessons, particularly that (I) energy cannot be created or destroyed but is conserved and (II) entropy of isolated systems is always increasing, striking the hours of the cosmic clock, and reminding us that both for humans and for energy matter, time exists and the future is distinct from the past by virtue of a higher value of S.

The second law of thermodynamics, still upheld as one of nature's fundamental laws, addresses the pathways we should avoid in order to keep life on Earth. It shows the universal, inescapable tendency toward disorder (in thermodynamics, the general trend toward an entropy maximum), which is also, again metaphorically, a loss of information and of usable or *available energy*. This tendency to the Clausius' "thermal death" speaks to the thermodynamic equilibrium, namely the death of biological systems and ecosystems, through the destruction of diversity and hence finally the removal of gradients. There are two ways to achieve such a condition when:

(a) through energy exchanges as heat fluxes, there are no more differences in temperature and nothing more can be done because no exchange of usable energy is allowed;
(b) a system, becoming isolated, consumes its resources, reaching a great increase in its internal entropy and, at the end, to self-destruction.

For this reason, living systems cannot exist at conditions near or at thermodynamic equilibrium, but keep themselves as far as possible from that state, self-organizing due to material and energetic fluxes, received from outside and from systems with different conditions of temperature and energy.

To live and reproduce, plants and animals need a continuous flow of energy. This is an obvious and commonly believed truism, but in fact organisms will also readily accept a discontinuous energy inflow, as life in a biosphere, driven by pulsed energy inputs that the periodic motions of the planet provide, demonstrates. The energy of the biosphere that originates in the discontinuous luminous energy of the sun is captured by plants and passes from one living form to another along the food chain. This radiant pathway that provides us with great quantities of food, fibers, and energy—all of solar origin—has existed for over four billion years, a long time if we think that hominids appeared on the Earth only circa six million years ago and that known history covers only 10,000 years. The ancestors of today's plants were the blue-green algae, or cyanobacteria, that began to practice photosynthesis, assuming a fundamental role in biological evolution.

All vegetation, whether natural or cultivated, has been capturing solar energy for millennia, yet the vast majority of the energy received by the Earth's surface from the sun is not part of the photosynthetic energy chain. Rather, most of the solar energy is dispersed: it is reflected, stored in the soil and water, used in the evaporation of water, and so forth. Approximately 1% of the solar energy that falls on fertile land and water is fixed through photosynthesis by primary producers in the form of high-energy organic molecules: solar energy stored in chemical bonds available for later use. Through additional biochemical processes (respiration) the plants transform this energy into other organic compounds and work.

The food chain considered in terms of energy flows has a logic of its own: the energy degrades progressively in the different phases of the chain (primary producers and secondary consumers including decomposers), giving back the elementary substances necessary to build again the molecules of living cells with the help of solar energy.

The organization of living beings in mature ecosystems slows the dispersal of energy fixed by plants to a minimum, using it completely for its complex mechanisms of regulation. This is made possible by large "reservoirs" of energy (biomass) and by the diversification of living species. The stability of natural ecosystems, however, means that the final energy yield is zero, except for a relatively small quantity of biomass that is buried underground to form fossils. Relatively small, true, but in absolute terms fuel enough to power modern civilization for centuries.

Photosynthesis counteracts entropic degradation insofar as it orders disordered matter: the plant takes up disordered material (low-energy molecules of water and carbon dioxide in disorderly agitation) and puts it in order using solar energy. It organizes the material by building it into complex structures. Photosynthesis is, therefore, the process that by capturing solar energy and decreasing the entropy of the planet paved the way for evolution. Photosynthesis is the green talisman of life, the bioenergetic equivalent of Maxwell's demon that decreases the entropy of the biosphere. On the Earth, living systems need a continuous or discontinuous flow of "negative entropy" (actually, energy from the outside which is used to bring the bounded system to a lower entropy state) and this flow consists of the very solar energy captured by photosynthesis. This input of solar energy is what fuels the carbon cycle. The history of life on the Earth can be viewed as the history of chemotropic life, followed by the photosynthesis and the history of evolution, as the history of a planet that learned to capture solar energy and feed on the negative entropy of the universe for the creation of complex self-perpetuating structures (living organisms).

Compared to us or our society, the sun is an enormous engine that produces energy and offers the Earth the possibility of receiving large quantities of the abovementioned "negative entropy" (organization, life), allowing a global balance that does not contradict the second law of thermodynamics. Every year, the sun sends the Earth 5.6310×10^{24} J of energy, over 10,000 times more energy than humans consume in a year. Wee should not consider this solar bounty, ours alone, though, as we are only one among millions of species relying on this flow.

2.3 PHYSICAL OPENNESS

An energy balance equation for ecosystems might be written as follows in accordance with the principle of energy conservation:

$$E_{\text{cap}} = Q_{\text{evap}} + Q_{\text{resp}} + \ldots + \Delta E_{\text{bio}} \tag{2.1}$$

Here, E_{cap} is the external energy captured per unit of time. A part of the incoming energy, solar radiation being the main source for the ecosystems on Earth, is captured and a part is reflected unused, determining the albedo of the globe. The more biological structure an ecosystem possesses, the more of the incoming energy it is able to capture, i.e., the lower the albedo. The structure acts as an umbrella or rather a satellite dish, capturing the incoming solar radiation.

In an ecosystem at steady state, the formation of biological compounds (anabolism) is in approximate balance with their decomposition (catabolism). That is, in energy terms:

$$\Delta E_{\text{bio}} \approx 0 \quad \text{and} \quad E_{\text{cap}} \approx Q_{\text{evap}} + Q_{\text{resp}} \tag{2.2}$$

The energy captured by a system can in principle be any form of energy (electromagnetic, chemical, kinetic, etc.), but for the ecosystems on Earth the short-wave energy of solar radiation (electromagnetic energy) plays the major role. The energy captured per unit of time is, however, according to Eq. (2.2) used to pay the maintenance cost per unit of time including evapotranspiration and respiration. The overall result of these processes requires that E_{cap} to be greater than 0, which entails openness (or at least nonisolation).

The following reaction chain summarizes the consequences of energy openness (Jørgensen et al., 1999): *source*: solar radiation → *anabolism* (charge phase): incorporation of high-quality energy, with entrained work capacity (and information), into complex biomolecular structures, entailing anti-entropic system movement away from equilibrium → *catabolism* (discharge phase): deterioration of structure involving release of chemical bond energy and its degradation to lower states of usefulness for work (heat) → *sink*: dissipation of degraded (low work capacity and high entropy) energy as heat to the environment (and, from Earth, to deep space), involving entropy generation and return toward thermodynamic equilibrium. This is how the energy cascade of the planet is usually described. Another way might be to express it in terms of gradient creation and destruction. The high-quality entering energy creates a gradient with baseline background energy. This enables work to be done in which the energy is degradiented and dissipated to space. On arrival there (at approximately 280 K) it locally "regradients" this new environment (at 3 K) but then rapidly disperses into the vacuum of the cosmos at large.

This same chain can also be expressed in terms of matter: *source*: geochemical substrates relatively close to thermodynamic equilibrium → *anabolism*: inorganic chemicals are molded into complex organic molecules (with low probability, meaning that the equilibrium constant for the formation process is very low, low entropy, and high distance from thermodynamic equilibrium) → *catabolism*: synthesized organic matter is ultimately decomposed into simple inorganic molecules again; the distance from thermodynamic equilibrium decreases, and entropy increases → *cycling*: the inorganic molecules, returned to near-equilibrium states, become available in the nearly closed material ecosphere of Earth for repetition of the matter charge—discharge cycle.

Input environments of ecosystems serve as sources of high-quality energy whose high contents of work and information and low entropy form of energy serve to raise the organizational states of matter far from equilibrium. Output environments, in contrast, are sinks for energy and matter lower in work capacity, higher in entropy, and closer to equilibrium. This is one possibility. On the other hand, since output environments also contain equilibrium-avoiding entities (organisms), their energy quality on a local basis might be just as great as that of organisms in input environments. Since, output environments feedback to become portions of input environments living systems operating in the ecosphere, which is energetically nonisolated but materially nearly closed, must seek an adaptive balance between these two aspects of their environmental relations in order to sustain their continued existence. That is, the charge—discharge cycle of the planet wraps output environments around to input environments, which homogenizes gradients and forces gradient-building (anabolic) biological activity.

The expression high-quality energy is used above to indicate that energy can either be applied to do work or it is what is sometimes called "anergy," i.e., energy that cannot do work. The ability to do work can be expressed by:

$$\text{Work} = \text{an extensive variables} \times \text{a difference in intensive variables}$$

For instance,

$$\text{Work} = mg(h_1 - h_2) \tag{2.3}$$

where m is the mass, g the gravity, h the height, and $(h_1 - h_2)$ the difference in height (see Table 2.1).

The concept exergy was introduced by Rant (1955, 1956) to express the work capacity of a system relative to its environment (see details presented in Wall, 1977; Szargut et al., 1988). It was particularly useful when the efficiencies of a power plant or the energy transfer should be expressed. We have therefore:

$$\text{Energy} = \text{exergy} + \text{anergy} \tag{2.4}$$

Q_{evap} and Q_{resp} in Eqs. (2.1) and (2.2) may be considered as anergy because it represents the energy lost and is heat at the temperature of the environment, i.e., no gradient. The temperature of the ecosystem would rise, if the ecosystem was not open at both ends, so to say. The heat is exported to the environment. The openness, or actually nonisolation (closed condition), of ecosystems makes it possible for the systems to capture energy for photosynthesis and also to export generated heat to maintain an acceptable temperature for life processes.

Exergy, as it is defined technologically, cannot be used to express the work capacity of an ecosystem because the reference (the environment) is the adjacent ecosystem. The eco-exergy expresses, therefore, the work capacity of an ecosystem compared with the same system as a dead and completely homogeneous system without gradients. See Box 2.1 for definition and documentation of "eco-exergy."

Eco-exergy expresses the development of an ecosystem by its work capacity (see Box 2.1). While we can measure the concentrations in the ecosystem proper, the concentrations in the reference state (thermodynamic equilibrium; see Box 2.1) must be estimated. For instance, such a theoretical value can be based on the usual use of chemical equilibrium constants. If we have the process:

BOX 2.1

ECO-EXERGY, DEFINITION

Eco-exergy was introduced in the 1970s (Jørgensen and Mejer, 1977, 1979, Mejer, 1979 and Jørgensen, 1982) to express the development of ecosystems through an increase of the work capacity. We presume a reference environment that represents the system (ecosystem) at thermodynamic equilibrium, which means that all the components are inorganic at the highest possible oxidation state: if sufficient oxygen is present (as much free energy as possible is utilized to do work) and homogeneously distributed at random in the system (no gradients), then the situation illustrated in Fig. 2.1 is valid. As the chemical energy embodied in the organic components and the biological structure contributes far most to the exergy content of the system, there seems to be no reason to assume a (minor) temperature and pressure difference between the system and the reference environment. Under these circumstances we can calculate the exergy content of the system as coming entirely from the chemical energy:

$$\sum(\mu_c - \mu_{co})N_i \tag{2.5}$$

where, μ_c and μ_{co} are the chemical potentials and N in the number of chemical compounds.

This represents the nonflow chemical exergy. It is determined by the difference in chemical potential (μ_c−μ_{co}) between the ecosystem and the same system at thermodynamic equilibrium. This difference is determined by the concentrations of the considered components in the system and in the reference state (thermodynamic equilibrium), as it is the case for all chemical processes.

$$\text{Component A} \leftrightarrow \text{inorganic decomposition products,} \tag{2.6}$$

then it has a chemical equilibrium constant, K:

$$\text{K} = [\text{inorganic decomposition products}]/[\text{Component A}] \tag{2.7}$$

The concentration of component A at thermodynamic equilibrium is difficult to find (see the discussion in Chapter 7), but we can, based on the composition of A, find the concentration of component A at thermodynamic equilibrium from the probability of forming A from the inorganic components.

Eco-exergy is a function of the reference state, often taken as the prevailing environment of the ecosystem which may vary and thus be different from ecosystem to ecosystem. Eco-exergy expresses, therefore, the work capacity relative to the same system but at (thermo-)dynamic equilibrium with the surroundings. Eco-exergy can furthermore, with the definition given, be applied far from thermodynamic equilibrium. It should be mentioned that eco-exergy cannot be measured, as the total internal energy content of a body or system cannot be measured. Even a small ecosystem contains many microorganisms and it is, therefore, hardly possible by determination of the weight of all components of an ecosystem to assess the eco-exergy of an ecosystem. The eco-exergy of a model of an ecosystem can, however, be calculated as it will be demonstrated in Chapter 7.

Using these calculations, we find the exergy of the system compared with the same system at the same temperature and pressure but in form of an inorganic soup without any life, biological structure, information, or organic molecules. As (μ_c) can be found from the definition of the chemical potential replacing activities by concentrations, we get the following expressions for eco-exergy:

$$Ex = RT\sum_{i=0}^{n} C_i \ln\left(C_i/C_{i,o}\right) \tag{2.8}$$

where R is the gas constant (8.317 J/K moles = 0.08,207 L atm K^{-1} moles), T the temperature of the environment (and the system; see Fig. 2.1), while C_i is the concentration of the ith component expressed in a suitable unit, e.g., for phytoplankton in a lake C_i could be expressed as mg/L or as mg/L of a specific nutrient under consideration. $C_{i,o}$ is the concentration of the ith component at thermodynamic equilibrium and n is the number of components. $C_{i,o}$ is a very small concentration (except for $I = 0$, which is considered to cover the inorganic compounds), it is therefore possible to use the probability ($p_{i,0}$) (see Chapter 7):

$$\frac{Ex}{V} = RT\sum_{i=0}^{n} p_i \ln\left(\frac{p_i}{p_{i,o}}\right) \tag{2.9}$$

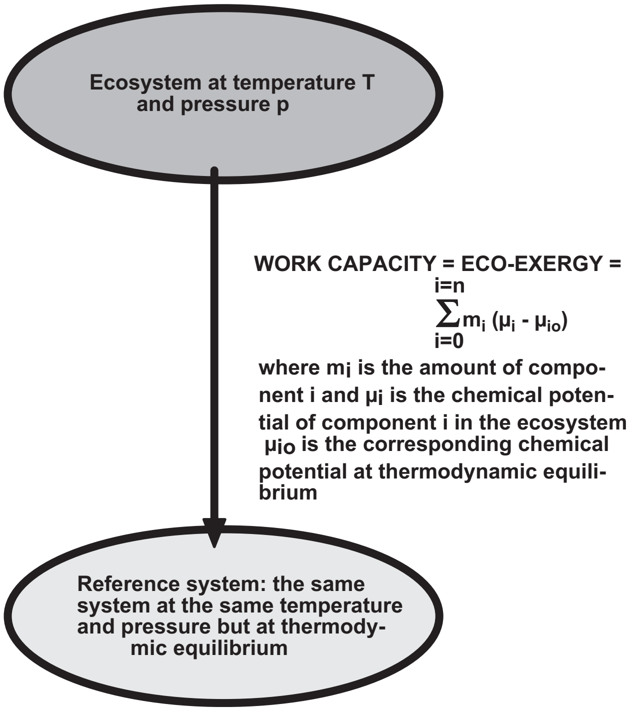

FIGURE 2.1 The exergy content of the system is calculated in the text for the system relative to a reference environment of the same system at the same temperature and pressure at thermodynamic equilibrium, it means as an inorganic soup with no life, biological structure, information, gradients, and organic molecules.¤

By using this particular eco-exergy based on the same system at thermodynamic equilibrium as a reference, the exergy becomes dependent only on the chemical potential of the numerous biochemical components that are characteristic for life. This is consistent with Boltzmann's statement that life is a struggle for free energy, which is the work capacity in classic thermodynamics.

As observed above, the total eco-exergy of an ecosystem *cannot* be calculated exactly, as we cannot measure the concentrations of *all* the components or determine all possible contributions to eco-exergy in an ecosystem. Nor does it include the information of interactions. If we calculate the exergy of a fox, for instance, then the above shown calculations will only give the contributions coming from the biomass and the information embodied in the genes, but what is the contribution from the blood pressure, the sexual hormones, and so on? These properties are at least partially covered by the genes but is that the entire story? We can calculate the contributions from the dominant biological components in an ecosystem, for instance, using a model or measurements, that covers the most essential components for a focal problem. The *difference* in exergy by *comparing* two different possible structures (species composition) is here decisive. Moreover, exergy computations always give only *relative* values, as the exergy is calculated relative to the reference system. These problems will be treated in further details in Chapter 7. For now, it is important to realize that it is the metaphorical quality of the exergy concept, and not its measurability that is most useful to ecologists. Entropy and exergy can both not be measured for ecosystems. It is not always necessary in science to be able to make exact measurements. Ecologists rarely do this anyway. Approximations can yield an approximate science, and that is what ecology is. Modeling approximates reality, not duplicates it, or reproduces it exactly because it is impossible due to high ecosystem complexity (see also next chapter). Approximate ecology—which can be quite useful and interesting—can be used to quantify (approximately), e.g., the influence of anthropogenic impacts on ecosystems. Often concepts and theories, not only measurements, make science interesting. With all the short-comings presented above, eco-exergy gives an approximate, relative measure of how far an ecosystem is from thermodynamic equilibrium and thereby how developed it is. Such assessment of important holistic ecosystem properties is important in systems ecology as well as in environmental management. This explains how eco-exergy has been applied several times successfully to explain ecological observations (see Jørgensen et al., 2002 and Chapter 9) and as indicator for ecosystem health (see Jørgensen et al., 2004 and Chapter 10).

2.4 THE SECOND LAW OF THERMODYNAMICS INTERPRETED FOR OPEN SYSTEMS

If ecosystems were isolated, then no energy or matter could be exchanged across their boundaries. The systems would spontaneously degrade their initially contained exergy and increase their entropy, corresponding to a loss of order and organization, and increase in the randomness of their constituents and microstates. This dissipation process would cease at equilibrium, where no further motion or change would be possible. The physical manifestation would ultimately be a meltdown to the proverbial “inorganic soup” containing degradation products dispersed equiprobably throughout the entire volume of the system. All gradients of all kinds would be eliminated, and the system would be frozen in time in a stable, fixed configuration. The high-energy chemical compounds of biological systems, faced suddenly with isolation, would decompose spontaneously (but not necessarily instantaneously) to compounds with high-entropy contents. The process would be progressive to higher and higher entropy states, and would, in the presence of oxygen, end with a mixture of inorganic residues—carbon dioxide, water, nitrates, phosphates, and sulfates, etc. These simpler compounds could never be reconfigured into the complex molecules necessary to carry on life processes without the input of new low-entropy energy to be employed in biosynthesis. An isolated ecosystem could, therefore, in the best case sustain life for only a limited period of time, less than that required from the onset of isolation to reach thermodynamic equilibrium. Observations of properties could not be made, only inferred, because observation requires some kind of exchanges between the system and an observer. There would be no internal processes because no gradients would exist to enable them. There would only be uninterrupted and uninterruptible stillness and sameness which would never change. The system would be completely static at thermodynamic equilibrium. Thus, in a peculiar way, isolated systems can only be pure abstractions in reality, submitting neither to time passage, change, nor actual observation. They are the first “black holes” of physics, and the antithesis of our systems plus their environments which are the core model for systems ecology. No ecosystem could ever exist and be known to us as an isolated system.

The second law of thermodynamics, though open to question, still retains its status as one of the most fundamental laws of nature. The law has been expressed in many ways. As indicated above, entropy will always increase and exergy will always decrease for an isolated system. Time has one direction. Tiezzi (2003b) concludes that entropy applied to far from thermodynamic equilibrium systems is not a state function since it has intrinsic evolutionary properties, strikingly at variance with classical thermodynamics. Work capacity is constantly lost as heat at the temperature of the environment that cannot do work. This implies that all processes are irreversible. The total reversibility of Newton’s Universe (and even of the relativity theories) is no longer valid (Tiezzi, 2003a,b; 2005). The introduction of irreversibility has, however, opened for new emergent possibilities. Without irreversibility there would have been no evolution (Tiezzi, 2005), which is one of the clearest examples of a totally irreversible process. The directionality of ecosystems that will be discussed in Chapter 6 is also a result of the second law of thermodynamics. The second law of thermodynamics and the irreversibility of all processes have given the world new, rich, and beautiful possibilities that a reversible world not could offer.

That is the current dogma, at least, and it is probably true. However, it is useful to at least briefly consider the attributes of a reversible world. Time travel would be possible; this has been amply fantasized in literature. There would be no “evolution” in the sense we understand and no path dependency; returning to former states could be seen as quite interesting and refreshing, especially if those states were more desirable, let us say further from equilibrium, than their current alternatives. Beauty and rich possibilities—what could be more enriching and beautiful than restoration of former systems, and lives, after wars or other privations, have driven them nearer to equilibrium. Reversibility could produce quite an interesting world, from many perspectives, replacing the humdrum grinding reality of movement toward equilibrium following exergy seeding.

The decrease in entropy or the increase in the eco-exergy in the biosphere depends on its capacity to capture energy from the sun and to retransmit it to space in the form of infrared radiation (positive entropy). If retransmission is prevented, in other words—if the planet were shrouded in an adiabatic membrane (greenhouse effect)—then all living processes would cease very quickly and the system would decay toward the equilibrium state, i.e., toward thermal death. A sink is just as necessary for life as a source to ensure the temperature that is required for carbon-based life.

Morowitz (1968) continues that all biological processes depend on the absorption of solar photons and the transfer of heat to the celestial sinks. The sun would not be an exergy source if there were not a sink for the flow of thermal energy. The surface of the Earth is at a constant total energy, reemitting as much energy as it absorbs. The subtle difference is that *it is not energy per se that makes life continue but the flow of energy through the system*. The global ecological system or biosphere can be defined as the part of the Earth's surface that is ordered by the flow of energy primarily through the process of photosynthesis.

The physical chemistry mechanism was elegantly described by Nobel Prize winner Albert Szent-György as the common knowledge that the ultimate source of all our energy and negative entropy is the sun. When a photon interacts with a particle of matter on our globe, it raises an electron or a pair of electrons to a higher energy level. This excited state usually has a brief life and the electron falls back to its basic level in 10^{-7} to 10^{-8} s, giving up its energy in one way or another. Life has learned to capture the electron in the excited state, to uncouple it from its partner and to let it decay to its fundamental level through biological processes, using the extra energy for vital processes.

All biological processes, therefore, take place because they are utilizing an energy source. With exception of the chemotrophic systems at submarine vents, the ultimate energy source is the solar radiation. Morowitz (1968) notes that it is this tension between photosynthetic construction and thermal degradation that sustains the global operation of the biosphere and the great ecological cycles. This entropic behavior marks the difference between living systems and dead things.

2.5 DISSIPATIVE STRUCTURE

The change in entropy for an *open* system, $\mathrm{d}S_{\mathrm{system}}$, consists of an external, exogenous contribution from the environment, $\mathrm{de}S = S_{\mathrm{in}} - S_{\mathrm{out}}$, and an internal, endogenous contribution due to system state, $\mathrm{di}S$, which must always be positive by the second law of thermodynamics (Prigogine, 1947, 1955, 1962, 1988, 1997, Prigogine and Stengers, 1979, 1984). Prigogine uses the concept of entropy and the 2nd law far from thermodynamic equilibrium, which is outside the framework of classical thermodynamics, but he uses the concepts only locally and still under conditions much closer to equilibrium than presented by biological or ecological systems.

There are three possibilities for the entropy balance:

$$\mathrm{d}S_{\mathrm{system}}/\mathrm{d}t = \mathrm{de}S/\mathrm{d}t + \mathrm{di}S/\mathrm{d}t > 0. \tag{2.10}$$

$$\mathrm{d}S_{\mathrm{system}}/\mathrm{d}t = \mathrm{de}S/\mathrm{d}t + \mathrm{di}S/\mathrm{d}t < 0, \tag{2.11}$$

$$\mathrm{d}S_{\mathrm{system}}/\mathrm{d}t = \mathrm{de}S/\mathrm{d}t + \mathrm{di}S/\mathrm{d}t = 0. \tag{2.12}$$

The system loses order in the first case, as is typically understood by the 2nd law. Gaining order (case 2), is *only* possible if $-\mathrm{de}S > \mathrm{di}S > 0$. Creation of order in a system must be associated with a greater flux of entropy out of the system than into the system. This implies that the system must be open or at least nonisolated.

Case 3, Eq. (2.11), corresponds to a stationary situation, for which Ebeling et al. (1990) used the following two equations for the energy (U) balance and the entropy (S) balance:

$$\mathrm{d}U\,/\,\mathrm{d}t = 0 \quad \text{or} \quad \mathrm{de}U/\mathrm{d}t = -\mathrm{di}U/\mathrm{d}t = 0. \tag{2.13}$$

and

$$\mathrm{d}S_{\mathrm{system}}\,/\,\mathrm{d}t = 0 \quad \text{or} \quad \mathrm{de}S/\mathrm{d}t = -\mathrm{di}S/\mathrm{d}t = 0. \tag{2.14}$$

Usually the thermodynamic processes are isothermal and isobaric. This implies that we can interpret the third case (Eqs. 2.11–2.13) using free energy:

$$\mathrm{de}G\,/\,\mathrm{d}t = T\,\mathrm{di}S/\mathrm{d}t > 0 \tag{2.15}$$

This means that a "status quo" situation for an ecosystem requires an input of free energy or exergy to compensate for the loss of free energy and corresponding formation of heat due to maintenance processes, i.e., respiration and evapotranspiration. If the system does not receive a sufficient amount of free energy, then entropy will increase. If the entropy of the system will continue to increase, then the system will die; see Section 2.2. This is in accordance with Ostwald (1931): life without the input of free energy is not possible.

An average energy flow of approximately 10^{17} W from solar radiation ensures the maintenance of life on Earth. The surface temperature of the sun is 5800 K and of the Earth on average approximately 280 K. This implies that the following export of entropy per unit of time takes place from the Earth to the open space:

$$10^{17}\mathrm{W}(1/5800\mathrm{K} - 1/280\mathrm{K}) \approx 4.10^{14}\mathrm{W/K} \tag{2.16}$$

corresponding to 1 W m^{-2} K.

Prigogine uses the term *dissipative structure* to denote self-organizing systems which tend to move toward a state of minimum entropy production, thereby indicating that such systems dissipate energy (produce entropy) for the maintenance of their organization (order). The following conclusions are appropriate:

All living systems, because they are subject to the second law of thermodynamics, are inherently dissipative structures. The anabolism combats and compensates for the catabolic deterioration of structure; the two processes operate against one another. Note that the equilibrium "attractor" represents a resting or refractory state, one that is passively devolved to if system openness or nonisolation are compromised (Jørgensen et al., 1999). The term is also commonly used to express the situation when a system is actively pushed or "forced" toward a *steady state*. Though widespread, we do not subscribe to this usage and make a distinction between steady states and equilibria for two reasons:

(1) The state-space system theory we outlined in the conservation chapter of *Ecosystems Emerging* (Patten et al., 1997) precludes anything in system dynamics but a unique input—state—output relationship. Therefore, given an initial state, state-space theory asserts that there exists one and only one sequence of inputs that will put an open system in a given state at a specified final time. For this terminal state to be an "attractor," many input sequences would have to be able to place the system in it, and from many initial states—the attractor would be hard to avoid. This is inconsistent with dynamical state theory.

(2) As observed above, a steady state is a forced (nonzero input) condition; there is nothing "attractive" about it. Without a proper forcing function, it will never be reached or maintained. A steady state that is constant may appear at equilibrium, but it is really far from equilibrium and maintained by a steady input of energy or matter. We regard equilibrium as a zero-input or resting condition. What are often recognized as local attractors in mathematical models really have no counterparts in nature. Steady states are forced conditions, not to be confused with unforced equilibria which represent states to which systems settle when they are devoid of inputs. The only true natural attractor in reality, and it is global, is the unforced thermodynamic equilibrium.

As an ecosystem is nonisolated, the entropy changes during a time interval, dt, can be decomposed into the entropy flux due to exchanges with the environment, and the entropy production due to the irreversible processes inside the system such as diffusion, heat conduction, and chemical reactions. This can also be expressed using exergy:

$$Ex\,/\,\mathrm{d}t = \mathrm{de}Ex/\mathrm{d}t + \mathrm{di}Ex/\mathrm{d}t, \tag{2.17}$$

where $\mathrm{de}Ex/\mathrm{d}t$ represents the exergy input to the system and $\mathrm{di}Ex/\mathrm{d}t$ is the exergy consumed (is negative) by the system for maintenance, etc. Eq. (2.16) —an exergy version of Eqs. (2.9) and (2.10) —shows among other things that systems can only maintain a nonequilibrium steady state by compensating the internal exergy consumption with a positive exergy influx ($\mathrm{d_e}Ex/\mathrm{d}t > 0$). Such an influx induces order into the system. In ecosystems, the ultimate exergy influx comes from solar radiation, and the order induced is, e.g., biochemical molecular order. If $\mathrm{d_e}Ex > -\mathrm{d_i}Ex$ (the exergy consumption in the system), the system has surplus exergy input, which may be utilized to construct further order in the system, or as Prigogine (1980) calls it: dissipative structure. The system will thereby move further away from thermodynamic equilibrium. Evolution shows that this situation has been valid for the ecosphere on a long-term basis. In spring and summer, ecosystems are in the typical situation that $\mathrm{d_e}Ex$ exceeds $-\mathrm{d_i}Ex$. If $\mathrm{d_e}Ex < -\mathrm{d_i}Ex$, the system cannot maintain the order already achieved, but will move closer to the thermodynamic equilibrium, i.e., it will lose order. This may be the situation for ecosystems during fall and winter or due to environmental disturbances.

2.6 QUANTIFICATION OF OPENNESS AND ALLOMETRIC PRINCIPLES

All process rates are in physics described as proportional to a gradient, a conductivity or inverse resistance and to the openness, compare for instance with Fick's laws of diffusion and Ohm's law. The import and export from and to an ecosystem is, therefore, dependent on the differences between the ecosystem and the environment, as well as of openness. For instance, the rate of the reaeration process of a water stream can be expressed by the following equation:

$$R_a = V\,\mathrm{d}C/\mathrm{d}t = K_a(T)A(C_s - C) \tag{2.18}$$

or

$$\mathrm{d}C\,/\,\mathrm{d}t = K_a(T)(C_s - C)/d \tag{2.19}$$

where R_a is the rate of reaeration, K_a a temperature constant for a given stream, A the area $= V/d$, V the volume, d the depth, C_s the oxygen concentration at saturation, and C the actual oxygen concentration. K_a is here the "conductivity" or inverse resistance. The faster the water flow in the stream, the higher is K_a. $(C_s - C)$ is the gradient and A, the area, is the openness. Numerous expressions for rates in nature follow approximately the same linear equation.

The surface area of the species is a fundamental property. The surface area indicates quantitatively the size of the boundary to the environment. Flow rates are often formulated in physics and chemistry as area times a gradient, which can be utilized to set up useful relationships between size and rate coefficients in ecology. For instance, loss of heat to the environment must be proportional to the surface area and to the temperature difference, according to the law of heat transfer. The rate of digestion, the lungs, hunting ground, etc. are, on the one hand, determinants for a number of parameters (representing the properties of the species), and on the other hand, they are all dependent on the size of the organism. It is, therefore, not surprising that many rate parameters for plants and animals are highly related to the size, which implies that it is possible to get very good first estimates for most parameters based only on the size. Naturally, the parameters are also dependent on several characteristic features of the species, but their influence is often minor compared with the size, and good estimates are valuable in many ecological models, at least as a starting value in the calibration phase. It is possible, however, to take these variations into account using a form factor = surface/volume. This form factor may vary considerably among species.

The conclusion of these considerations must, therefore, be that there should be many parameters that might be related to simple properties, such as size of the organisms, and that such relationships are based on fundamental biochemistry and thermodynamics (Figs. 2.2–2.6).

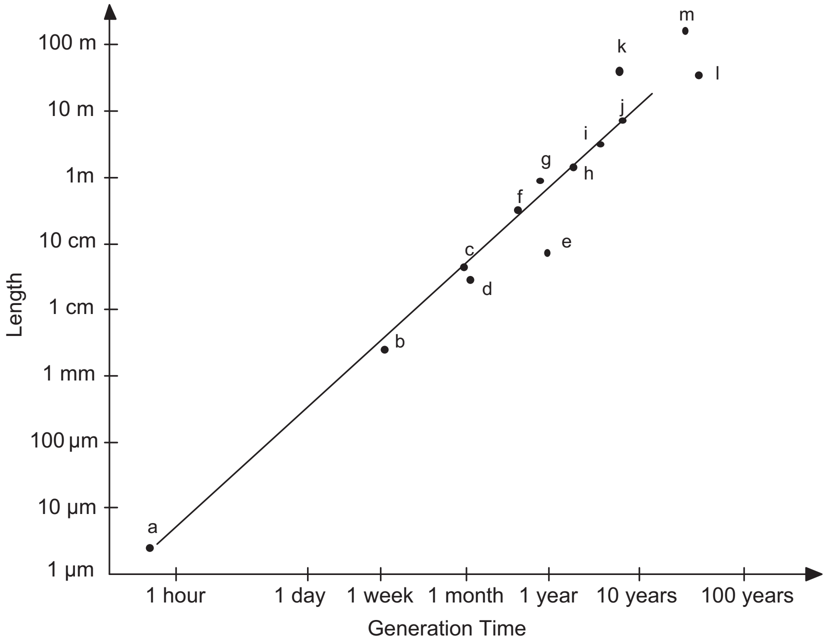

FIGURE 2.2 Length and generation time plotted on log–log scale: (a) *Pseudomonas*, (b) *Daphnia*, (c) bee, (d) housefly, (e) snail, (f) mouse, (g) rat, (h) fox, (i) elk, (j) rhino, (k) whale, (l) birch, and (m) fir (Peters, 1983). *Reproduced from Jørgensen, S.E., 2000a. Principles of Pollution Abatement. Elsevier, Oxford, UK, 520 pp.*

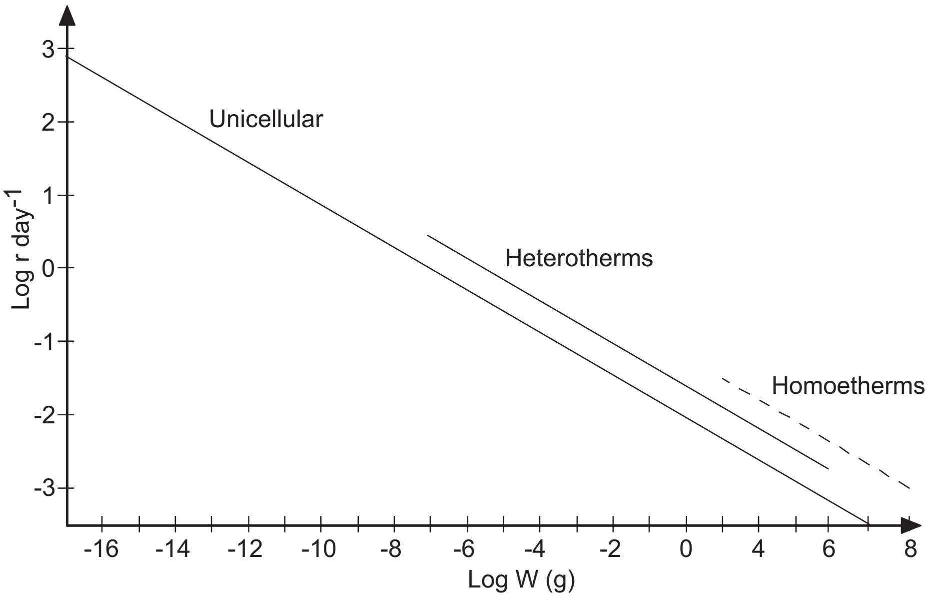

FIGURE 2.3 Intrinsic rate of natural increase against weight for various animals. After Fenchel (1974). Source: *Fundamentals of Ecological Modeling by Jørgensen and Bendoricchio.*

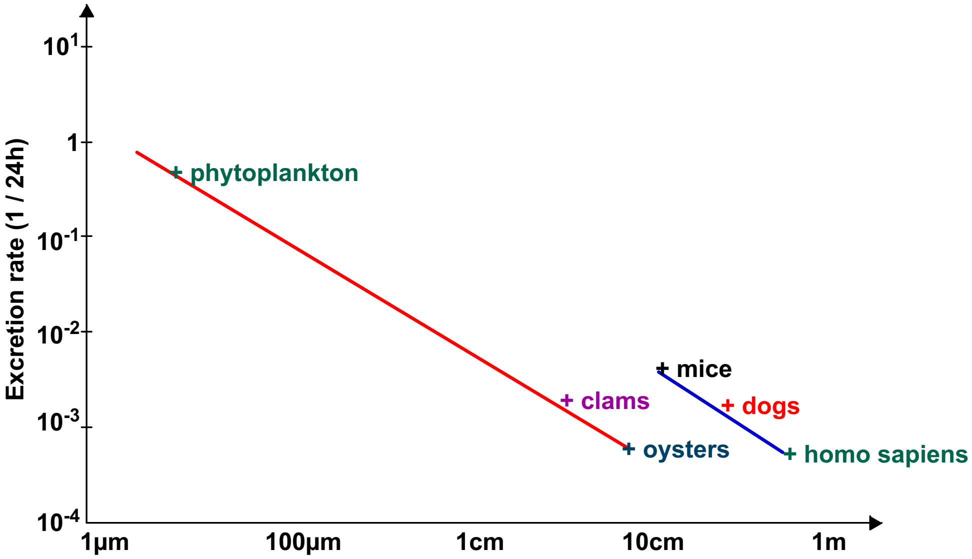

FIGURE 2.4 Excretion of Cd $(24\ \mathrm{h})^{-1}$ plotted against the length of various animals: (1) *Homo sapiens*, (2) mice, (3) dogs, (4) oysters, (5) clams, and (6) phytoplankton (Jørgensen, 1984).

Above all there is a strong positive correlation between size and generation time, T_g, ranging from bacteria to the biggest mammals and trees (Bonner, 1965). This relationship can be explained using the relationship between size (surface) and total metabolic action per unit of body weight mentioned above. This implies that the smaller the organism the greater the metabolic activity. The per capita rate of increase, r, defined by the exponential or logistic growth equations is again inversely proportional to the generation time:

$$\mathrm{d}N / \mathrm{d}t = rN \tag{2.20}$$

$$\mathrm{d}N / \mathrm{d}t = rN(1 - N/K) \tag{2.21}$$

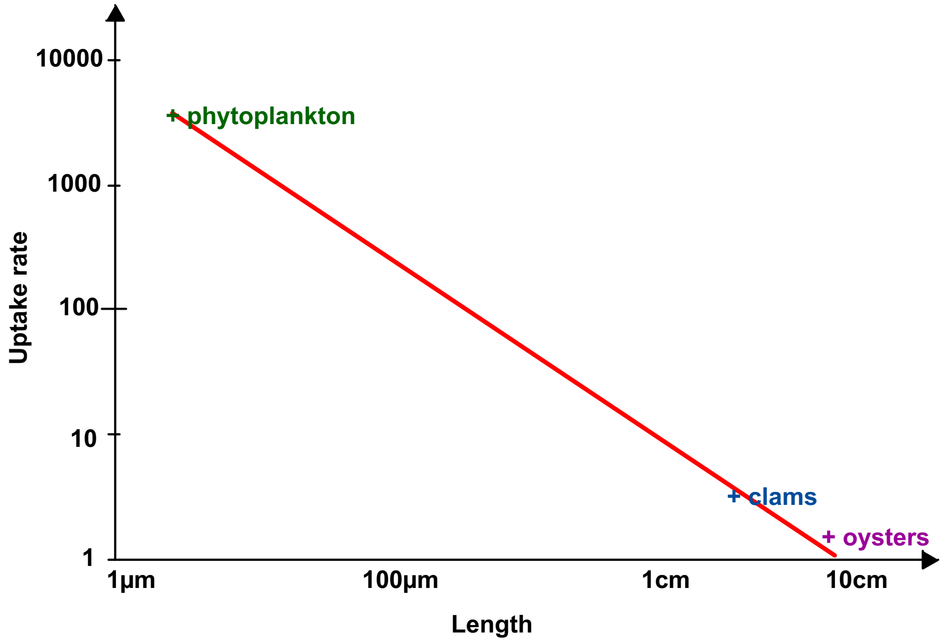

FIGURE 2.5 Uptake rate (mg g^{-1} $(24\ h)^{-1}$) plotted against the length of various animals (Cd): (1) phytoplankton, (2) clams, (3) oysters. After Jørgensen (1984). Source: *Fundamentals of Ecological Modeling by Jørgensen and Bendoricchio.*

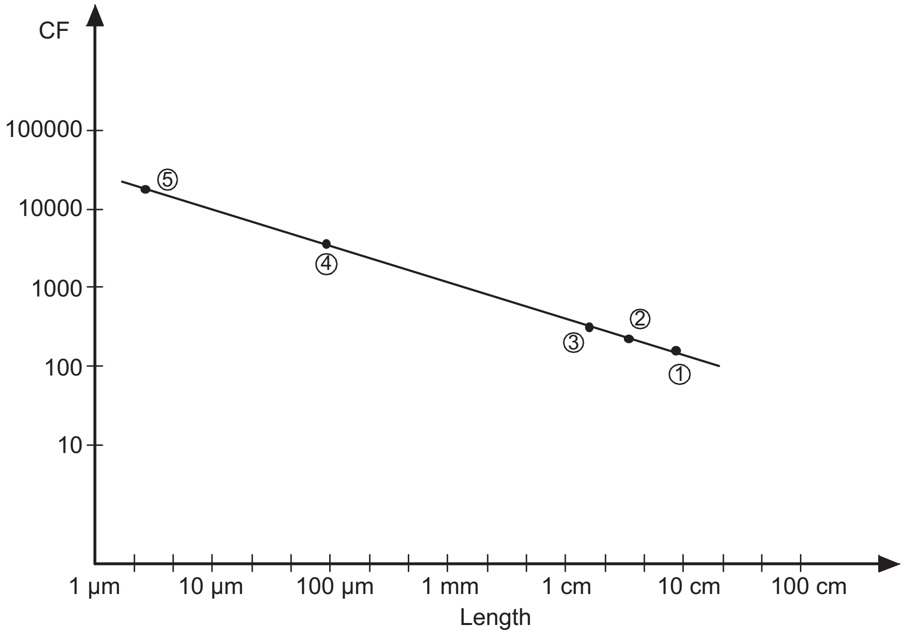

FIGURE 2.6 Biological concentration factor (BCF) denoted CF for Cd versus length: (1) goldfish, (2) mussels, (3) shrimps, (4) zooplankton, (5) algae (brown-green). After Jørgensen (1984). Source: *Fundamentals of Ecological Modeling by Jørgensen and Bendoricchio.*

where N is the population size, r the intrinsic rate of growth, and K the environmental carrying capacity. While r is related to the size of the organism, Fenchel (1974), showed that it falls into three groups: unicellular, heterotherms, and homeotherms (see Fig. 2.3).

The same allometric principles are expressed in the following equations, giving the respiration, food consumption, and ammonia excretion for fish when the weight, W, is known:

$$\text{Respiration} = \text{constant} \times W^{0.80} \tag{2.22}$$

$$\text{Feed Consumption} = \text{constant} \times W^{0.65} \tag{2.23}$$

$$\text{Ammonia Excretion} = \text{constant} \times W^{0.72} \tag{2.24}$$

It is also expressed in the general equation (Odum, 1959, p. 56):

$$m = kW^{-1/3} \tag{2.25}$$

where k is roughly a constant for all species, equal to approximately 5.6 $\mathrm{kJ/g^{2/3}}$ day, and m the metabolic rate per unit weight W.

Similar relationships exist for other animals. The constants in these equations might be slightly different due to differences in shape, but the equations are otherwise the same. All these examples illustrate the fundamental relationship in organisms between size (surface) and biochemical activity. The surface determines the contact with the environment quantitatively, and by that the possibility of taking up food and excreting waste substances.

The same relationships are shown in Figs. 2.4—2.6, where biochemical processes involving toxic substances are applied as illustrations. The excretion rate and uptake rate (for aquatic organisms) follow the same trends as the metabolic rate. This is of course not surprising, as excretion is strongly dependent on metabolism and the direct uptake dependent on the surface.

These considerations are based on allometric principles (see Peters, 1983; Straškraba et al., 1999), which in other words can be used to assess the relationship between the size of the units in the various hierarchical levels and the process rates, determining the need for the rate of energy supply. All levels in the entire hierarchy of an ecosystem are, therefore, due to the hierarchical organization, characterized by a rate which is ultimately constrained by their size.

Openness is proportional to the area available for exchange of energy and matter, relative to the volume = the inverse space scale (L^{-1}). This may also be expressed as the supply rate=k*gradient*area relative to the rate of needs, which is proportional to the volume or mass. An ecosystem must, as previously mentioned, be open or at least non-isolated to be able to import the energy needed for its maintenance. Table 2.3 illustrates the relationship between hierarchical level, openness, and the four-scale hierarchical properties presented in Simon (1973). The openness is expressed here as the ratio of area to volume.

For the higher levels in the hierarchy, approximate values are used. As we move upwards in the hierarchy, the exchange of energy (and matter) becomes increasingly more difficult due to a decreasing openness. It becomes increasingly more difficult to cover needs. This explains why energy density, time scale, and dynamics decrease according to the inverse space scale or openness, which are expressed differently as the rates are adjusted to make the possible supply of energy sufficient (Fig. 2.7). These considerations are consistent with the relationship between size and time scale of levels in the hierarchy, as presented by O'Neill et al. (1986) and Shugart and West (1981).

TABLE 2.3 Relationship Between Hierarchical Level, Openness (Area/Volume Ratio), and Approximate Values of the Simon's (1973) Four Scale-Hierarchical Properties: Energy/Volume, Space Scale, Time Scale, and Behavioral Frequency.

Hierarchical Level	Openness[1,3] (A/V, m^{-1})	Energy[2] (kJ m^{-3})	Space Scale[1] (m)	Time Scale[1] (sec)	Dynamics[3] (g m^{-3}sec)
Molecules	10^9	10^9	10^{-9}	$<10^{-3}$	10^4–10^6
Cells	10^5	10^5	10^{-5}	10–10^3	1–10^2
Organs	10^2	10^2	10^{-2}	10^4–10^6	10^{-3}–0.1
Organisms	1	1	1	10^6–10^8	10^{-5}–10^{-3}
Populations	10^{-2}	10^{-2}	10^2	10^8–10^{10}	10^{-7}–10^{-5}
Ecosystems	10^{-4}	10^{-4}	10^4	10^{10}–1^2	10^{-9}–10^{-7}

[1] *Openness, spatial scale, and time scale are inverse to hierarchical scale.*

[2] *Energy and matter exchange at each level depend on openness, measured as available exchange area relative to volume. Electromagnetic energy as solar photons comes in small packages (quanta,* hν, *where h is Planck's constant and ν is frequency), which makes only utilization at the molecular level possible. However, cross-scale interactive coupling makes energy usable at all hierarchical levels.*

[3] *Openness correlates with (and determines) the behavioral frequencies of hierarchical levels.*

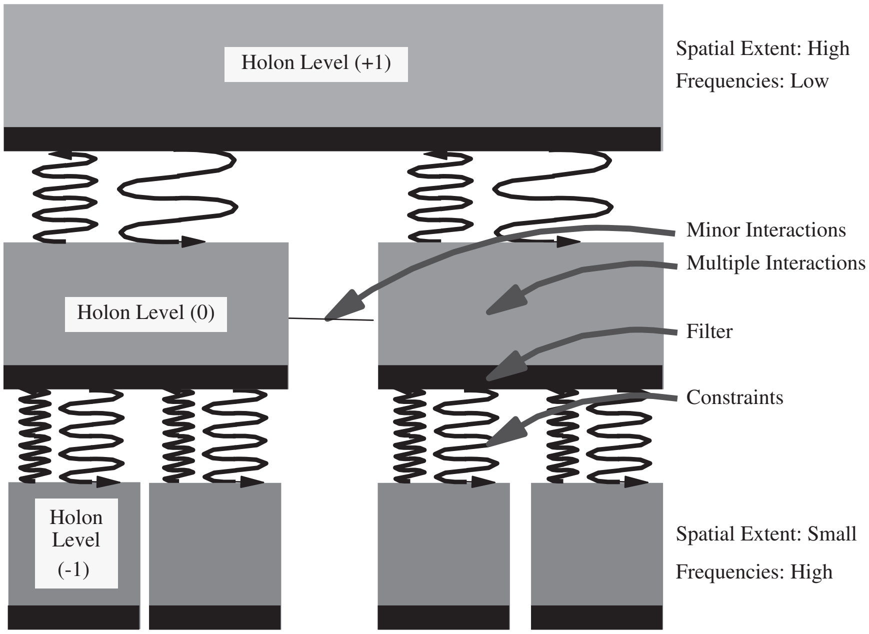

FIGURE 2.7 A schematic representation of interacting hierarchical levels.

Exchange of matter and information with the environment of open systems is in principle not absolutely necessary, thermodynamically, as energy input (nonisolation) is sufficient (the system is nonisolated) to ensure maintenance far from equilibrium. However, it often gives the ecosystem some additional advantages, for instance, through the input of chemical compounds needed for certain biological processes or by immigration of species offering new possibilities for a better ordered structure of the system. All ecosystems are open to exchange of energy, matter, and information with their environment.

The importance of the openness to matter and information is clearly illustrated in the general relationship between number of species, SD (species diversity), of ecosystems on islands and the area of the islands, A:

$$\mathrm{SD} = C \times A^{z}(\text{number}), \tag{2.26}$$

where C and z are constants. The perimeter relative to the area of an island determines how "open" the island is to immigration or dissipative emigration from or to other islands or the adjacent continent. The unit (L^{-1}) is the same as the above used area to volume ratio as a measure of openness.

Different species have very different types of energy use to maintain their biomass. For example, the blue whale uses most of the energy available (97%) for increasing biomass and only 3% for reproduction. Whales are what we call *K*-strategists, defined as species having a stable habitat with a very small ratio between generation time and the length of time the habitat remains favorable. This means that they will evolve toward maintaining their population close to the carrying capacity. *K*-strategists are in contrast to *r*-strategists which are strongly influenced by any environmental factor. Due to their high growth rate they can, however, utilize suddenly emergent favorable conditions and increase the population rapidly. Many fishes, insects, and other invertebrates are *r*-strategists. The proportion of energy going into reproduction can be over 50%.

2.7 THE CELL

The cell is the basic biological unit, as the elementary particles and the elements are the basic units of chemistry. In spite of the enormous variation in the structure and function of different organisms, the fundamental unit, the cell, is with some variations basically the same. Why is the cellular structure the same? First, early in evolution the cell demonstrated its functionality. But the use of structural units of small size has also ensured effective transportation

TABLE 2.4 Some Differences Between Prokaryotic and Eukaryotic Cells.

	Prokaryotes	Eukaryotes
Size	1—10 μm	10—100 μm
Nucleus	None. The chromosomal region is called nucleolus	Nucleus separated from cytoplasm by nuclear envelope
Intracellular organization	Normally, no membrane-separated compartments and no supportive intracellular framework	Distinct compartments, e.g., nucleus, cytosol with cytoskeleton, mitochondria, endoplasmic reticulum, Golgi complex, lysosomes, plastids
Gene structure	No introns; some polycistronic genes	Introns and exons
Cell division	Simple	Mitosis or meiosis
Ribosome	Large 50S subunit and small 30S subunit	Large 60S subunit and small 40S subunit
Reproduction	Parasexual recombination	Sexual recombination
Organization	Mostly single-cellular	Mostly multicellular, with cell differentiation

After Klipp, E., Herwig, R., Kowald, A., Wierling, C., Lehrach, H., 2005. Systems Biology in Practice. Concepts, Implementation and Application. Wiley-VCH Verlag GmbH, Weinheim, Germany, 465 pp.

by diffusion. Most cells have a diameter between 1 and 20 mm (Table 2.4). Cells have, therefore, a relatively high openness (see Table 2.3), which is necessary for the biochemistry of organisms to work. The hierarchical structure, which was presented in Fig. 2.7 and will be further discussed in Chapters 5 and 8, is a precondition for the needed openness for each level in the hierarchy.

Let us, however, demonstrate the importance of openness by focusing on the cell. The problem for the cells is to have an openness that would match the need for diffusive transportation for the matter needed for the biochemical syntheses that take place in the cells, first of all for the synthesis of proteins.

Protein synthesis takes place in about 10 steps from primary gene expression in DNA inside the nucleus to final production of the mature protein at its final destination outside the nucleus but within the plasma membrane. First there is transcription in which the DNA region encoding the gene is transcribed into a complementary messenger RNA (mRNA). Next, in eukaryotes, initial pre-mRNA is spliced and processed to mature mRNA. This is exported across the nuclear envelope into the cytosol. There, codons in ribosomes progressively translate the genetic code into a mature cytosolic protein. This is followed by several steps of sorting and modification involving cytoplasmic ultrastructures such as the endoplasmic reticulum and Golgi apparatus. All the genes of an organism make up its genome. Of these, only certain ones will be expressed at a given time or for a specific cell type. Some genes which perform basic functions are always required; these are constitutive or housekeeping genes. Others are expressed only under certain conditions (Klipp et al., 2005, pp. 45—47).

Openness in the scenario just given is particularly pronounced at the nuclear and cytoplasmic boundaries, but in fact is expressed all along the way as intracellular structures receive, process, and pass along the various intermediary products in protein synthesis. Is the openness sufficient to ensure uptake of oxygen and nutrients needed for protein synthesis? Matter needed for the biochemistry is proportional to the volume (we presume that the cell is a sphere where d is cell diameter):

$$\text{Volume} = \pi d^3/6 \tag{2.27}$$

The transport from the surface to the cell takes place by a fast, active transport and the concentration at the surface is, therefore, 0. The area of the sphere is πd^2. The flux of matter toward the cell is considered constant, which implies that the concentration gradient will decrease with the distance from the cell in the exponent 2:

$$\mathrm{d}C\,/\,\mathrm{d}r = k\,r^{-2} \tag{2.28}$$

where r is the distance from the center of the cell (radius). The concentration is 0 at the surface of the cell, i.e., $r = \mathrm{d}/2$. The concentration at the distance r from the center of the cell C_r can be found after differentiation of Eq. (2.28) to be:

$$C_r = C(1 - \mathrm{d}/2r). \tag{2.29}$$

The diffusion rate, corresponding to the uptake rate is a diffusion coefficient (D) times the concentration gradient ($\mathrm{d}C/\mathrm{d}r = Cd/2r$ or at the surface $= 2C/d$) times the openness = area $= \pi d^2$, or therefore $2\pi dDC$, where D is the diffusion coefficient and C the concentration in the environment. The uptake rate relative to the need, denoted UR/N, is found as:

$$UR/N = 12DC/(fd^2) \tag{2.30}$$

where f is the need per unit of time and volume. The relative uptake rate will be four times smaller, if the diameter is doubled. Relatively small cell sizes are necessary to obtain a sufficient relative uptake rate. This equation demonstrates the importance of the cell size and explains, therefore, indirectly the hierarchical structure because small cells are the prerequisite for a sufficient supply of nutrients, although there are many additional explanations.

2.8 WHAT ABOUT THE ENVIRONMENT?

Openness is a requisite for moving substance across boundaries, and boundaries imply an inside–outside dichotomy. That is, in departure from thermodynamic equilibrium energy and matter move from outside to inside and dissipation signifies movement in the reverse direction, from interiors to exteriors.

The term “environment” has appeared 46 times previously in this chapter, in a book on ecology, the biological science of environment, and yet we have not once anywhere done anything explicitly with this concept except take it for granted as a reference source and sink from which some older more or less accepted thermodynamics, without its modern challenges, proceeds to operate in the organization of ecosystems. We use the concept of environment, but have not attempted to define it scientifically or explore it in any deep way. There is little in theoretical ecology that elaborates it in substantive scientific terms. It is just a convenient category of “surroundings” that openness requires—some place to derive inputs and exhaust outputs.

Particular scales aside, it is relevant in the context of openness to ask the hard question— “What is environment?” We look around the room or outside the window and see what everyone agrees is “environment.” Seeing is only part of it, however; there is also touching and smelling, etc. In other words, there are sensory stimuli involved. What about these? Our household pets and the plants in the garden that began this chapter have considerably different sensory apparatus from us. Does that mean environment is relative, something that can only be defined by perception? Or are certain aspects of it accessed differently by different open systems? It is clear from the perspective of reality as a collection of physics’ particles, and from mass–energy conservation, that what comes to me at a given moment as visual, auditory, tactile, etc. stimuli cannot also come to you or your dog or plant. At this level, it must be acknowledged that there is a certain uniqueness that attaches to the “environments” of particular open-system receivers of sense-data. Not only is this true for sensory stimuli, but also for the masses of matter that enter our bodies as food and exit as biodegradable products useful as food for other organisms. So, environment, it would seem, courses in and out of open systems, and the ultimate uniqueness of the substance and signals both confer a central place on the *open system* as the focal arbiter of environment. Afferent input environments coming from the past are originated the moment a unit of high-quality energy or matter crosses the boundary of a receiving open system. This increases the exergy and lowers the entropy of the receiving system. Reciprocally, efferent environments that unfold with the future are founded the moment a unit of energy or matter exits the said open system. This dualistic concept of environment is operationalized in the mathematical theory of *environs* (Patten, 1978; 1982), about which now numerous papers have been published describing the properties of such structures. The dualism is central, and so is the unity of the focal entity–environ triad. Environments and the things with which they are associated can never be separated in environ theory—they are a unit of nature, however intractable, but sometimes with surprising holistic properties which are explored in detail in Chapter 4.

2.9 CONCLUSION

Openness of systems to exchange of energy and matter implies certain foundational properties in natural organization:

- It is a necessary but not sufficient property for ecosystems.
- It presumes boundaries;
- Boundaries imply bounded entities—something kept in;

- Entities imply an elemental discreteness in natural organization (note Table 2.3);
- Therefore, human sensory apparatus operates correctly in perceiving an essentially particulate world.

Or does it? … since it is also true that:

- Boundaries imply environments—something kept out;
- Environments are unbounded, thus inherently nondiscrete;
- Therefore, human perception is mismatched to environmental reality.

This may be why we know more about disconnected objects than we do about object–environment relationships, and why science is more reductive than holistic. It appears that the property of openness, the subject of this chapter, returns us to the same kind of enigma as the wave–particle duality, giving ecology a deep challenge for its future to unravel.

C H A P T E R

3

Ecosystems Have Ontic Openness

…next to music and art, science is the greatest, most beautiful and most enlightening achievement of the human spirit ***Popper (1990)***

3.1 INTRODUCTION

This chapter's title may mean little to many persons, yet the essence may be understood fairly easily on an intuitive basis. The adjective "ontic," which hardly appears in any dictionary, clearly relates to the term ontology, which is used in philosophy in its widest sense to designate "the way we view the world and how it is composed." Ontic bears the slight difference that it refers to intrinsic properties of the world as we construct it and its behavior, such that it addresses phenomenology as well. Therefore, this chapter complements the concepts of thermodynamic openness addressed in the previous chapter, by including the physical openness available to ecosystem development.

In fact, everybody knows something about openness. We know how it is to be open to another person's opinions, to be open minded, or open to new experiences. We enjoy that surprising things may happen on our (field) trips and journeys (in nature). In fact, any person who has tried to plan exact details for a trip into the wilderness will know how difficult this is. First, we may address the aspect of realizing such a trip and stress that this also implies the acceptance of the fact that unexpected things may or rather will occur. But, second, we have also to address the fact that once an event occurs, it is an outcome of many unexpected events. It is impossible to predict which one and how often such events actually occur. We may expect to bring extra dry socks to use after one incident, an unexpected event. How many persons will be able to foresee exactly how many pairs to bring? Or in other cases, we may return with unused socks but found that we needed extra shirts instead. Any of us will know that it is eventually not possible to make such a detailed plan.

In fact, one could have chosen another title to the present chapter: "anything may—but does not—happen." Of which the first part deals with, as we shall see in the following, the enormous number of possibilities that exist in general and also in biological systems. The second part indicates that all possibilities have not been realized, partly because it is not physically possible, and partly due to constraints that are described in other chapters of this book.

This chapter is about the ontic openness of ecosystems. It relates directly to the theme of this book and the systemness of ecosystems because ontic openness results, in part, due to the complex web of life constantly combining, interacting, and rearranging in the natural world to form novel patterns. Furthermore, ontic openness is at least a partial cause of indeterminacy and uncertainty in ecology and thus the reason that we are not able to make exact predictions or measurements with such a high accuracy as, for instance, in physical experiments. Therefore, when understanding ecosystems from a systems perspective, one cannot overlook the importance of physical openness.

3.2 WHY IS ONTIC OPENNESS SO OBSCURE?

In referring to the above title of this chapter we have already mentioned that it likely will pose a question to the vast majority of readers, not only the ecologically oriented ones: what is the meaning of the title of this chapter? We have tried to foresee this question already by giving a first vague and intuitive explanation. We guess it is likely that

https://doi.org/10.1016/B978-0-444-63757-4.00003-6

only a few readers have met this "phenomenon" before as far as the term ontic openness is concerned. We also expect that very few, if any, of the readers are familiar with texts that deal with the role of ontic openness in an ecological context.

To our knowledge, no such thorough treatment of this topic exists. Rather a number of treatments of more or less philosophical character exist—all of which may be taken into account—and which all together may add up to a composite understanding of what ontic openness may mean and what its importance and consequences to ecological science may be.

Should we attempt to further explain ontic openness very briefly (which is impossible) we would start with openness, and turn the attention to another related word like open-minded. We normally use this word to designate a person who is willing to try out new things, accept novel ideas, maybe a visionary person able to think that the world could be different, that matters may be interdependent in other ways than in which we normally think. Many scientists make their breakthrough, thanks to such mental openness. Discoveries are often unexpected or unplanned—a phenomenon known in the philosophy of science as *serendipities*. Kuhn also addresses this issue of the scientific procedure when he stresses that paradigm shifts in the evolution of science involves that scientists come to look at the same object from a different angle or in a different manner.

We now would like, if possible, to remove the psychology element. If we remove the role of *subjectivity*, i.e., that openness relies on one or more person's ability or willingness to see that the surrounding world may be different or could have other possibilities realized than hitherto, then we are really on the right track.

We are now left with an *objective* part of openness. If we can now accept the physical existence of this and that it is a property that penetrates everything, then we are really getting there. The openness is an objectively existing feature not only of the world surrounding us but also ourselves and our physical lives (e.g., biochemical individuality introduced by Williams (1998)). This is the ontic part of the openness.

Another reason for ontic openness not to be so commonly known among biologist and ecologist is the fact that the progenitors of this concept were dominantly physicists and in particular those in the areas of quantum mechanics, particle physics, and relativity theory. Furthermore, we typically do not view these areas as being directly relevant to biology or ecology. Also, these theories are not easy to communicate to "outsiders," so even if ecology is considered to be a highly trans-, inter-, and multidisciplinary science, it is perfectly understandable that no one has thought that these hard-core subdisciplines of physics today could possibly have a message for ecology.

Luckily, one might say, some of the physicists from these areas turned their attention in other directions and started speculating about the consequences of their findings to other areas of natural science such as biology. On several occasions we have found physicists wondering about the distinction between the physical systems and living systems, such as Schrödinger's *What is life*. Living systems are composed of basically the same units, atoms, and molecules, and yet they are so different. One physicist, Walter Elsasser, will receive an extra attention in this chapter. Studying his works, in particular from the later part of his productive career, may turn out to be a gold mine of revelations to any person interested in how biology differs from physics and about life itself.

Still have not understood or got the idea of what ontic openness is about? Do not worry—you most probably have experienced it and its consequences already. Let us investigate some well-known examples.

Most Ecologists Have Experienced Ontic Openness Already!

Most ecologists will have met ontic openness already—somewhat in disguise—as often our background comes from the gathering of empirical knowledge, an experience we may have achieved through hard fieldwork.

To start, let us consider a hypothetical "test ecologist." Given the information about latitude and a rough characteristic ecosystem type—terrestrial or aquatic—she will be able to decide whether she is expert "enough" in the area to forecast the system state or if she prefers to enlist aid from a person considered to be more knowledgeable in the area. If deciding to be an "expert," then she will for sure be able to tell at least something about the basic properties of the ecosystem, such as a rough estimate of the number and type of species to be expected. Given more details, such as exact geographical position, we may now narrow in on ideas considering our background knowledge. There will be a huge difference in organisms, species composition, production, if we are in the arctic or in the tropics. Likewise, being, for instance, in the tropics there will be a huge difference between a coral reef in the Pacific Ocean or in a mangrove swamp in the Rufiji River Delta. We will be able to begin to form images of the ecosystem in our minds, conceptual models of trophic interactions, community linkages, and functional behavior. Meanwhile, we know very well that to get closer in details with our description we will need additional knowledge, for instance, about ecological drivers, such as hydrodynamics, depth, and other external influences, such as human impacts from fisheries, loadings of both organic and inorganic in type, etc.

Nevertheless, given as much information as we possibly **can** get and, for instance, focusing in on a particular geographic position, such as the Mondego River Estuary in Portugal, we will not be able to answer simple questions accurately such as Which plant species are present at a certain locality, how are they distributed, or what are their biomass and production? We will more likely be able to give an answer something like "that under the given conditions we would consider it to be most likely that some rooted macrophyte will be present and that it would probably be of a type that do not break easily, probably with band-shaped leaves, probably some species of Zostera, etc. We will be able, based on experience and knowledge, to give only an estimate in terms of—what we shall later call the propensity—the system to be of a certain 'kind'." BUT we will never be completely sure. This is due to ontic openness.

Examples from the World of Music

Sometimes, when introducing new concepts, it is useful to make an entrance from an unexpected and totally different angle. In this case, we will consider the world of music—a world with which most people are familiar and have specific preferences. We only know very few people to whom music does not say anything and literally does not "ring a bell."

We consider—in a *Gedanken Experiment*—the situation of an artist set to begin a new composition. To illustrate the universality of the approach we may illustrate the situation by the possible choices in two situations—a small etude for piano or a whole symphony. We shall start by looking at both the situations from a statistical and probabilistic angle. The two situations may look quite different from a macroscopic point of view, but in fact they are not.

In the case of a short piece for piano, a normal house piano has a span of approximately 7 (or 7¼) octaves of 12 notes each giving 84 (or 88) keys in all. If an average chord on the piano has five notes in it, then it is theoretically possible to construct 3,704,641,920 or approx 3.7 billion chords on it (4.7 billion in the case of 88 keys). (Note that we already here deal with a subset of the $84! = 3.3 \times 10^{126}$ possibilities). Meanwhile, if the assumption that a chord consists of five notes on average is valid, then it does not take long to reach almost the same level of complexity *sensu lato*. Putting a small piece of music together, assuming that we work in a simple 4/4 and change chords for each quarter, after 16 notes or 4 bars have reached a level 126×10^{153} of possible ways to construct the music. Many of these possible combinations of notes and chords would not sound as music at all, and luckily we are faced with constraints. A physical constraint, such as the human physiology, will serve to limit the number of notes than can be accessed in a single chord (a good piano player will be able to span maybe over one octave per hand, thereby lowering the number of possible variations considerably). Psychological constraints of various kinds do also exist depending on the decisions of the composer or our personal taste—we do want the music to sound "nice."

The situation does not change a lot considering a symphony orchestra although complexity really rises much faster. Considering a relatively small symphony orchestra of say 50 musicians—each having a span of approximately 3 octaves or (36 notes)—even before starting we have 36^{50} or 6.5×10^{77} possibilities of how the first chord may sound. By the second note we have already exceeded any of the above numbers.

Almost no physical constraints exist in this case. The task of the composer is very simple, picking a style of music like the choices between classic or 12-tone music, between piano concerto, opera, or string quartets. The point is now that for each note, for each chord, there are many possibilities of what the composer **could** write on the sheet, but in fact only one ends up being chosen, one "solution" out of an enormous number of possibilities. As we shall see later, the number of possibilities to choose from is so large (*immense*) that it makes no physical sense. Therefore, in the end the choice of the composer is *unique*. The fact that we anyway will be able to determine and talk about such a thing like style is that the composers have had a tendency (see *propensities* later) to choose certain combinations out the possible.

Let us end this section with a situation most people will know. Considering yourself a skilled person, familiar with the many styles of music, you listen to an unknown piece of music in a radio broadcast. It is a very melodic piece of music in a kind of style you really like and with which you are familiar. You, even without knowing the music, start to hum along with some success, but eventually you will not succeed to be totally right throughout the whole piece. Do not worry, it is not you that is wrong, neither is the music—you are just experiencing the ontic openness of someone else, in this case the composer.

3.3 ONTIC OPENNESS AND THE PHYSICAL WORLD

As mentioned above, a number of treatments of this topic exist that all add up to our possible understanding of the importance of ontic openness and what it means in the context of our everyday life. Putting them together and taking the statements to a level where we really see them as ontological features, i.e., as ontic, we will be, on one hand forced to reconsider what we are doing, on the other hand, we can look upon the world, and in particular the uncertainties, the emergent properties that we meet, in a much more relaxed manner.

Unfortunately, to ecology and the ecologists, as previously mentioned, the statements that have already been made on openness almost all originate from physicists. In fact, seen from a philosophy of science point of view, this means that the statements are often dominated by arguments deeply rooted in reductionist science, often literally close to an atomistic view. Interesting things happen when the arguments are taken out of the reductionist realm to other levels of hierarchy, i.e., the arguments are taken out of their physical context and extended to biology and eventually—following our purpose of the present book—into ecology.

The basic contributions we think of here may be represented by a number of scientists. A sketch of a few essential ideas that it may be possible to relate to the issue of ontic openness as well as the originators is given in Table 3.1.

In the following, we will take a more detailed look at a few of these perspectives. From the table it is evident that we deal with quite recent contributions and some noteworthy overlaps in time. It would, of course, be interesting to know if and how these persons have influenced each other, a thing which may become clear only from close, intensive studies of the time development of their works and biographies. Meanwhile, this would be a tedious task and the possible mutual influence has not been considered in this paper.

TABLE 3.1 A Non-exhaustive List of Various Authors Who Have Addressed the Issues of Ontic Openness of Natural, Physical, and Biological Systems.

Originator	Era	Idea	Remark
N. Bohr	1885—1962	Complementarity—the idea that the more descriptions are needed	Derived from the wave—particle duality
E. Schrödinger	1887—1961	Order from disorder and order from order	Relates to Elsasser's immense numbers and historical aspects
W. Heisenberg	1901—1976	The principle of uncertainty or indeterminacy, e.g., the simultaneous determination of position and momentum of an electron is not possible	Argued to be valid also for ecosystems by Jørgensen
K.R. Popper	1902—1994	**a)** End of fixed probabilities— we need to work with propensities **b)** The open universe	Basic assumption behind Ulanowicz's concept of ascendency
W.M. Elsasser	1904—1991	Biological systems are heterogeneous and therefore possess immense possibilities which are coped with by agency and history	The combinatorial explosions shaping this phase-space occurs at almost any level of hierarchy
I.A. Prigogine	1917—2003	The understanding of biological systems as dissipative structures and far from equilibrium systems	Assumes that the "Onsager relation" may be extended to the conditions of life (Chapter 6)
C.S. Holling	1930—	The idea that evolution happens through breakdowns that opens up to new possibilities through an ordered/cycling process	See creative destruction (Chapter 7). Similar to H.T. Odum pulsing paradigm
S.E. Jørgensen	1934—2016	The Heisenberg uncertainty principle extended to ecosystem measurements	
S.A. Kauffman	1939—	The continuous evolution of biological systems toward the edge of chaos	

At first, the ideas may appear disparate, but in fact all illustrate the necessity to view systems as ontically open.

It Is Not Possible to Measure Everything

In the world of physics, the importance of uncertainty and our interference with systems through experiments has been recognized for less than a century. The introduction of concepts such as complementarity and

BOX 3.1

THE HEISENBERG UNCERTAINTY PRINCIPLE OR PRINCIPLE OF INDETERMINACY

The basic proof shows that the product of position and momentum will always be larger than the Planck's constant. This is given explicitly by the following mathematical terms:

$$\Delta s \times \Delta p \geq \frac{1}{2}\hbar = \frac{h}{4\pi} \tag{3.1}$$

where s refers to space, p is the momentum, and h is the Planck's constant (6.626×10^{-34} J s).

irreversibility has offered solutions to many problems but has simultaneously involved the recognition of limits to the Newtonian paradigm. Below, we deal with some important findings in physics from the 20th century such as the Heisenberg uncertainty principle, the Compton effects, and the relaxation of systems that may have future parallels in ecology.

The Heisenberg Principle

The Heisenberg uncertainty relation tells that we cannot know exactly both the position and the velocity of an atom at the same time. At the instant when position is determined, the electron undergoes a discontinuous change in momentum. The smaller the wavelength of the light employed, the greater the change. Thus, the more precise the position is determined, the less precise the momentum is known, and vice versa (Box 3.1).

The Compton Effect

The Compton effect deals with the change in wavelength of light when scattered by electrons. According to the elementary laws of the *Compton effect*, p_1 and λ_1 stand in the relation:

$$p_1 \times \Delta\lambda_1 \cong h \tag{3.2}$$

$$\Delta E_1 \times \Delta T_1 \cong h \tag{3.3}$$

where p_1 is the momentum of the electron, $\Delta\lambda_1$ is the wavelength increase due to the collision, E_1 is the energy, and T_1 is the time.

Eq. (3.2) corresponds to Eq. (3.3) and shows how a precise determination of energy can only be obtained at the cost of a corresponding uncertainty in the time (Box 3.2).

Spin Relaxation

Spin relaxation is possible because the spin system is coupled to the thermal motions of the "lattice," be it gas, liquid, or solid. The fundamental point is that the lattice is at thermal equilibrium; this means that the probabilities of spontaneous spin transitions up and down are not equal, as they were for rf-induced transitions (Box 3.3).

Given the remarks made at the start of this section, one may indeed start to wonder and speculate about the relations of these physical systems that obey universal laws when involved at the level of chemistry and biology and how or if these affect living systems at all. This is exactly what the physicist Walter M. Elsasser did, and it may be worthwhile to spend a few moments studying his work and conclusions.

BOX 3.2

THE COMPTON EFFECT AND DIRECTIONALITY

From the uncertainty relation between position and momentum, another relation may be derived. Let v and E be the velocity and energy corresponding to momentum p_x, respectively, then:

$$v\Delta p_x \frac{\Delta x}{v} \geq h$$

$$\Delta E \times \Delta t \geq h$$

where ΔE is the uncertainty of energy corresponding to the uncertainty of momentum Δp_x and Δt is the uncertainty in time within which the particle (or the wave packet) passes over a fixed point on the x-axis (Fong, 1962). Thus, irreversibility of time is not taken into account since in the quantum mechanics paradigm time is assumed to be reversible.

We want to point out that if we take as an axiom the irreversibility of time, it is an error to calculate the limit:

$$\lim_{\Delta t \to 0} \frac{\Delta s}{\Delta t}$$

because this means that

$$\forall \varepsilon > 0, \quad \exists \delta > 0 : \left|\Delta t\right| < \delta \Rightarrow \left|\frac{\Delta s}{\Delta t}\right| < \varepsilon$$

where

$$|\Delta t| < \delta \Leftrightarrow |t_1 - t_0| < \delta \Leftrightarrow -\delta < t_1 - t_0 < \delta \Leftrightarrow t_0 - \delta < t_1 < t_0 + \delta$$

Simply speaking, it is not possible to think t_1 as approximating t_0 from right, in fact, the state $S(t_0)$ that the function S reaches when t_1 becomes t_0 from right cannot be the same state $S(t_0)$ that the function assumes as t_1 reaches t_0 from left.

It is well known that if the left and right limits of a function are not identical, then the limit does not exist. Hence, we must redefine the time derivative of a function as the left limit, if it exists

$$\lim_{\Delta t \to 0} \frac{\Delta s}{\Delta t}$$

This translates in practice to the statement that in the Cartesian graph, it is impossible to cover the t-axis in both sense from left to right and right to left, but in the first manner only.

3.4 WHAT REALLY DIFFERS BETWEEN PHYSICS AND BIOLOGY: FOUR PRINCIPLES OF ELSASSER

The one contributor from Table 3.1 that literally takes the step from physics into biology was Walter M. Elsasser whose "roaming" life is quite impressive. The details of his life are described in a biography[1] by Rubin (1995), who was acquainted with Elsasser the last 10 years of his life. Most of the information on Elsasser mentioned below is based on this biography and Elsasser's own autobiography (Elsasser, 1978). From these works, one cannot help sense that Elsasser's contributions were sparked by ontic openness on his own "body and soul" throughout his career. Rubin (1995) summarized Elsasser's (1987) four basic principles of organisms: (1) ordered heterogeneity, (2) creative selection, (3) holistic memory, and (4) operative symbolism. The first principle is the key reference to ontic openness, while the other points address how this order arises in this "messy" world of immense numbers. In other words, the latter three seem more to be ad hoc inventions necessary to elaborate and explain the first.

Background

According to Rubin, Theophile Khan influenced Elsasser's understanding of the overwhelming complexity dominating biological systems as compared with the relative simplicity of physics. Probably, he was also influenced by Wigner from whom he is likely to have picked up group or set theory.

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[1] This excellent biography is available on the Internet in several forms. Philosophy of science students will be provided with a deep insight in how production of a scientist may not necessarily depend on skill or education, but may rather be determined by political and sociological regimens throughout his life.

BOX 3.3

RELAXATION OF SYSTEMS

Denoting the upward and downward relaxation probabilities by $W_{\alpha\beta}$ and $W_{\beta\alpha}$ (with $W_{\alpha\beta} \neq W_{\beta\alpha}$), the rate of change of N_α is given by

$$\frac{dN_\alpha}{dt} = N_\beta W_{\beta\alpha} - N_\alpha W_{\alpha\beta}$$

At thermal equilibrium $dN_\alpha/dt = 0$, and denoting the equilibrium population by $N_{0\alpha}$ and $N_{0\beta}$ we see that

$$\frac{N_{0\beta}}{N_{0\alpha}} = \frac{W_{\alpha\beta}}{W_{\beta\alpha}}$$

The populations follow from Boltzmann's law, and so the ratio of the two transition probabilities must also be equal to $\exp(-\Delta E/kT)$. Expressing N_α and N_β in terms of N and n ($n = N_\alpha - N_\beta$), we obtain

$$\frac{dn}{dt} = -n\left(W_{\beta\alpha} + W_{\alpha\beta}\right) + N\left(W_{\beta\alpha} - W_{\alpha\beta}\right)$$

This may be rewritten as

$$\frac{dn}{dt} = -\frac{(n - n_0)}{T_1}$$

in which n_0, the population difference at thermal equilibrium, is equal to

$$n_0 = N\left[\frac{W_{\beta\alpha} - W_{\alpha\beta}}{W_{\beta\alpha} + W_{\alpha\beta}}\right]$$

and $1/T_1$ is expressed by

$$\frac{1}{T_1} = W_{\alpha\beta} + W_{\beta\alpha}$$

T_1 thus has the dimensions of time and is called the "spin-lattice relaxation time." It is a measure of the time taken for energy to be transferred to other degrees of freedom, that is, for the spin system to approach thermal equilibrium: Large values of T_1 (minutes or even hours for some nuclei) indicate very slow relaxation (Carrington and McLachlan. Introduction to Magnetic resonance).

It is now possible to say something about the width and shape of the resonance absorption line, which certainly cannot be represented by a Dirac δ function.

First, it is clear that, because of the spin relaxation, the spin states have a finite lifetime. The resulting line broadening can be estimated from the uncertainty relation:

$$\Delta v \, \Delta t \approx 1$$

and thus we find that the line width due to spin—lattice relaxation will be in the order of $1/T_1$.

These studies, together with periodical influence from von Neumann, caused him to realize a fundamental difference between physical systems on the one side and living systems on the other. Due to his early life education in atomic physics, he considered physical systems as homogenous sets—all atoms and molecules of a kind basically posses the same properties and behavior. At this level, and always near to equilibrium conditions, the world is deterministic and reversible processes dominate.

As opposed to this view, he considered living systems to differ in this fundamental aspect of the homogenous sets. Living systems, he argued, are highly heterogeneous and far more complex than physical systems. Their behavior as opposed to physical systems is nondeterministic and irreversible. This is what we today would designate as far from equilibrium systems or dissipative structures.

The views of Elsasser are at this point derived from studies and knowledge about biological systems at cellular and subcellular level, i.e., the boarder between the "dead" physicochemical systems and the living systems. The "distinction" falls somewhere between the pure chemical oscillations, such as in the Beluzov—Zhabotinsky reaction and the establishing of biochemical cycles (autocatalytic cycles or hypercycles of Eigen and Schuster) together with chirality and the coupling to asymmetries introduced by separation of elements and processes by membranes. Part of the living systems indeterminacy is caused by an intrinsic and fundamental (ontic) property of the systems—(ontic) openness.

Ordered Heterogeneity

Around the late 1960s, Elsasser directed his attention to the question of what possibly could have happened since the beginning of the universe, i.e., since the Big Bang—the thinking is much along the same line as Jørgensen formulated some decades later where Heisenberg's uncertainty relation is transferred[2] to ecosystems (see Section 3.2).

Elsasser's starting point was to calculate, roughly at least, how many quantum-level events could have taken place since the Big Bang. Since events at quantum level happens within one billionth of a second, he calculates a number to be in the order of 10^{25}. Then considering that the number of particles in the form of simple protons that may have been involved in these events to be approximately 10^{85}, he calculates the number of possible events to be 10^{110}. Any number beyond this "simply loses its meaning with respect to physical reality" (Ulanowicz subm). Elsasser puts a limit at around 10^{100} (a number known as Googol). Any number beyond this is referred to as an *immense number*. In Elsasser's terminology, an immense number is a number whose logarithm itself is large. Such numbers make no sense we claim. And yet, as we saw with the examples from music, any simple everyday event, such as a piece of music, breaks this limit of physical events easily—almost before it is started.

But where does the relevance to ecosystems come in one may ask? Good question—and for once—a very simple answer. The point is that any ecosystem easily goes to a level of complexity where the number of possible events that may occur reaches or exceeds immense numbers. Again, Ulanowicz points out that "One doesn't need Avogadro's number of particles (10^{23}) to produce combinations in excess of 10^{110}, a system with merely 80 or so distinguishable components will suffice" (Ulanowicz, subm.) as 80! is in the order of 7×10^{118}.

Now, as the vast majority of ecosystems, if not all, exceed this number of components it means that far more possibilities could have been realized, so that out of the phase space of possibilities only a few combinations have been realized. Complicating things further is that events entail path dependency; thus, some states that did not occur the first time even lose the possibility to occur in the future. Any state that has occurred is also likely to occur only once—and is picked out of superastronomical number of possibilities. The other side of the story, as the title indicates, is that we are also left with a large number of possibilities that have never been and are never going to be realized. In other words, almost all events we may observe around us are literally *unique*. There are simple, repeatable events in nature within the domain classical probability, but they are sets of a measure zero in comparison to *unique* events.

Meanwhile, we cannot foretell the possibilities of the next upcoming events. If we consider any particular situation, then we face a world of unpredictability—a world that is totally ontic open. In fact, taken together, the above means that we should forget about making predictions about ecosystem development or even trying to do this. Luckily, as we shall see later, Karl Popper (1990) advocated a "milder" version of ontic openness.

Although we up to now have dealt with heterogeneity at the level of probabilities, the following points from Elsasser try to explain how nature copes with this situation.

Creative Selection

This point addresses the problems that arise from the immense heterogeneity. How do living systems "decide" among the extraordinary large number of possibilities that exist? Elsasser was precisely aware that living systems were nondeterministic, nonmechanist systems, whereas opposed to the physical systems that are always identical. As Rubin (1995) states, they "repeat themselves over and over again … but each organism is unique."

Thus, Elsasser gives *agency* to the organisms, although judging from this point alone it is not very easy to see where or how the "creativity" arises. Therefore, this point cannot be viewed as isolated from the two additional points below. Selection mechanisms are not ignored in this view that just stresses the intrinsic causes of evolution.

Holistic Memory

With memory Elsasser addresses part of what is missing from agency. Again, according to Rubin, the criterion for living system to choose is information stability. Some memory system has to be introduced, as the living systems have to ensure the stability. This point, in addition to agency, also involves history and the ability to convey this history, i.e., heredity to living, organic systems. Although again a part misses on how this information is physically going to be stored, preserved, and conveyed.

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[2] This transfer would in the context of philosophy of science be designated as a theoretical reduction—indeed with large epistemic consequences. This is opposed to Elsasser's approach that we here consider within the normal paradigm of physics.

Operative Symbolism

Last, symbolism provides the mechanism for storing this information by introducing DNA as "material carrier of this information." This cannot be seen as isolated from the history of science in the area of genetics. Much of the Elsasser's philosophical work has been written when the material structure and organization of our hereditary material, the chromosomes, was revealed.

The above arguments could be taken as if Elsasser was still basically a true reductionist as we have now gotten everything reduced into "simple" mechanisms for the conveyance of history. Elsasser was indeed aware of this point and saw the process in a dualistic (not to say dialectic) manner as he stated this mechanism to be holistic in the sense that it had to "involve the entire cell or organism" (see Section 3.6).

Ecology and Heisenberg

According to Jørgensen (1995), "some of the principles of quantum mechanics are (silently and slowly) introduced in ecology" during the last 15 years (this was probably written significantly earlier than 1995!). This is stated to be valid in particular to the area of modeling with the following remarks: "An ecosystem is too complex to allow us to make the number of observations needed to set up a very detailed model—even if we still consider models with a complexity far from that of nature. The number of components (state variables) in an ecosystem is enormous." Taking this argument there is a clear correlation to the ontic openness of Elsasser, for instance, through the presentation by Ulanowicz quoted above. Again, the number of components in an ecosystem alone is enough to form a system that is ontic open.

To the empiricist, this means that we have to use our limited resources in time and in particular money in the best possible manner. Who wants to spend unnecessary efforts? Who does not want to be as economically efficient as possible given that research money is always a limiting constraint? Meanwhile, the calculations made by Jørgensen imply a theorem of intrinsic empirical incompleteness. The argument goes as follows (Box 3.4).

According to Jørgensen, the Heisenberg Uncertainty Principle may now be reformulated, so that it refers to two other measures: uncertainty in time and energy (note the product of the two is consistent with Planck's constant, namely energy times time). The analogous formula reduces to

$$\Delta t \times \Delta E \geq \frac{1}{2}\hbar \tag{3.7}$$

BOX 3.4

SAMPLING UNCERTAINTIES

Given that the amount resources that can be spent on examining an ecosystem is limited to a finite amount of measurement. For this calculation, a limit is set to 10^8, an arbitrarily chosen number, which on one hand seems to be very high in terms of fieldwork, but may be rather realistic when processes such as data logging is involved.

Considering the number of dependent variables in the system (n) we need to determine the full "phase space" we need make at least m, measurements, where

$$m = 3^{n-1} \tag{3.4}$$

This assumes that our knowledge about a given system is so little determined that we have no a priori knowledge about the interrelations in the ecosystem, i.e., the physical flows or the regulatory feedbacks in the system. Therefore, we have to assume the worst case—that everything is literally linked to everything. In this case, Jørgensen calculates that with the limits of 10^8 number of measurements we can only deal with a system with fewer than 18 components (as $3^{18} = 387.420.489$).

Assuming that our sample is taken from a statistical population with a normal distribution and the standard deviation (σ) of the sample mean (x streg) is given by:

$$\text{S.D.} = \frac{\sigma}{\sqrt{\#samples}} \tag{3.5}$$

Eq. (3.5) may be reorganized into

$$\frac{\sigma}{\text{S.D.} \cdot \sqrt{\#samples}} = 1 \tag{3.6}$$

After all, in the end, the amount of empirical work we can do is dependent on the energy available (not only our own energy) and the time used per measurement.

First, we may now calculate the cumulative amount of energy received by the Earth since its creation and the number of measurements that could hypothetically have been made since this creation. If we consider the amount of energy we could have spent in measuring to be equivalent to the amount of energy received for the past 4.5 billion years, and using 1.731×10^{17} J s^{-1} as the value for incoming radiation, then this gives a total value of

$$\begin{aligned} \Delta E &= \#\text{years} \times \#\text{days} \times \#\text{hours} \times \#\text{seconds} \times \text{energy s}^{-1} \\ &\left(= \ 4.5 \times 10^{9} \times 365.3 \times 24 \times 3600 \times 1.73 \times 10^{17}\right) \\ &= 2.5 \times 10^{34}\ \text{J} \end{aligned} \tag{3.8}$$

Inserting the value of Planck's constant and solving Eq. (3.7), we may—again hypothetically—calculate the time necessary for every measurement which will now be

$$\Delta t = \frac{h/4\pi}{\Delta E} = \frac{\left(6.626 \times 10^{-34}\right)/4\pi}{2.5 \times 10^{34}} = 10^{-67}\ \text{s} \tag{3.9}$$

Thus, we could possibly make a measurement or sample in 10^{-67} of a second.

If we could have exercised this practice ever since the creation of the Earth, we could have made 4.7×10^{84} measurements.

Returning to Eq. (3.5), this means that we will have a standard deviation, S.D. (accuracy) of

$$\text{S.D.} = \frac{10^{-17}}{\sqrt{4.7 \times 10^{84}}} \approx 10^{-59}$$

or in referring to Eq. (3.4), that we may never succeed in measuring systems with more than $n = 237$! (here, the exclamation is an exclamation, not factorial symbol).

To make an intermediate summary, there are many ways to express ontic openness. At the same time, it has consequences to many relevant aspects of ecology such as the time we use for empirical work as well as the expectations we may have to issues such as accuracy and predictability.

3.5 ONTIC OPENNESS AND RELATIVE STABILITY

After introducing Elsasser's immense numbers and applying Heisenberg's principle to ecology, we end up with a rather pessimistic message to ecologists. In order not to fall totally in despair, let us turn to Popper. Although seemingly agreeing mostly with Elsasser, he does present a modified interpretation of the classical probability concept that at the same time offers us a somewhat more optimistic view of what can be done.

Popper, although also a physicist, is best known for his philosophy of science work and the problem of the logics connected to the epistemic of carrying out research studies like "Logik der Forschung," etc. He is considered to be the father of the research strategy known as falsification.

Popper (1990—reprinted from his lectures in 1930s), in a minor publication "A world of Propensities," states that he established a common research agenda with Carnap based on "Logik der Forschung." In this agenda, they agreed to distinguish sharply between, on the one hand, probability as it is used in the probabilistic hypotheses of physics, especially of quantum theory, which satisfies the mathematical "calculus of probabilities," and, on the other hand, the so-called probability of hypotheses, or their degree of confirmation (Popper, 1990, p. 5, see also Ulanowicz, 1996).

In fact, Popper himself, by addressing our failure to prove anything with a 100% certainty, i.e., the total dominance of uncertainty and the higher likelihood of falsification of experiments rather than the opposite, is addressing an openness that is part of the everyday life of all scientists. But again, if this is a property inherent in the systems we work, then indeed we will be forced to return to the pessimist view presented above. If a true, real feature of the world, then why do science at all? Popper refers to the findings of Heisenberg as "objective indeterminacy," but argues against the solution of translating everything into probabilistic terms. Popper claims that most scientists picking up the probabilities turned it into a question of "lack of knowledge" (the information as entropy approach that is strongly connected to Shannon and von Neumann—our comment) leading to what he calls a subjectivist theory of probability (Popper, 1990, p.8).

After working with probability theory for more than 35 years, he claims to have come up with "satisfactory and very simple solutions." One of which he refers to as "the propensity interpretation of probability," a concept that originated back in 1956. Ulanowicz later used this interpretational framework in the development of his ascendency concept (Box 4.1) proposed to be an indicator of ecosystem development (Ulanowicz, 1986, 1997).

In his explanation of the propensity interpretation, Popper began with an example of tossing a coin or throwing dice, in which we deal with known equiprobable outcomes—probability of ½ or 1/6 of any of the possible outcomes, respectively. Most of us will be familiar with these examples and consider them rather trivial, but what happens in the case when either the coin or the die is manipulated, i.e., loaded.

First of all, it is clear that in this case our assumption of equiprobable outcomes ends. One may introduce a very simple solution to this situation and just continue to work with the new weighted possibilities. We could hope that it would be as simple as that. But the consequence of such a situation on our work is much greater than we may imagine.

At least two major problems originate from the character of the situation: (1) How are the weights determined? (2) What is the consequence to our ability to forecast such a system? In determining the weights, a feasible method may easily be found. We may just continue "normal" coin tossing or dice throwing a considerable number of times, registering the outcome of each event. The point is now that this procedure will eventually take more time (more tosses or throws) in order to reach a reliable result and yet the determined weights will still be connected to a relatively high uncertainty. Popper stated, "instead of speaking of the possibility of an event occurring, we might speak, more precisely, of an inherent propensity to produce, upon repetition, a certain statistical average" (Popper, 1990, p. 11). Each event will happen with a more or less certain probability, a tendency—or as we now know it—a propensity. The immediate effect will be that our chances of successfully predicting a number of sequences will be very small.

We may now consider that the evolving world around us is a composite of events that all have nonfixed probabilities. Assigning weights is further complicated if the weights are not fixed, but rather varying, say on the external conditions in which the event is cast. In fact, adaptation is an inherent property of biological systems, thus, we must consider that the propensities themselves may change with time. This should lead to the understanding that propensities are entailed in the situation not the object. Our ability to predict, or our hopes to do this, will vanish within a short time, just as our abilities to predict the development of music is disappearing after just a few bars of playing as described earlier.

3.6 THE MACROSCOPIC OPENNESS—CONNECTIONS TO THERMODYNAMICS

Although there is possibly a connection between thermodynamic (Chapter 2) and ontic openness, the relation between the two is definitely nontrivial and attempts to distinguish the two will therefore not be included here.

An energy flow can lead to organization (decrease in entropy, e.g., photosynthesis) or destruction (increase in entropy, e.g., a cannon ball). The same quantity of energy can destroy a wall or kill a man; obviously the loss of information and negentropy is much greater in the second case. Energy and information are never equivalent as demonstrated, for instance, through Brillouin's refusal of Maxwell's Demon.

The classical example of the mixing of gases in an isolated system shows us that there can be an increase in entropy without energy input from outside. The point is that energy (E) and entropy (S) are both state functions in classical thermodynamics, but energy is intrinsically reversible, whereas entropy is not. Entropy has the broken time symmetry (Blum, 1951). In other words, entropy has an energy term plus a time term that energy does not have. Herein lies the physical connection to the concept of exergy dealt with in Chapters 2 and 6.

Energy and mass are conservative quantities; thus, it follows that total energy and mass cannot change with time. They may transform to other types of energy and mass, but the overall quantities remain the same: they are reversible. Entropy has an intrinsic temporal parameter. Energy obeys spatial and material constraints; entropy obeys spatial, material, and temporal constraints.

If history and the succession of events are of scientific relevance, then the concept of a state function should be revised at a higher level of complexity. The singularity of an event also becomes of particular importance: if a certain quantity of energy is spent to kill a caterpillar, at the same time we lose the information embodied in the caterpillar. But were this the last caterpillar, we would lose the direct evolutionary line to replicate that information. Nowadays, its unique genetic code may have been preserved through sequencing, but that is not the same as the species in its ecological role. The last caterpillar is different from the nth caterpillar.

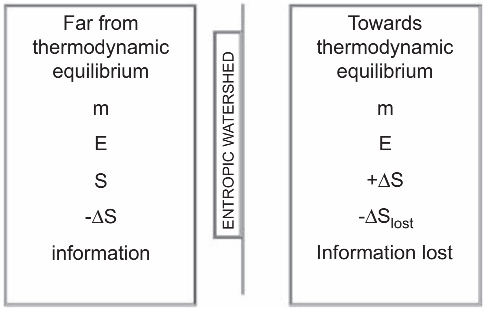

FIGURE 3.1 The death of the deer, an example showing the difference between a living, far from equilibrium system compared with the situation after its death where irreversible changes becomes dominant. *Courtesy of WIT Press from Tiezzi E : Steps Towards an Evolutionary Physics, 2006, 157 p.*

The Entropy Paradox

Stories take place in a setting, the details of which are not irrelevant to the story. What happens in the biosphere, the story of life, depends on the biosphere constraints. Hence it is important to have global models of the biosphere in terms of space, time, matter, energy, entropy, information, and their respective relations.

If we consider the evolutionary transition from anaerobic to aerobic living systems, then the ratio of energy to stored information is clearly different. The information that led to evolution and the organization of the two types of system is not proportional to the flow of energy, due to dissipative losses that also introduce irreversibility.

Thus, entropy breaks the symmetry of time and can change irrespective of changes of energy—energy being a conservative and reversible property, whereas entropy is evolutionary and irreversible per se. The flow of a nonconservative quantity, negentropy, makes life go and the occurrence of a negentropic production term is just the point that differs from analysis based on merely conservative terms (energy and matter).

The situation is explained in Fig. 3.1 "The death of the deer": mass and energy do not change, whereas entropy does. There is an "entropic watershed," a gradient, between far from equilibrium (living) systems and classical systems (the dead deer or any inorganic nonliving system). The essence of the living organism resides in its being a "configuration of processes."

We may conclude that in far from thermodynamic equilibrium systems (biological and ecological), entropy is not a state function, since it has intrinsic evolutionary properties, strikingly at variance with classical thermodynamics.

It is important to study energy and matter flows, quantities that are intrinsically conserved; it is also important to study entropy flows, an intrinsically evolutionary and nonconserved quantity. But if energy and mass are intrinsically conserved and entropy is intrinsically evolutionary, how can entropy be calculated on the basis of energy and mass quantities (entropy paradox)? This question is still unanswered and all we can do is to note that the ecodynamic viewpoint is different from that of classical physics and classical ecology.

The Probability Paradox

The following illustrates that—for even simple far from equilibrium systems—unforeseen consequences to predictability may arise from various aspects of heterogeneity. An event occurs in a stochastic manner because others precede it. Evolutionary events proceed in a manner that depends on time: they show a direction of time; they are irreversible. History determines the environmental and genetic constraints making the future largely unpredictable, as demonstrated several times above. Stochastic or probabilistic elements are unavoidable (although compare the views of Elsasser, Popper, etc.).

Novelty abounds in biological and ecological systems. Ontic openness allows for the emergence of new form and patterns. Previously unobserved events cannot be predictable, while rare and extreme events may or will completely change the dynamics of complex systems.

Fig. 3.2 shows the emergence of a probability paradox in the presence of events:

a) Suppose that an oxidation (chemical event), unknown to the observer, arises in the classic "white and black spheres" game: the probability white/black is no more fifty-fifty (only if the oxidation is changing the white sphere, e.g., to gray, may we know what happened);

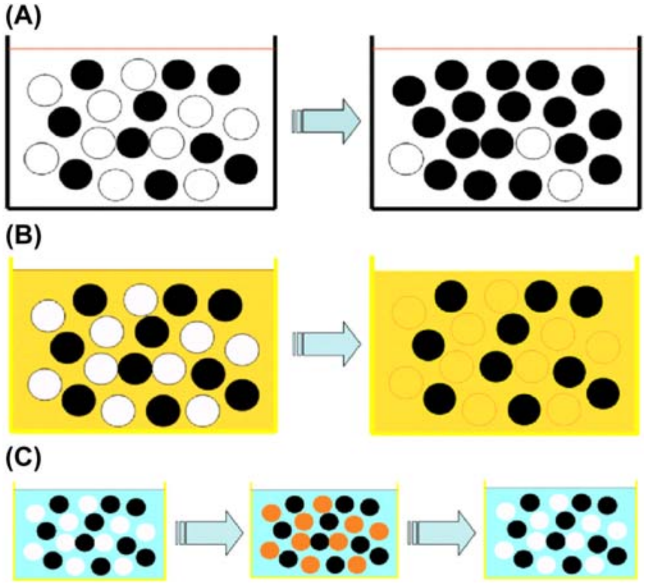

FIGURE 3.2 Unexpected events that may occur in living systems: (A) oxidation; (B) chameleon effect; (C) oscillating reaction. *Courtesy of WIT Press from Tiezzi E : Steps Towards an Evolutionary Physics, 2006, 157 p.*

b) Suppose that an evolutionary event also occurs, related to the "chameleon" effect (sensible to the environment): again, the probability is no more fifty-fifty; moreover, the event's interval depends on the "chameleon";

c) Suppose an oscillating event occurs, similar to the Beluzov−Zhabotinsky reaction: the situation is more complex and depends on many parameters. Again, the observer has no possibility to predict which sphere will be picked up from the container.

It is possible to conclude that in the far from equilibrium framework a classical probability approach does not apply, and new models have to be developed for the Boltzmann's relation $S = k \ln W$.

3.7 ONTIC OPENNESS AND EMERGENCE

At all levels of nature, we see the emergence of "narrative elements." We are reminded of Scheherazade who interrupts her beautiful story to start another one, even more beautiful. In nature, we have the cosmological history that includes the history of matter, of life, of humans, and so on till we come to our individual history associated to our consciousness. At all levels, we observe events associated with the emergence of novelties, which we may associate with the creative power of nature.

These narrative historical aspects are part of complexity. Complex systems share the feature to exhibit a great variety of behaviors. Take an example from chemistry: the Belousov−Zhabotinsky reaction mentioned above. The details are irrelevant here. Let us suppose that there are two species of molecules: "red" ones and "blue" ones; moreover, they transform one into the other. The behavior of the system depends on the external constraints. Close to equilibrium the collisions are random. There may only appear short living local flashes of color. But far from equilibrium the behavior of this system changes radically. It becomes in succession red then blue then again red. This periodicity indicates the existence of long-range correlations due to the nonequilibrium conditions. "At equilibrium matter is blind, far from equilibrium it begins to see" (Ilya Prigogine[3]).

The fascination of these physical experiments lies in the fact that small variations in a tiny building block of matter manifest themselves as large changes in biological processes. The paradox of modern scientific research in this field lies in the fact that the greater the detail in which we seek "pure" mechanisms or given subparticles, the more confirmation we have of the validity of quantum mechanics and the more important information we have on the structure of matter. On the other hand, starting from elementary particles, the more we study interactions with biological systems and ecosystems, the more we discover the complexity, irreversibility, and intrinsic aleatory character of nature.

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[3] From the foreword to E. Tiezzi, The Essence of Time, WIT Press, Southampton, 2003.

In chaos, we rediscover the spontaneity of evolutionary history: a universe in which God plays dice, to invert Einstein's phrase.[4]

God was the supreme guarantee of physical determinism. For Einstein, protagonist of the first "heroic" phase of quantum physics, physical determinism applied to any process. However, Max Born[5] once told Einstein that a deterministic universe was innately anathema to him. Born admitted that Einstein might be right, but added that determinism did not seem to hold in physics, much less in other fields. Born criticized Einstein's comment that God plays dice,[6] observing that Einstein's deterministic world needed chance. Born's wife, Hedwig, had previously written to their "dear friend Albert" that she could not admit a universal law according to which everything was predetermined, including whether or not she vaccinated her child against diphtheria.[7]

Both uncertainty equations are related to the complex relation between the observer and the experiment. The first one deals with position and momentum, the second one deals with energy and relaxation time. Both equations assume time reversibility and are valid in a given instant: the momentum is related to the derivative of space with respect to time and the relaxation time is related to the lifetime of the elementary particle in the excited state. Both equations are valid in the quantum physics paradigm and deal with conservative quantities (mass, energy), but not with living systems or evolutionary quantities.

Space and time are categories belonging to different logical types, which should not be confused. By nature, time is evolutionary and irreversible, whereas the space is conservative and reversible. A reversible quantity cannot be differentiated with respect to an irreversible one. It is not possible to compare evolving quantities, such as the life span of the Einstein's twins, in the framework of reversible mechanics. If we deal with evolutionary (living) systems, then we may introduce a third concept: Thermodynamic uncertainty related to the intrinsic irreversible character of time (Tiezzi, 2006a,b).

Let us say that a thermodynamic uncertainty arises from the experimental existence of the arrow of time and from the experimental evidence that, during the measurements, time goes by. Since during the interval of the experiment (measurement) time flows, also the conservative quantities (energy or position) may change leading to a further uncertainty.

Recently, astrophysics discovered that the mass of a star is related to the life span of the star itself. The larger is the mass, the less is the life span. This finding may also be related to the uncertainty principle. It seems that there is a sort of uncertainty relation between space and time, where space is related to mass, energy, and the conservative quantities.

3.8 ONTIC OPENNESS AND HIERARCHIES

The above section shows the necessity of an extended view of biological systems focusing on the property of heterogeneity and order at the same time. The pertinent mechanisms are encompassed within Elsasser's four principles, but already here the pitfall of a return to reductionism was pointed out. Rather, let us begin with an assumption that includes as given the genetic-level apparatus.

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[4] On December 4, 1926, Einstein wrote to Max Born that although quantum mechanics was worthy of respect, an inner voice told him that it was not yet the right solution because it did not enable us to penetrate the secret of the Great Old Man, who he was sure did not play dice with the world (Science and Life, Letters, 1916–1955, letter no. 52 in A. Einstein, H. and M. Born). Max Born considered that there was a profound divergence of viewpoint between Einstein and the following generation, to which Born regarded himself as belonging, though only a few years younger than Einstein. In a previous letter (April 29, 1924, no. 48 of the above collection), Einstein observed that the ideas of Niels Bohr on radiation were interesting but he himself did not wish to be led away from rigorous causality. He added that he could not tolerate the idea that an electron exposed to radiation could freely choose when and in which direction to jump. Were this so, he said he would prefer to be a shoemaker or a gambler rather than a physicist. In the introduction to this collection of letters, Werner Heisenberg comments that Einstein agreed with Born on the fact that the mathematical formalism of quantum mechanics, which originated in Göttingen and was subsequently elaborated at Cambridge and Copenhagen, correctly represented the phenomena occurring inside the atom, but that he did not recognize quantum mechanics as a definitive or even exhaustive representation of these phenomena. The theme that God does *not* play dice recurs elsewhere in the Born–Einstein correspondence (e.g., Einstein's letters of September 7, 1944, and October 12, 1953, nos. 81 and 103, respectively).

[5] October 10, 1944 (letter no. 84 to Science and Life).

[6] The expression "God plays dice" obviously had an irrational overtone for Einstein, but, as we shall see, not for us.

[7] October 9, 1944 (letter no. 82 in Science and Life).

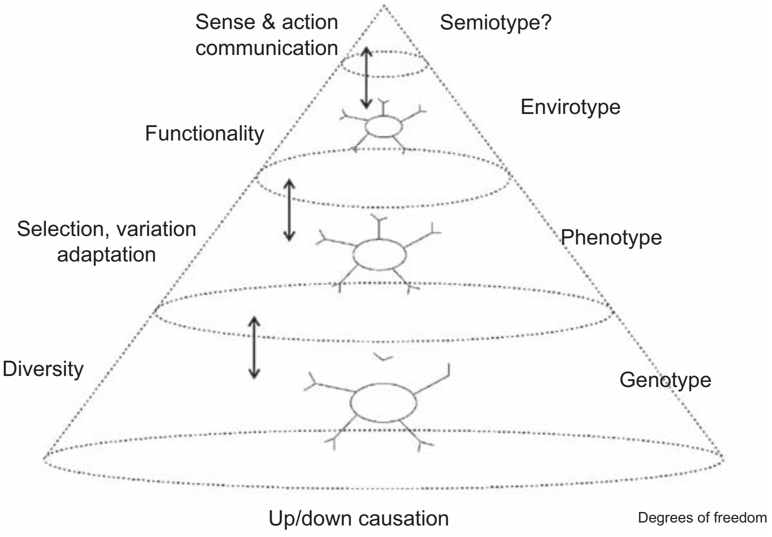

FIGURE 3.3 A biological hierarchy suggesting that interactions with the environment and finally the semiotics determine the development of the ecosystem. *From Nielsen, 2007, with permission from Elsevier.*

It is easy to see from the composition of nucleic acids or triplet codes that the genome combinatorics will exhibit *immense numbers*. These are also the numbers reached in calculations by Jørgensen et al. (1995) and the many attempts that have followed to calculate an exergy index for ecosystems based on the information content of the genome. Ontic openness is definitely a reality at this level.

Patten later suggested another hierarchical level in addition to the genotype and phenotype levels, namely and the exosomatic envirotype reflecting that an organism's genetic template and physiological manifestation is only realized with respect to its ultimate surroundings and the ecosystems, respectively. Recently, Nielsen (in print) has extended this view by adding a semiotic level above (Fig. 3.3). This layer includes all kinds of communicative and cognitive process, i.e., semiotics in a wide sense. This represents the ultimate layer of realizing ecosystem openness.

Thus, at each layer of the biological hierarchy we meet a new side of ontic openness. Interactions between hierarchical levels may, as indicated, take place in both upward and downward directions. The traditional view is that as we move up the hierarchy we are narrowing the number of possibilities. Therefore, as O'Neill et al. (1986) state, hierarchies are systems of constraints, which only are able to provide system regulations at steady-state conditions. Whenever rare events or system transformations occur, the hierarchies are broken, and uncertainty takes place in a broad extent. Emergence due to ontic openness always exists but is just realized in other ways that are not covered by the reductionist view.

3.9 MESSAGES FROM ONTIC OPENNESS TO ECOLOGY AND ECOLOGISTS/MANAGERS

That the concept of ontic openness appears to complicate ecology ramifies as well to ecosystem management (see also Chapters 5 and 7). This complexity arises both from structural systems components (ontology) and from their interrelationships and resulting behaviors (phenomenology). Ontic openness implies that we should simply not expect description to be easy—neither in terms of composition nor in their behaviors. Such expectation would be fatuous!

Because ecosystems are causally open, we should not expect regular systematic behavior to be the rule. We do see some trends, however, as formulated by early ecologists, such as Warming and Odum and by several contributors to this volume. Our aim is to synthetize the knowledge we have gained up to now into several simplified take-home messages, all based upon the fact that ecosystems and their components are ontologically open. The arguments that follow are taken mainly from Ulanowicz (2009, 2014, 2016), Nielsen (2009), Nielsen and Ulanowicz (2011), Nielsen and Emmeche (2013).

Variation

Ontic openness guarantees that variation will be part of any system so designated. Variation, for example, is an essential presumption that undergirds (Neo-)Darwinian evolution in its widest sense, and, more specifically, adaptation and selection. For some odd reason, such a variation has always been taken for granted, and the reason behind its existence has been ignored. It has simply been assumed to be there. That the numbers of combinations in genetic systems are immense lies at the crux of ontic openness and provides us with an explanation for the emergence of variation.

Uncertainty

At the same time, this ever-persistent variation imparts a high degree of uncertainty about any type of biological system. About the only thing one can be certain is that a given situation will never be repeated. A state once realized will never again appear precisely as it was. One is reminded of Heraclitus' River; change is the only constant. Ontic openness imparts, therefore, innumerable deviations and nonrepetitiveness to our observations and studies. That we ourselves are ontically open systems who interfere with our study objects (or rather subjects) *sensu Bohr* does not diminish uncertainty. To the contrary, it enlarges and exposes it.

Indeterminacy

Systems that are ontically open not only generate uncertainty but are themselves indeterminate—in fact in two senses of the word, each of which generates its separate consequences: First, we will never be able to make exact forecasts about such systems; they are simply unpredictable. Second, we are left with an inability to identify or specify exact system conditions—neither in terms of states nor flows. We simply do not have the time or energy to elaborate the precise situation. Attempts to describe the system in terms of fixed probabilities are also not possible, i.e., we are left in a world of Popperian propensities.

Nondirectionality

It is also important to note that the variations arising from ontic openness may carry with them no priorities or directionalities. That is, whatever happens may occur as a result of total and true randomness. Such variation then acts in a neutral manner among the ontological components and assumes no value. Introduction of direction and evaluation of something in either a positive or negative manner involve, on one hand, a governing mechanism (such as autocatalysis) and an evaluative function that makes it possible to judge if a given direction is good or bad. Directionality and normative judgment may arise in either an objective or a subjective manner (see later in this section).

The ubiquity of ontic openness at all levels also means that in order for a system not to end up as an indeterminate "chaotic" system (one characterized by noise only) or in a situation where all emergent states will be considered equally valid and good in quality, something else—another kind of process—must take action in or on the system.

Voidness

First of all, not all possible states can be realized. They are too enormous in number. Part of system phase space—in fact most of it—will never be filled. Whether such lacunae represent lost opportunities or simply unrealistic solutions is not relevant to this discussion. Still, mere intuition dictates that out of all the realized possibilities, some must be working better than others. Some constellations of processes will arise—be they good or bad—but not all will be realized (hence the void space). The quality of their functions can be evaluated based on objective functions required, for example, by thermodynamic laws (at least at the lower levels of cells and organisms). That such constraints may be extended to work at higher level systems is one of the goals of this book.

Patterns and Constraints

Because both directionality and evaluation (interpretation/cognition?) do occur in ontic open systems, one must conclude that agencies and constraints exist that serve to exclude some possibilities and favor others. Normally, such constraint is the result of objective criteria that promote functionality or optimality in a biophysical sense. More subjectively, we tend to overlay these constraints with an anthropocentric viewpoint. For example, when considering the relationships between genomes and physiology, we usually view changes that lead to improvements of the system as healthy and those that lower functionality as malign (e.g., genetically induced diseases or syndromes).

Hierarchy and Causality

It is also important to note that ontic openness emerges at *all levels* of the biological hierarchy because an immense number of combinations among ontological units is usually a characteristic of each focal level under consideration. To demonstrate a direct linkage between outcomes at a specific level and causality elsewhere in the hierarchy will be difficult to trace, predict, or identify. Tentatively, we may expect to find materials and efficient causes at work in lower levels, whereas formal and final causes should be operative at higher levels.

Ontic Openness Stresses the Precautionary Principle

These perspectives centered around ontic openness, and, in particular, those addressing uncertainty, unpredictability, and indeterminacy, point to the need for extra caution when dealing with such systems. Should we choose to remain with the traditional view of biological systems (or even ecosystems) as Newtonian systems that are determinate and predictable, not only would we be grievously in error philosophically and scientifically, but we would also offer advice that is guaranteed to result in bad management. Now, fully aware that ecosystems are ontically open at all hierarchical levels, we appreciate how the precautionary principle must be taken more seriously than ever.

That ecosystems seem to "have a life on their own" that we hardly understand makes it even more important that we act with respect for nature—for hard-core scientific reasons as well as ethical considerations.

3.10 CONSEQUENCES OF ONTIC OPENNESS: A TENTATIVE CONCLUSION

Here we summarize the consequences of ontic openness that will have a deep impact on ecology:

1) Immense numbers are easily reached
2) Possible development and uncertainty
3) Uniqueness of the ecosystem
4) Agency—how is this uniqueness chosen
5) Emergent properties are common

In the following section, we will attempt to address the above points in context of applying a systems perspective to ecology and ecological theory.

Immense Numbers Are Easily Reached

Much of the material given above clearly demonstrates that achieving numbers of interacting elements in ecological systems that are above Googol (10^{100}), and thereby do not in themselves carry any physical meaning, is fairly common if not ubiquitous. A combinatorial view on any level of hierarchy of biological systems is not sufficient in explaining "the meaning of life"—in fact, 42 makes more sense and is a better estimate.[8]

Possible Development and Uncertainty

As pointed out by several calculations above, ecosystems have too many distinguishable parts for classical understanding. Even if middle-number systems, they possess enough components to exceed the limits we may have considering our capabilities of doing experiments and sampling. In order to accept this, we need to recognize that we do have to live a high uncertainty, e.g., often expressed in the fact that our standard deviations on any measurement that we make are far beyond the levels accepted by our "colleagues" from physics and chemistry.

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[8] Meaning of Life given in Douglas Adams', *Hitchhikers Guide to the Galaxy.*

The Uniqueness of Ecosystems

This issue could be seen as rather trivial. At each state in its evolution, the ecosystem transitions to a new state. The one thing we now can be sure of is that the next state will be just as unique as the previous one, the system will never repeat itself exactly. An event may happen once and never again.

In fact, we did implicitly address this point indirectly in the introduction, without putting much attention to it, when we described a situation familiar to most of us: our inability to describe precisely a system without measurements. Meanwhile, not to fall in despair, we may find some satisfaction in the world of propensities. We may not know exactly what happens, but approximately what happens.

Agency of Ecosystems

This topic is probably the most problematic. In fact, many of us probably would like the idea that "nature has a life on its own," and this may also correspond nicely with what we observe or have observed. But how to give agency to ecosystems without being accused of romanticism, teleology, etc. or alternatively getting involved in a debate about intelligent design?

Uniqueness as Emergence

Given the sum of the possible conclusions from the above—unexpected things are bound to happen in ecosystems and likewise in ecological research. In fact, when Odum (1969) made his proposal to follow the study of emergent properties of ecosystems as a research strategy he was "only" introducing a suggestion of studying the impact of ontic openness to ecosystems (QED).

The Messages of Ontic Openness to Ecology

A view of our world as possessing an essential property such as being ontically open does carry several important messages to ecologists. The ubiquity of emergent properties or unexpected, rare events should, as such, be no surprise to us any longer. Meanwhile, we should not fall in despair; some predictability is still possible, although we should expect accuracy to be small and uncertainty to be high. Probably, understanding the world as propensities rather than fixed possibilities is the way out of this dilemma. The biological world as we see it around us now, its (bio)diversity consists of the part of the openness that was actually realized. It is, together with its individual components, unique, and is "locked-in" from many path-dependent evolutionary events. It will never emerge again, and as such it should be appreciated a lot more than seems to be the case in the moment.

C H A P T E R

4

Ecosystems Have Connectivity

Life did not take over the globe by combat, but by networking. ***Margulis and Sagan.*** **Microcosmos**

4.1 INTRODUCTION

The web of life is an appropriate metaphor for living systems, whether they are ecological, anthropological, sociological, or some integrated combination—as most on Earth now are. This concept immediately conjures up the image of interactions and connectedness both proximate and distal: A complex network of interacting parts, all playing off one another, providing constraints and opportunities for future behavior, wherein the whole is greater than the sum of the parts. The term "network" has received much attention recently in human affairs, especially with the Internet, cell phones, etc. In ecology it has a long history, dating back at least to Darwin's "entangled bank", and with the 20th-century rise of systems ecology and ecological modeling, and burgeoning current interest in problems of biodiversity, stability, sustainability, and global change, etc. networks and how they reflect an interconnected biosphere are hard to avoid as central research topics for ecology. Adopting them as research areas for study immediately opens a box of technical scientific tools to be applied—graph theory, matrix algebra, differential equations and simulation modeling, and growing methodologies for network analysis.

Networks, as used in *Ecological Network Analysis* (ENA) and *Network Environ Analysis* (NEA), are in the first instance *transactional*. That is, they consist of sets of energy–matter storage *compartments* coupled together by adjacent, pairwise intercompartmental interchange *transactions*. Energy and matter are conserved, hence the interchanges are zero-sum. These two properties anchor ENA and NEA to basic physics. Subsequent catenated exchanges from points of introduction (boundary inputs) give rise to nonconservative, nonzero-sum *relations*. In these, ecology begins to leave the realm of physics and empirical science and enters a zone where theory must be employed to compensate an inability to directly observe and measure. Relations like competition and mutualism are virtual, hence empirically intractable. The predation relation is, by comparison, real and concrete. Because networks are nothing if not virtual vehicles for transporting causality away from its origins, they serve also as vehicles for transporting ecology away from what is directly and empirically observable and measurable. Reductive science leaves off in this process, and holistic science must take over in its place, but this is widely, not only in ecology but everywhere in science, only in its nascent stages. Holistic ecology—"holoecology"—is still ahead to be created as part of the *New Ecology* conception of this book.

Although transactional exchange involves discrete substance transfer, transactions taken in total directly and indirectly link elements together in interconnected webs, giving rise to network structure. This structure, and the relationships it carries, both concrete and virtual, can outlast the component parts that do the work, providing habituated patterns of history and context for life's continuity. The web of life, all life, has important impacts on both the objects within the networks and science's attempts to understand the whole–part relationships. If the immanent web goes unseen, and unconnected organisms or their tangible groupings are the only categories favored by scientific attention, then system-level effects of wider interconnection, one pole of bipolar determination, will go unseen also. For example, in a holistic investigation of the Florida Everglades, Bondavalli and Ulanowicz (1999) showed that the American alligator (*Alligator mississippiensis*) has a mutualistic relationship with several of its prey, such that influence of the network trumps the direct, observable act of predation, which actually initiates network propagations leading to the ultimate mutualisms. The connected web makes this so because each isolated act of predation concatenates, bifurcates, converges, and cycles to complexly link together the entire system. In this,

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indirect effects mediated by higher order relations propagated over network distances by pathways that extend through many other objects can dictate overall relations (see sections Grounding Hypotheses and CH-2: Network Nonlocality). While this might seem irrelevant to the nourished alligator and the hapless organisms that end their lives in its gut, as a whole the prey population benefits from the alligator's presence in the web since it also feeds on other organisms that in turn are predators on or competitors with the prey. In NEA, this process of emergent positive relations deriving from zero-sum adjacent transactions is referred to as "network synergism" and "network mutualism" (see sections Relational Hypotheses, CH-13: Network Synergism and CH-15: Network Mutualism).

Such discoveries as these, involving virtual elements, are not possible without viewing the ecosystem as a connected network, and as these are immanent and virtual structures one can readily appreciate the problems this raises for empirical research, which effectively cannot take inquiry where it needs to go for understanding and prediction. This chapter deals with ecological connectivity essential for understanding and prediction. It provides an overview of systems approaches, introduces quantitative ENA/NEA methods to investigate connectivity, and concludes with a set of hypotheses formulated from viewing ecosystems as networks. Insights from networks often appear at first glance to be esoteric, surprising, and unintuitive, but once understood through examination by network methods they usually fall into place in the growing body of systems-ecological knowledge now under construction from holism, rather than from the atomistic reductionism that has dominated past ecology. The new problems of the day, from regional to global scales, are complex systems problems, and they do require the paradigm, not shift, but evolution, now underway. We hope this chapter's treatment of nature's connectivity will give further impetus to ecology's adopting the systems perspective promoted throughout this book.

4.2 ECOSYSTEMS AS NETWORKS

Ecosystems are conceptual and functional units of study that entail the ecological community together with its abiotic environment. Implicit in the concept of any system, such as an ecosystem, is that of a system boundary that demarcates objects and processes occurring within the system from those occurring outside the system. This inside—outside perspective gives rise to a first dualism in the concept of environment, one environment existing outside the focal system and another inside. The latter is explicit in the state variables of mathematical descriptions, but the external environment is relegated to having presence only in afferent and efferent boundary-crossing phenomena (inputs and outputs). Mathematizing intraboundary influences gives rise to a second dualism, which sees a system's internal environment as the external environments of component parts. These were named *environs* by Patten (1978), and there are two of them, one incoming, the other outgoing. We typically are not concerned with events beyond the system boundary that start and end there without entering the system by crossing its boundary. Moreover, as open systems, fluxes do occur across boundaries, and these provide needed energy—matter inputs as well as outputs to sinks for waste heat or unusable organic compounds. In addition to continuous energy input and output, allochthonous inputs of dead organic matter are important in some ecosystems like streams and deltas, and biotic dispersal can also play important boundary-crossing roles.

The spatial extent of ecosystems varies greatly and depends often on the functional processes inside boundaries. O'Neill et al. (1986) defined an ecosystem as the smallest unit that can persist in isolation with only its abiotic environment, but this does not give an indication about the necessary area required. Cousins (1990) proposed the home range or foraging range of locally dominant top predators as an arbiter of ecosystem size, referred to as an ecosystem trophic module, or "ecotrophic module." Similar to the watershed approach in hydrology, Power and Rainey (2000) proposed a "resource shed" to delineate the spatial extent of an ecosystem. In the extreme, one could eliminate the environment altogether by expanding boundaries indefinitely outward to subsume all boundary flows, thus making the very concept of environment a paradox (Gallopin, 1981). The idea is not to make the "resource shed" so vast as to include everything inside the system boundary, but rather to establish a demarcation line based on gradients of interior and exterior activities. In fact, as open systems an external reference state is a necessary condition for framing the ecosystem of interest (Patten, 1978). We give the last word to Post et al. (2005), who stated that different organisms within ecosystems based on their resource needs and mobility will operate at different temporal and spatial scales, typically leaving the scale context-specific for research questions at hand.

Definitional difficulties aside, following O'Neill's prescription of identifying the smallest unit that could sustain life, a minimum set of functional categories might be said to be autotrophs alone. However, on a finite planet with finite resources, unprocessed metabolic residues would accumulate and ultimately choke off any possibilities for autonomous continuance. Adding decomposers seems necessary, therefore autotrophy and saprotrophy together might be taken as minimum process constituents for a sustainable functioning ecosystem. But ecosystems also universally possess heterotrophic consumers. Why and how did these emerge if not needed? Returning to the saprovores, one could argue that evolution produced them not because they were needed (though they were) but because the prior established autotrophs represented an open niche—"opportunity" in economy-of-nature terms, and "nature abhors a vacuum." Such opportunistic emergence of a new trophic category without regard for its necessity for indefinite sustainability could also then apply to (unneeded) consumers. So, by the simple logic of opportunity, or if preferred goal orientation (see sections Amplification Hypotheses, CH-4: Network Aggradation, CH-5: Network Throughflow Maximization, CH-6: Network Storage Maximization, Integrative Hypotheses and CH-8: Network Interior Amplification), we arrive rather quickly at the observable trophic constituents of virtually all ecosystems, classified in accordance with their network-relational properties:

1. *Reflexive* autotrophic primary producers that draw in and organically fix external energy and matter;
2. *Symmetric* saprotrophic decomposers that ingest dead organic matter and close cycles of substance flow to add network pathways; autotrophs and saprotrophs together are a sufficient set to enable indefinitely sustainable ecosystems; and
3. *Transitive* heterotrophic consumers of live organisms, forming trophic networks that build upward in trophic-dynamics extended from primary fixed energy and matter; recent research (Patten, 2019; Section 4, TSUNAMI Effect—see later, CH-8: Network Interior Amplification) shows transitive (+,−) agonism (consumption) or its sign-opposite (−,+) altruism (saprovory) to be necessary processes for maximizing gains in the energy−matter economy of nature.

Biotic communities made up of these relational categories entail networks of relationships in ecosystems built on interactions between individuals in populations, individuals of multiple species, and active and passive interactions of individuals with their environment.

In ecosystem studies two approaches are employed. The first, a "black-box" approach, concerns exosystem inputs and outputs without elucidating the processes that generate these (Likens et al., 1977). The second, generally termed ENA, gives a detailed accounting of energy and material flows within ecosystems. In these studies, the focus is usually at the scale of species or "trophospecies" (functional feeding groups) and how these interact, rather than on interactions between individuals of the same species, although these are considered in individual-based studies and models. ENA could even be called "reductionistic holism" because it takes fine-scale details of ecosystem constituents and their interconnections and uses these to reveal or fashion global patterns that shape system structure and function.

Although interaction networks are ubiquitous, observing them is difficult (their virtuality), and this has led to slow recognition of their importance. For example, empirical observations reveal direct transactions between individuals, but do not immediately reveal the contextual network in which they play out. Sitting in a forest, one does not see networks, but rather an occasional act of grazing, predation, or death. While watching wolves hunt deer, it is not apparent what shrubs the deer browsed on, now assimilated by the deer and soon the wolf, not to mention energy tracebacks to solar radiation or nutrients in soil pore water. Since food web components form a connected reticulum, it is necessary to study and understand them in relation to the latter, not in isolation or as a limited subset of the whole. Networks are abstract quantities, and paradoxically empirical science must admit abstraction also in order to inform about "real" reality.

Every component, in fact, must be connected to others through both its input and output transactions. There are no trivial, isolated components in an ecosystem, not in the sense of being needed, but in the sense of contributing to overall function when present. Pulling out one species is like pulling one intersection of a spider's web, such that although that one particular crosshair is brought closer for inspection, the entire web becomes distorted by the disturbance. Those sections of the web more closely and strongly connected to any selected node are more affected, but the entire system is warped as each node is embedded within the whole network of webbed interactions. The indicator species approach works because it focuses on those organisms that are deeply embedded in the web (Patten, 2006) and thereby produce large systemic deformation. The food web is, therefore, in fact, more than just a metaphor; it acknowledges the inherent connectivity of ecosystem interactions.

4.3 FOOD WEBS

Food web ecology has been a driving force in studying the interconnections among species (e.g., MacArthur, 1955; Paine, 1980; Cohen et al., 1990; Polis, 1991). In fact, we typically think of the abundance and distribution of species in an ecological community as being heavily influenced by interactions with other species (Andrewartha and Birch, 1984). But a species is more than just a locus in an envirogram; it is its interactions with other species and with the environment that provide the connectivity that constructs the ecosystem. The diversity, stability, and behavior of the whole complex are governed by such interactions. Wholeness is of the essence. In this section we introduce the standard food web treatment in ecosystem ecology, discuss some of its weaknesses and suggest improvements, and end with an overview of general insights gained from understanding ecosystem connectivity as revealed by ENA.

Food webs are typically depicted as directed graphs ("digraphs") representing "who eats whom." Species and other trophic categories are graph nodes and the arcs denote transactional flows of energy or matter in response to the binary relation $E =$ "eats", E' its negation. E has the following relational properties:

- *Irreflexive:* $a\ E'\ a$—self-consumption is atypical, cannibalism an exception;
- *Asymmetric:* $a\ E\ b \nRightarrow b\ E\ a$—again, exceptions occur in carnivorous plants, and also species with mutually predatory life-cycle stages, such as frogs eating dragonflies, and dragonfly larvae eating tadpoles;
- *Intransitive:* $a\ E\ b$ and $b\ E\ c \nRightarrow a\ E\ c$. However, similar relations like $N =$ "nourishes" and $T =$ "transfers energy to" are transitive: $a\ (N \vee T)\ b$ and $b\ (N \vee T)\ c \Rightarrow a\ (N \vee T)\ c$.

These simple distinctions show how aphysical relations arise from physical energy−matter transactions in networks. For example, let $C =$ "competes with" be another relation. Then $a\ E\ b$ and $c\ E\ b \Rightarrow a\ C\ c$. The relation C is irreflexive, symmetric, and intransitive. In ecological networks, relational transformations frequently occur. For example, $a\ E\ b$ and $b\ E\ c \Rightarrow a\ H\ c$, where $H =$ "helps" is a new relation, generally reflexive, typically asymmetric, and always transitive.

Fig. 4.1 is a food web diagram typifying what one would find in an introductory biology textbook. Energy enters the primary producer compartment (Phytoplankton) and is transferred "up" the trophic chains by feeding (E) interactions, first grazing and then several levels of predation, losing energy (not shown) along each step, where after a few steps it has reached a terminal node called Top Predator. The reader can demonstrate how relational intricacy emerges in networks by attempting to superimpose the above simple relations E, C, and H (and also any made-up ones) onto the trophic diagram, even with its deficiencies. The latter would come to light if one wanted to understand the entire connectedness as established by the matter−energy flow pattern of the ecosystem; here are some of them:

- First, the diagram excludes any representation of decomposers, identified above as a more fundamental element of ecosystems than more familiar consumer groups like herbivores, carnivores, and omnivores. While decomposers have been an integral part of some ecological research (e.g., microbial ecology, eutrophication models, network analysis, etc.), their role in community food web ecology is just now gaining stature. Prejudices

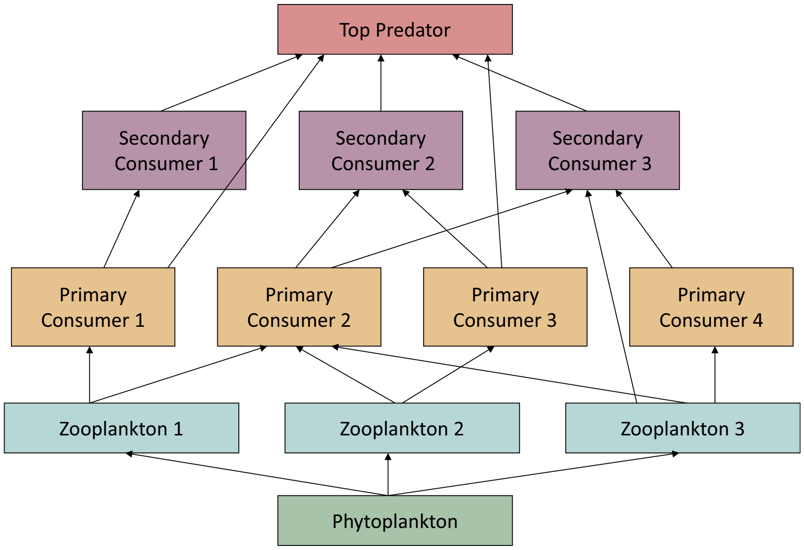


FIGURE 4.1 Typical textbook depiction of an aquatic food web. Models of this type are simplistic as revealed in ecological network analyses, but they still provide baseline thinking for much of mainstream food-web theory. A short list of omitted universals enjoyed by all actual food webs is: no system boundary, therefore no external inputs or outputs; no microbes or other saprovores. Therefore no energy or matter cycling; the five trophic levels are discrete, whereas in reality they are always distributed; the pathways from bottom to top compartments are few and short, in reality they are many (astronomical) and long; and no other transfer processes than feeding are shown, whereas in nature trophic and nontropic processes are always commingles and must be unravelled in any realistic food-web analysis. This is a 19th Century diagram appropriate for 21st Century use only at the most elementary levels of primary education, and then only if erroneous imprinting subject to later correction is to be allowed.

and biases often work to shape science; for example, few food web ecologists would be likely to classify our species (*Homo sapiens*) as saprovorous (detritus-feeding) based on our diet of predominantly dead or not freshly killed organisms (living microbes, parasites, and inquilants in our food aside).

- Second, the diagram shows the top predators as dead ends for resource flows; if that were the case, there would be a continual accumulation of top predator carcasses throughout the millennia that biological entities called "top predators" have existed. Nature would be littered with residues of lions, hawks, owls, cougars, wolves, and other such animals, even the fiercest of the fierce like *Tyrannosaurus rex* (not to mention other nongrazed or directly eaten materials such as tree trunks, excreta, etc.). Ours would be a different organic world than it is. Obviously, this is not the case because in reality there is no "top" as far as food resource and energy flow are concerned. The bulk of the energy from "top-predator" organisms, like all others, is consumed by other organisms, although perhaps not as visibly or dramatically as in active predation. Although there have been periods in which accumulation rates exceed decomposition rates, resulting in among other things the formation of fossil fuels and limestone deposits, most organic matter most of the time is oxidized to carbon dioxide. Considering the network organization of ecosystems, the relevance of flows from top predators, in fact all life forms, to detritus is that they provide additional intrasystem connectivity.
- Third, when decomposers are included in ecosystem models, as is happening more and more, they are treated as source compartments only. Resources flow out of compartments to exploiting organisms, but are not returned as the products and residues of such exploitation. For example, in a commonly studied data set of 17 ecological food webs (Dunne et al., 2002), 10 included detrital compartments, but all of these had node in-degrees equal to zero, meaning they received no inputs from other compartments. In reality, all organic compartments in food webs are sources for dead organic material (Lindeman, 1942; Fath and Halnes, 2007). It is easy to correct these flow structures by allowing material from each compartment to flow into detritus compartments. However, this introduces cycling into the network and gives a significantly different picture of connectance patterns and resulting system dynamics.

The point is that while food webs have been one way to examine feeding relations in ecology, they are just a starting point for investigating the full connectivity of ecosystems. Other, more complete, descriptive, and analytical methodologies are needed. On the last point, it is noteworthy that a substantial ENA/NEA-based literature on "network trophic dynamics" has been produced in systems ecology that (1) introduces the mathematics of true Lindeman (1942) food cycles (Higashi et al., 1989, Patten et al., 1990); (2) enables the description, by a "network unfolding" procedure, of the real nondiscrete, distributed nature of trophic pyramids wherein each trophic level is made up of elements from many cross-feeding (omnivorous) compartments, and each compartment is made up of elements in multiple trophic levels (Burns, et al., 1991; Higashi et al., 1991; 1993a,b); and (3) discriminates trophic and nontrophic processes that combine to produce the true network trophic dynamics of realistic food webs (Whipple and Patten, 1993). This failure over a quarter century to incorporate new technical developments into mainstream studies has multiple causes:

- First, food webs as complexly reticulated networks are difficult to describe and quantify empirically. Multiple scientific specialties—different for terrestrial, marine, and freshwater environments—spanning biogeochemistry, and microbial-to-predator—prey biology and ecology involving a broad phylogenetic spectrum of organisms, are hard to assemble, coordinate, support, and sustain.
- Second, the visionary, conceptual, mathematical, institutional, and other technical and human management requirements of true complex-systems study are daunting and hard to acquire and maintain in today's world where applied agenda science is favored in the competition for scientific resources.
- Third, imprinting to existing scientific culture, social forces for group membership, conformity, and career advancement, together with limiting material and human resources combine to make reactionary avoidance and retreat into simplicity an easy practical path. Old ecology has strong forces to keep it in place. New ecology, as espoused in this book, will accordingly be slow in coming to our rapidly changing world now being shaped by three accelerations—in technology, economic globalization, and global change (Friedman, 2016).

4.4 SYSTEMS ANALYSIS

If the environment is organized and can be viewed as networks of ordered and functioning systems, then it is necessary to have analysis tools and investigative methodologies that capture this wholeness. Just as one cannot see statistical relationships by visually observing an ecosystem or a mesocosm experiment, one must collect data on the local interactions that can be estimated or measured, then analyze the connectivity and properties that arise from this. In that sense, systems analysis is a tool, similar to statistical analysis, but one that allows the identification of holistic, global properties of organization.

Historically, there are several approaches employed to do just that. One of the earliest was Forrester's (1971) box-and-arrow, feedback-dynamics diagrams. Building on this approach, Meadows et al. (1972) showed the system influence primarily of human population on environmental resource use and degradation. The Forrester approach also later formed the basis for Barry Richmond's STELLA modeling software first developed in 1985, a widely used simulation modeling package. This type of modeling is based on a simple, yet powerful, "4 Cs" of modeling approach—Compartments, Currencies, Connections, Controls. One of Richmond's main aims with this software was to provide a tool to promote systems thinking. The first chapter of the user manual is an appeal for increased systems thinking (Richmond, 2001). In order to reach an even wider audience, he developed a "Story of the Month" feature which applied systems thinking to everyday situations such as terrorism, climate change, and gun violence. In such scenarios, the key linkage is often not the direct one. System behavior frequently arises out of indirect interactions (held in NEA to be dominant in causation: CH-2: Network Nonlocality) that are difficult to incorporate into connected mental models. Many societal problems, be they environmental, economic, or political, stem from the lack of a systems perspective that goes to remote distributed causes rather than stopping at proximate derivative ones.

Many systems analysis approaches are based on state-space theory (Zadeh and Desoer, 1963), which provides a conceptual and mathematical foundation to understand how input-state-output sequences work to generate system dynamics. Linking multiple states together creates networks of causation (Patten et al., 1976), such that input and output orientation and embeddedness of objects influence the overall behavior.

Box 4.1 from course material of Patten (pers. comm.) describes a progression from a simple causal sequence in which one object, through simple connectance, exerts influence over another. Causal chains and networks exhibit indirect causation, followed by a degree of self-control in which feedback ensures that an object's output environ wraps around to its input environ. Lastly, with holistic causation, systems influence systems. Using network analysis several holistic control parameters have been developed (Patten and Auble, 1981; Fath, 2004; Schramski et al., 2005). Further testing is necessary but these approaches are promising for understanding the overall influence each species (or other compartment) has in the system.

Another approach to systems analysis is HT Odum's use of energy flow diagrams, which spawned the entire subfield of emergy (embodied energy) flow analysis for ecosystems, industrial systems, and urban systems (e.g., Odum, 1996; Bastianoni and Marchettini, 1997; Wang et al., 2005; Huang, and Chen, 2005; Tilley and Brown, 2006).

The systems analysis approach is also an organizing principle for much of the work at the International Institute of Applied Systems Analysis (IIASA) in Laxenburg, Austria. This institute was established during the height of the Cold War as a meeting ground for East and West scientists and found common ground in the systems approach (www.iiasa.ac.at). Although its focus is not ecology, IIASA has produced several large-scale interdisciplinary environmental models such as Greenhouse Gas – Air Pollution INteractions and Synergies (GAINS), GLObal BIOsphere Management Model (GLOBIOM), and the long-term energy planning model MESSAGE.

Another systems approach, Food Web Analysis, is the main one from ecology, but as stated earlier has limited perspective by including only the feeding relations of organisms easily observed and measured, largely ignoring decomposition processes and abiotic resources, and operating with a limited analysis toolbox. For example, without a basis in first principles of thermodynamics or graph theory (which are now starting to be incorporated) the discipline has been trapped in several "debates" such as "top-down" versus "bottom-up" control, and

BOX 4.1

DISTRIBUTED CAUSATION IN NETWORKS

1. *The causal connective:* $B \rightarrow C$
   There is only a direct effect of B on C
2. *The causal chain:* $A \rightarrow B(A) \rightarrow C$
   B affects C directly, but A influences C indirectly through B, and C has no knowledge of A
3. *The causal network:*$\{A\} \rightarrow B(\{A\}) \rightarrow C$
   $\{A\}$ is a system, with a full interaction network giving potential for holistic determination
4. *Self-influence:*$\{A(C)\} \rightarrow B(\{A(C)\}) \rightarrow C$
   C is in network $\{A\}$ and exerts indirect causality on itself
5. *Holistic influence:*$\{A(B,C)\} \rightarrow B(\{A(B,C)\}) \rightarrow C$
   B is also in $\{A\}$ so that B, C and all else in $\{A\}$ influence C indirectly.

interaction-strength determination, which have ready alternatives in ENA methodologies. Specifically, regarding top-down versus bottom-upcontrol, Patten and Odum (1981), Fath (2004), and Schramski et al. (2006) all used network analysis to demonstrate and try to quantify the cybernetic and distributed nature of ecosystems. ENA arose specifically to address issues of wholeness and connectivity. It has two major directions, *Ascendency Theory* (Ulanowicz, 1986a; 1997), which is concerned with ecosystem growth and development, and *Environ Theory* or NEA (Patten, 1978), an environmental system theory. Ascendency Theory is summarized elsewhere in this volume (see Box 6.1). After some general remarks on ENA, the remainder of this chapter will sketch connectivity perspectives from "20 Cardinal Hypotheses" (CHs) developed in Environ Theory.

4.5 ECOSYSTEM CONNECTIVITY AND ECOLOGICAL NETWORK ANALYSIS

The exploration of network connectivity has led to the identification of many interesting, important, and nonintuitive properties. Reiterating previously made, and important, distinctions in this chapter, ENA starts with the assumption that a system can be represented as a network of nodes (vertices, compartments, components, etc.) and the connections between them. When there is an exchange (flow) of matter or energy between any node pair, we say there is a "direct" transfer, a *transaction*, between them. This empirical transfer is, however, typically made up of multiple indirect transfer threads originating at many sources. Empirical directness is better referred to as *adjacent directness*, meaning macroscopically direct between two nodes. Adjacency matrices, $A = (a_{ij})$, in NEA mark the presence ($a_{ij} = 1$) or absence ($a_{ij} = 0$) of such binary links between all (i, j) node pairs in a system. The binary transactions that convey adjacent causation are conservative and zero-sum. They give rise to both adjacent and nonadjacent, meaning empirically and macroscopically indirect, *relations*, which are nonconservative and nonzero-sum. Adjacency matrices are the basis for pathway analysis in ENA. There is an important distinction to be made in transactional flows between *analytical (microscopic) directness* and *empirical (macroscopic) directness*, both of which occur in adjacent links, $a_{ij} = 1$, between (i, j) compartment pairs. This is illustrated in Fig. 4.2. Basically, empirically direct refers to a bulk transfer of substance from j to i, whereas analytically direct refers to the first transfer of substance from j to i after its boundary introduction at compartment j.

Nobel Prize—winning economist Wassily Leontief first developed a form of network analysis called *Input—Output Analysis* (Leontief, 1936, 1951, 1966). Based on system connectivity, this has been applied to many fields. For example, there is a large body of research in the area of social network analysis, which uses the input—output methodology to investigate how individual lives are affected by their web of social connections (Wellman, 1983; Wasserman and Faust, 1994; Trotter, 2000). Input—output analysis has also successfully been applied to study the flow of energy or nutrients in ecosystem models (e.g., Wulff et al., 1989; Higashi and Burns, 1991).

Bruce Hannon (1973) is credited with first applying economic input—output analysis techniques to ecosystems. He pursued this research primarily to determine the interdependence of organisms in an ecosystem based on their direct and indirect energy flows. Others quickly picked up on this powerful new application and further refined and extended the methodology. Some of the earlier research studies in this field include Finn (1976, 1980), Patten et al. (1976), Levine (1977, 1980, 1988), Barber (1978a, b), Patten (1978, 1981, 1982, 1985, 1992), Matis and Patten (1981), Higashi and Patten (1986, 1989), Ulanowicz (1980, 1983, 1986, 1997), Ulanowicz and Kemp (1979), Szyrmer and Ulanowicz (1987), and Herendeen (1981, 1989). Both Environ Analysis and Ascendancy Theory rely on the Input—Output Analysis basis of ENA.

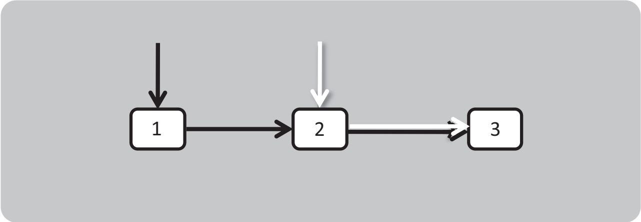


FIGURE 4.2 Distinction between adjacent, nonadjacent, and direct and indirect transactional flows. The link flow from compartment 1 to 2 is both adjacent (next to) and analytically direct (first transfer after boundary input). The link flow from compartment 2 to 3 is adjacent (empirically or macroscopically direct) but with analytically direct (white) and indirect or nonadjacent (black) components. This is a composite flow, not a direct flow in the analytical (microscopic) sense even though empirically it appears "direct." Most empirical flows in ecological networks, including adjacent link flows, have many sources and thus are actually composite flows with a high proportion of (analytically) indirect elements.

Network-related software developments such as ECOPATH (Christensen and Pauly, 1992), EcoNetwork (Ulanowicz, 1999), WAND (Allesina and Bondavalli, 2004), NEA.m (Fath and Borrett, 2006), EcoNet (Kazanci, 2007), and ena.R (Borrett and Lau, 2014; version 3.0, 2017) are available to perform computations and will ease the dissemination of these techniques.

4.6 NETWORK ENVIRON ANALYSIS PRIMER

Details of NEA have been presented elsewhere (e.g., Patten, 1978, 1981, 1982, 1985, 1991, 1992), so here we will provide only a general overview. This will give background for this chapter's concluding section describing NEA's "CHs." Ecosystem connections, such as flow of energy or nutrients, provide the conceptual framework. The directed connections between ecosystem compartments provide necessary and sufficient information to construct a network diagram (digraph) and its alternative representation as an adjacency matrix—as explained above, an $n \times n$ matrix with 1's or 0's in each element depending on whether or not the corresponding compartment pairs are adjacently connected.

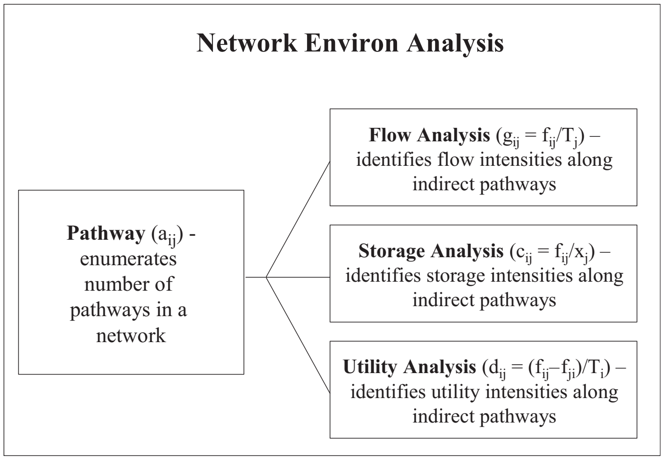
Using this information, *structural analysis* is employed to identify the number of indirect pathways and the rate at which these increase (as they do, exponentially) with increasing path length. With quantitative information regarding the storages and flows (internal and boundary) of the system compartments, functional analyses become possible—for flows, storages, and utilities (Box 4.2). Each of these analyses relies on a base matrix, the "ABCDs" of NEA as described below. Structural analysis proceeds from the direct adjacency matrix, $A = (a_{ij})$. Functional analyses follow:

- for flows, from intensive flow matrix, $B = (b_{ij})$ (or with diagonal elements zeroed, in probabilistic form, $G = (g_{ij})$);
- for storages, from a partial turnover rate matrix $C = (c_{ij})$, nondimensionalized to a probabilistic form, $P = (p_{ij})$;
- and for utilities, $D = (d_{ij})$.

The network parameters, g_{ij}, p_{ij}, and d_{ij}, are all dimensionless, enabling them to be manipulated algebraically at will without carrying along any complicating physical units. Contributions along pathways of lengths $m = 0, 1, 2, \ldots$ are revealed through powers of the direct matrices, G, P, and D. For example, G represents analytically direct flow intensities; G^2 gives second-order indirect flow contributions that have traveled over 2-step pathways from boundary introduction, represented by the zero'th-order term, $\mathbf{G^0}$**;** G^3, third-order indirect over 3-step pathways; and … G^m, mth order over m-step pathways. Given the series constraints provided by boundary outputs > 0 (thermodynamic dissipation, a universal property of ecological systems), higher order terms approach zero as the series

BOX 4.2

OVERVIEW OF NETWORK ENVIRON ANALYSIS



BOX 4.3

BASIC NOTATIONS FOR NETWORK ENVIRON ANALYSIS

Flows: f_{ij} = within system flow directed from j to i, comprise a set of transactive flows.

Boundary transfers: z_j = input to j, y_i = output from i.

Storages: x_j represent n storage compartments (nodes).

Throughflow: $T_i^{(in)} = z_i + \sum_{n}^{i=1} f_{ij}$

$$T_i^{(out)} = \sum_{n}^{i=1} f_{ij} + y_i$$

At steady state: $T_i^{(in)} = T_i^{(out)} \equiv T_i$

Nondimensional, intercompartmental *flow intensities* are given by $g_{ij} = f_{ij}/T_j$

Nondimensional, intercompartmental, intensive *utilities* are given by, $d_{ij} = (f_{ij} - f_{ji})/T_i$.

Nondimensional, *storage*-specific, intercompartmental flows are given by $p_{ij} = c_{ij}\Delta t$, where, for $i \neq j$, $c_{ij} = f_{ij}/x_j$, and for $i = j$, $p_{ii} = 1 + c_{ii}\Delta t$, where $c_{ii} = -T_i/x_i$.

Nondimensional integral flow, storage, and utility intensity matrices, N, Q, and U, respectively, can be computed as the convergent power series:

$$N = G^0 + G^1 + G^2 + G^3 + \ldots + G^m + \ldots = (I - G)^{-1}$$

$$Q = P^0 + P^1 + P^2 + P^3 + \ldots + P^m + \ldots = (I - P)^{-1}$$

$$U = D^0 + D^1 + D^2 + D^3 + \ldots + D^m + \ldots = (I - D)^{-1}$$

The mth order terms, $m = 1, 2, \ldots$, account for interflows over all pathways of lengths m in the system. The terms $m = 0$ denote identity matrices I; these allow cross-boundary flows to enter the system from its surrounding environment.

converges; that is, $G^m \to 0$ as $m \to \infty$. This makes it possible to sum the direct ($m = 1$) and *all* indirect contributions ($m = 2$ to ∞) to obtain an integral, or holistic, system evaluation (see Box 4.3, and later, Fig. 4.4). In the functional analyses, integral flow, storage, or utility values are the summation of the direct plus all indirect contributions (in Box 4.3, N, Q, and U, respectively). In this manner it is possible to quantify the total indirect contribution and compare it to the direct flows. The result in well-conditioned realistic models is almost always direct < indirect, and most often direct << indirect, prompting the conclusion (see section CH-2: Network Nonlocality) that indirect effects are dominant in nature (Higashi and Patten, 1989), and holism therefore reigns supreme, leading to the need for holistic methodologies that account for and quantify wholeness and indirectness.

Although nuanced conceptually, NEA analysis is not very demanding computationally, though it does require some familiarity with matrix algebra and graph theory concepts. The notations and methodology of the two main ENA approaches, *ascendency* and *environ analyses*, differ slightly and have been developed in detail in the above-cited references, among others. Box 4.2 lists the main lines of NEA development, in chronological order from top to bottom at the right, and also shows how all of these are anchored in pathway analysis. Box 4.3 summarizes the principal notations, and Fig. 4.4 illustrates these for a simple compartment model (upper left) and also how they are related to the defining system equations (upper right), in both time-forward and time-backward directions. The first is input (z)-driven and generates output environs to boundary outputs (y); the second is output (y)-referenced and back-traces input environs to boundary inputs (z). Note that the F matrix used in the defining equations has negative throughflows (T) on the principal diagonal, and is the form used to calculate the B and B' matrices of throughflow analysis. When the diagonals of F are zeroed, $F0$, this is the form used to compute the G matrices. Note that the throughflow and storage analyses have completely parallel development. In fact, all four analyses of NEA (Box 4.2) have parallel treatments throughout the theory, including the generation (Fig. 4.4) of direct and indirect relationships of all orders ($m = 0, 1, \ldots, \infty$) by power series, M^m, comprising the core "ABCDs" of environ analysis. $M = \{A, B, C, D\}$ is the set of base matrices for, respectively, pathway (A), throughflow (B), storage (C), and utility (D) analyses. These are the primary methodologies for investigating system structure, function, and organization employing NEA.

Fig. 4.5 illustrates the breakout of three output and three input environs from the three-compartment system previously employed to illustrate discussions in connection with Figs. 4.3 and (later) 4.10. The environs are virtual, but the compartments that form as their cumulative aggregates are concrete, and just so, the physical biota and abiota of nature are made up from such threads of substance transformation and passage from histories to futures through the tangible objects in the systems they collectively become, which in their turn also move and change through time. It is a complex conception, unregistered in human cognition—invisible threads of energy—matter flow and flow delay

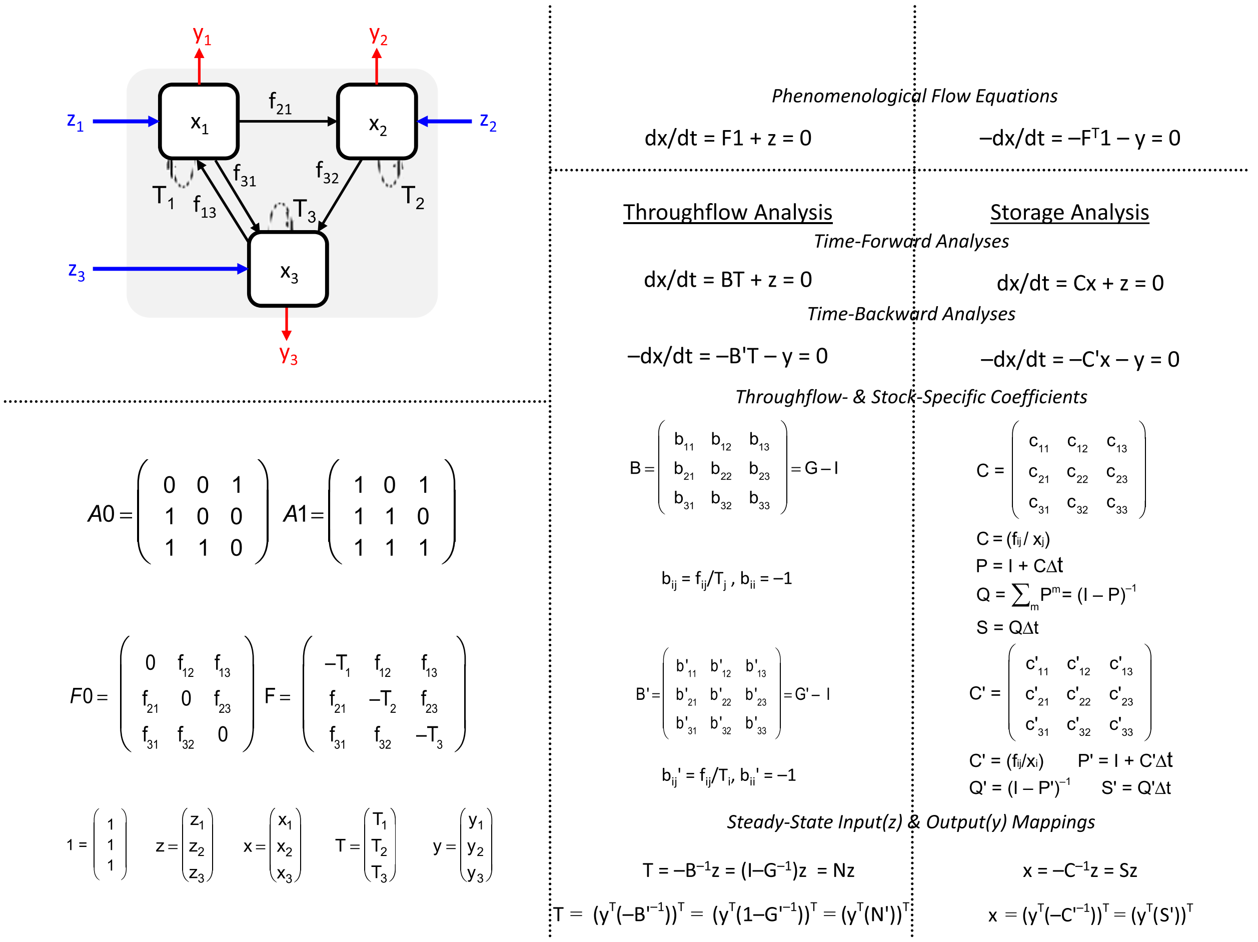


FIGURE 4.3 Summary of basic matrices and formulas for steady state throughflow (T) and storage (x) environ analyses (NEA). All matrices are oriented from column (j) to rows (i). The upper left panel displays a three-compartment digraph as an example. The lower left panel shows matrices and vectors associated with this digraph. $A0$ and $A1$ are adjacency matrices, respectively, without (diagonal elements $= 0$) and with (diagonal elements $= 1$) self-loops used to represent storage; $F0$ (zero diagonals) and F (negative throughflow diagonal elements) are flow matrices; $1 =$ vector of ones, $z =$ input vector, $x =$ state (storage) vector, $T =$ throughflow vector, and $y =$ output vector. The middle and right-hand panels display the time-forward (upper left) and time-backward (upper right) defining flow equations for, respectively, input-driven output environ analysis, and output-referenced input environ analysis. These are followed by equation forms derived from them for throughflow (middle panel) and storage (right panel) analyses, then the coefficient matrices for these equations: B, B' and G, G' for throughflow generation, and C, C', Q, Q', and S, S' for storage generation. Lastly, the steady-state mappings of boundary inputs (z) and outputs (y) into the throughflows and storages are shown. The mapping matrices are convergent sums of infinite series (Fig. 4.4) representing m^{th} order transfers ($m = 0, 1, \ldots, \infty$) of substances over all pathways of all lengths m leading from points of entrance to points of exit in the system. Source: *Patten (2016, Fig. 3.1, p. 67).*

(storage) that comprise these environs that are, in effect, extended building blocks of systems' component parts defined at the system boundaries.

The succeeding sections provide two numerical examples to illustrate typical results generated by NEA. Then, the chapter concludes with a summary of NEA's "20 CHs" to show the span of new ecological insights emergent from the study of network organization. There is unarguably very "New Ecology" in this, not established, certainly, but hypothesized from formal theory, and it remains for the mainstream field to connect to these new perspectives and begin to evaluate them for permanent standing or not in the edifice of ecological knowledge.

Network Example 1—Aggradation

Using NEA, it is possible to demonstrate how increasing connections in networks are beneficial for both system components and the whole. Fig. 4.6 presents a very simple example, presuming steady-state (input = output for compartments and the system) and first-order donor-determined flows. The latter are often used in ecological modeling to cut through to and reflect the fundamental (thermodynamic) gradient dynamics (Müller, 1998) that

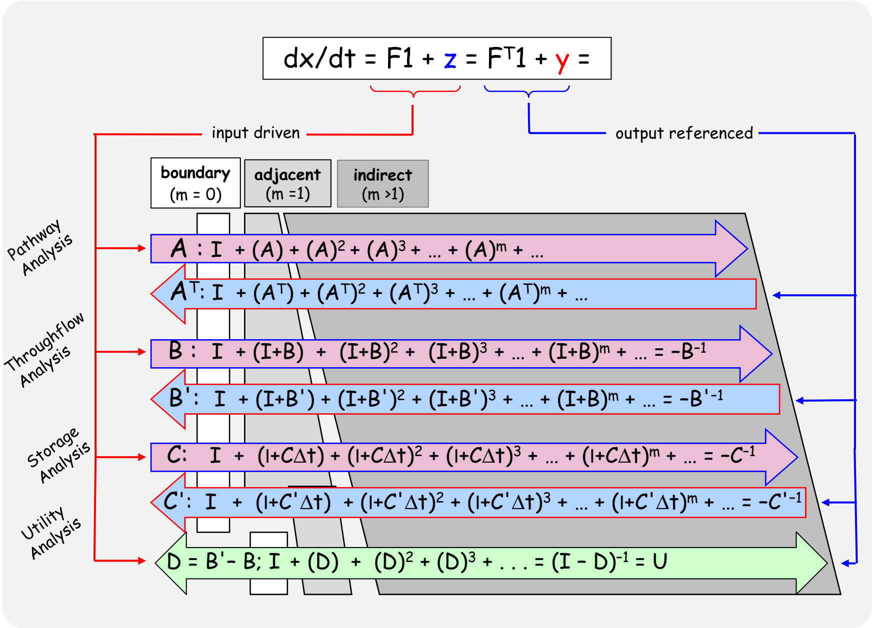


FIGURE 4.4 The “ABCDs” of steady-state network environ analysis. Matrix pairs are for forward (from inputs) and reverse (from outputs) directions. A, A^T (transpose) are adjacency matrices used in *pathway analyses*. B, B' are throughflow-specific flows used in *throughflow analyses*. C and C' are storage-specific flows used in *storage analyses*. $D = B' - B^T = C' - C^T$ (representing throughflow- and storage-specific net flows, respectively) is the generating matrix for environ utility analyses which provides the metrics for network synergism, the ultimate goal function in the Janus Hypothesis (see section CH-16: Network Janus Enigma Hypothesis). Note that D brings both reverse (B', C') and forward environ orientations into this equivalently flow- or storage-based value oriented analysis, the key to which is sum(D) = 0 (zero-sumness) whereas sum(U) >>0 (nonzero-sumness).

are in fact the ultimate causes behind whatever other kinds of coupling functions modelers with a more mechanistic, proximate-causal view prefer. Fig. 4.6A shows the throughflow and energy (as exergy) storage (based on a retention time of five time units) in the two components with no coupling, i.e., no network interconnections. Making a connection between the two compartments links them physically, and not only changes their individualistic behavior but also alters the overall system performance. In this case, the throughflow and exergy storage both increase because the part of the flow that previously exited the system is now used by the second compartment. Total system throughflow (TST; “function”as flow), exergy stored (“function”as storage), and average path length (“structure”) all increase. The advantages of extending structure and function in integrated systems is well known from industrial ecology, in which, as in saprotrophy, waste from one industry is used as raw material for another industry (e.g., Gradel and Allenby, 1995; McDonough and Braungart, 2002; Jørgensen, 2006).

Network Example 2—Cone Spring Ecosystem

For the second example, we look at the same Cone Spring ecosystem model from the previous chapter, where it was used to demonstrate Ascendency Analysis calculations. This will also serve to show some similarities and differences between ascendency and environ analyses. Figure B3.1 (in Box 4 of Chapter 3) shows only the system flows as modeled in the original ecosystem study. Since standing stocks (storages) were omitted there (they are shown in Fig. 4.7), we limit ourselves here to NEA’s flow and utility analyses. First, referring to Fig. 4.7, the left panel contains code for online simulation software, EcoNet (Kazanci, 2009), to simulate and analyze the Cone Spring model for NEA’s and some other measures. The reader is encouraged to open the EcoNet link (http://eco.engr.uga.edu/), copy and paste the Fig. 4.7 program into it, and run the model. This will generate the digraph shown in the upper right panel, and also the selected results (and quite a few more) shown in the lower right-hand panel. EcoNet documentation will also serve as an instructional resource for interested readers.

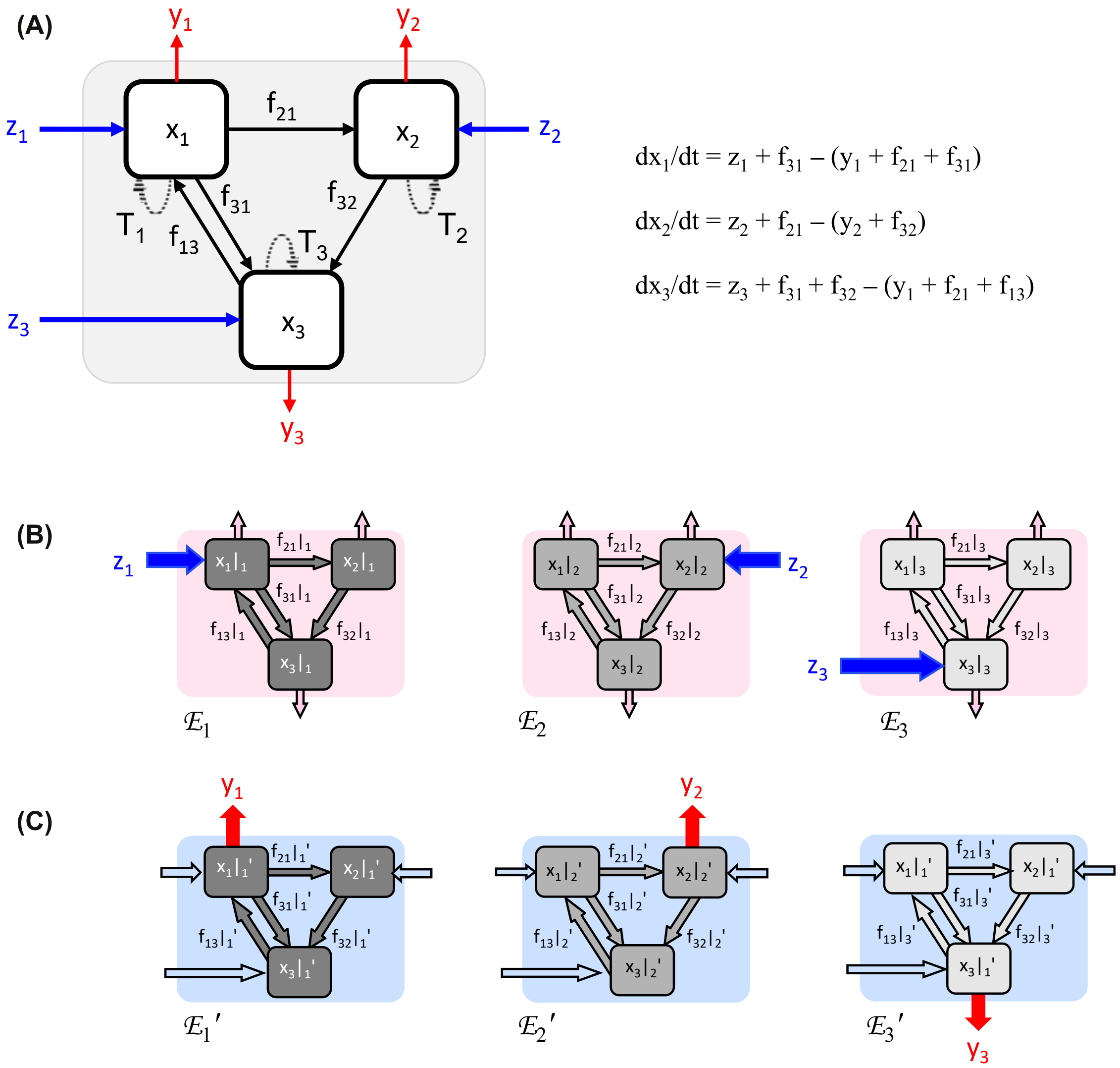
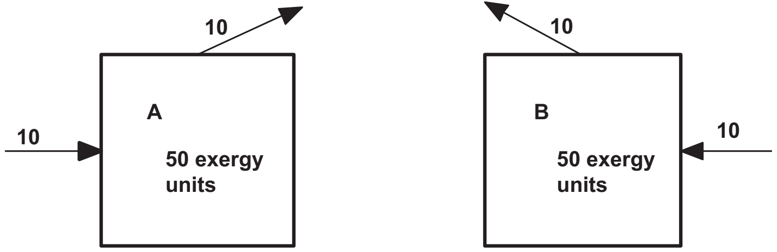


FIGURE 4.5 Depiction of the 2n environs of an $n = 3$ compartment model. (A) Composed model showing compartment stocks (x_i), boundary inputs (z_i), outputs (y_i), interior flows (f_{ij}), throughflows (T_i), and state-transition equations. (B) Partition of model (A) into its three output environs $E_{k=1,2,3}$ encompassing all the stock ($x_i|_k$) and flow ($f_{ij}|_k$) elements generated by each labeled input (z_k), $k = 1, 2, 3$. (C) Partition of model (A) into its three input environs $E_{k'=1,2,3}'$ encompassing all the stock ($x_i|_{k}'$) and flow ($f_{ij}|_{k}'$) elements reachable against the direction of the arrows from each labeled output (y_k). Each of the six environs shown has unique structural and dynamic characteristics that sum to the whole system (A) expressed as composite stocks and flows with empirically measurable aggregate properties. Source: *Modified after Patten (2015, Fig. 2, p. 49).*

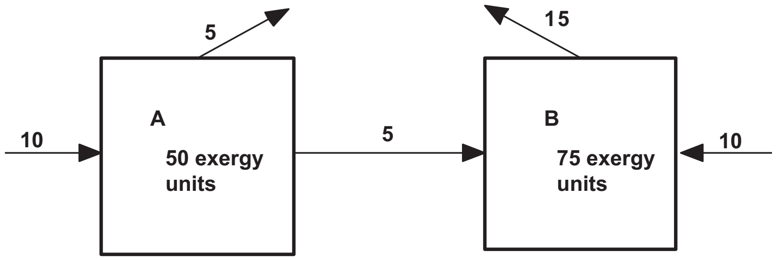
From Fig. 4.7 (and also the EcoNet run) we obtain the following information (recall the book's convention that flows are oriented from columns to rows; also, the matrices A and F here correspond to $A0$ and $F0$ of Fig. 4.3):

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 1 & 1 & 1 \\ 0 & 1 & 0 & 0 & 0 \\ 0 & 1 & 1 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 \end{bmatrix} \quad F = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 8881 & 0 & 1600 & 200 & 167 \\ 0 & 5205 & 0 & 0 & 0 \\ 0 & 2309 & 75 & 0 & 0 \\ 0 & 0 & 370 & 0 & 0 \end{bmatrix} \quad z = \begin{bmatrix} 11184 \\ 635 \\ 0 \\ 0 \\ 0 \end{bmatrix}$$

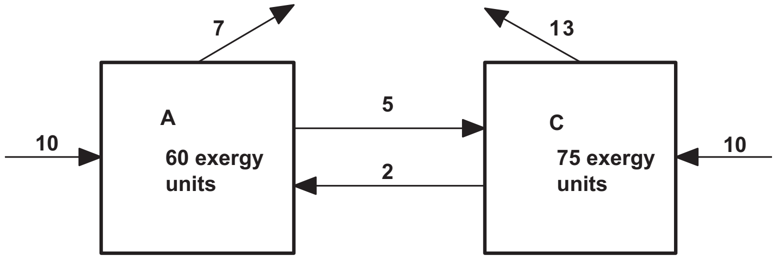
$$y = [\,2303 \quad 3969 \quad 3530 \quad 1814 \quad 203\,]$$



(A) No coupling between A and B. The throughflow is 20 and the exergy storage is 100 exergy units



(B) A coupling from A to B . The throughflow is now 25 and the exergy storage is 125 exergy units.



(C) A coupling from A to B and a coupling from B to A.The throughflow is now 27 and the exergy storage is 135 exergy units

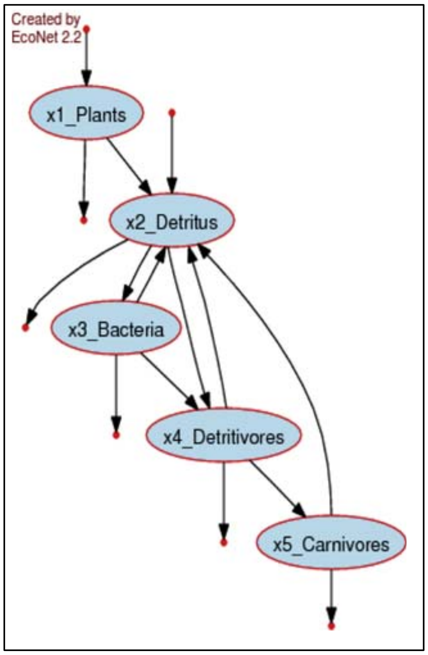
FIGURE 4.6 Two-compartment system illustrating network aggradation as increased total system throughflow and, let us say, usable energy (exergy) storage relative to boundary inputs resulting from internal transactional coupling. (A) No coupling; (B) single-link coupling; (C) cyclic coupling.

Compartmental throughflow is the sum of either entering or exiting flows to or from the compartments because at steady state these are equal; therefore, $T_i = z_i + \sum_j f_{ij} = \sum_j f_{ji} + y_i$. TST is the sum of all compartmental throughflows: $\text{TST} = \sum_i T_i$, $i = 1, \ldots, n$ compartments, which here where $n = 5$ is 30,626 kcal $\text{m}^{-2}\,\text{y}^{-1}$. (Note, in Ascendency Analysis, that compartmental *throughput*. TP_i, is a concept that includes both inputs (z_i) and outputs (y_i): $\text{TP}_i = z_i + \sum_{n}^{j=1} f_{ji} + y_i$). Continuing on with the NEA we present (refer to Box 4.3 and Fig. 4.3) the nondimensional flow and utility matrices, $G = I + B$ and $D = G' - G^{\text{T}}$ (transposed), respectively:

$$G = \begin{bmatrix} 0 & 0 & 0 & 0 & 0 \\ 0.794 & 0 & 0.308 & 0.084 & 0.451 \\ 0 & 0.453 & 0 & 0 & 0 \\ 0 & 0.201 & 0.014 & 0 & 0 \\ 0 & 0 & 0 & 0.155 & 0 \end{bmatrix} \quad D = \begin{bmatrix} 0 & -0.794 & 0 & 0 & 0 \\ 0.773 & 0 & -0.314 & -0.184 & 0.015 \\ 0 & 0.693 & 0 & -0.014 & 0 \\ 0 & 0.885 & 0.0315 & 0 & -0.155 \\ 0 & -0.451 & 0 & 1.00 & 0 \end{bmatrix}$$

http://eco.engr.uga.edu

```
# CONE SPRING ENERGY MODEL
# Flow units kcal/m^2*y^-1
# M Williams & D Crouthamel
# In BC Patten (Ed) 1971 Simulation & Systems
Analysis in Ecology, VI
# Academic Press, NY 607 pp
# Data from Patten 1982 Elementary particles for
ecology.
# Am. Nat. 119: 179-219
#
# INPUTS
* -> x1_Plants                    c=11184.0
* -> x2_Detritus                  c=635.0
#
# INTERFLOWS
x1_Plants -> x2_Detritus          c=31.1649123
x2_Detritus -> x3_Bacteria        c=1.4539588
x2_Detritus -> x4_Detritivores    c=0.6450522
x3_Bacteria -> x4_Detritivores    c=0.6440823
x3_Bacteria -> x2_Detritus        c=13.7238422
x4_Detritivores -> x2_Detritus    c=3.3333333
x4_Detritivores -> x5_Carnivores  c=6.1666667
x5_Carnivores -> x2_Detritus      c=9.8235294
#
# OUTPUTS
x1_Plants ->  *             c=8.0771930
x2_Detritus ->  *           c=1.1094689
x3_Bacteria ->  *           c=30.2675815
x4_Detritivores ->  *       c=30.2333333
x5_Carnivores ->  *         c=11.9411765
#
# INITIAL CONDITIONS
x1_Plants          = 285.0
x2_Detritus        = 3579.4
x3_Bacteria        = 116.6
x4_Detritivores    = 60.0
x5_Carnivores      = 17.0
```



Link Density	1.6
Connectance	0.32
Total System Throughflow	30626.1
Finn's Cycling Index	0.0919357
Indirect Effects Index	0.912593
Ascendency	56076.8
Development Capacity	130264
Aggradation Index	2.59126
Synergism Index	7.11204
Mutualism Index	2.125
Homogenization Index	1.87497

FIGURE 4.7 EcoNet code and selected results for the Cone Spring energy-flow model. EcoNet (Kazanci, 2009) is an online modeling, simulation, and analysis tool for transactional network models. Directions for its use together with examples are included, enabling convenient self-instruction.

Running the analysis gives the integral flow intensity matrix:

$$N = \begin{bmatrix} 1.000 & 0 & 0 & 0 & 0 \\ 0.958 & 1.207 & 0.374 & 0.186 & 0.545 \\ 0.434 & 0.547 & 1.169 & 0.084 & 0.247 \\ 0.199 & 0.251 & 0.092 & 1.039 & 0.113 \\ 0.031 & 0.039 & 0.014 & 0.161 & 1.018 \end{bmatrix}$$

along with the following information (which appears also in Fig. 4.7):

- the Finn Cycling Index is 0.0919, meaning about 9% of flow is cycled flow;
- the ratio of indirect to direct flow is 0.9126, meaning an almost equal amount (0.91:1.00) of TST travels over indirect versus direct paths. This is actually a rare exception to the rule as in most models indirect flow contributions usually exceed direct ones; and

- the network evenness measure (homogenization) is 1.8750, meaning values in the integral flow matrix, N, are nearly twice as evenly distributed as values in the direct flow matrix, G—which is obvious just from inspecting the two matrices. Another analysis possible with the flow data, but not displayed here, is calculation of the actual unit environs, i.e., flow decompositions showing the amount of flow within each system environ (Fig. 4.5) generated by one unit of input or needed to generate one unit of output at each compartment. The jth columns of N give this for each jth output environ, and the ith rows of N' give it for the ith input environs. Regarding utility, this particular example is one in which the powers of D do not enjoy guaranteed convergence (the maximum eigenvalue of D is greater than 1), which was originally thought to be require to compute valid network synergism metrics. However, Kazanci and Adams (2017) have recently shown that convergence may not be a needed property in order to interpret valid utility information from the inverse integral utility matrix, $U = (I - D)^{-1}$. This is another area of NEA that calls to attention how unexpected and unintuitive results frequently come to be generated in network analyses. Although this is an area of ongoing research, we can still speculate about the proximate and ultimate ecological relations in such cases by looking at paired signs across the principal diagonals of, respectively, the proximate (D) and ultimate (U) utility matrices:

$$\mathrm{sgn}(D) = \begin{bmatrix} 0 & - & 0 & 0 & 0 \\ + & 0 & - & - & + \\ 0 & + & 0 & - & 0 \\ 0 & + & + & 0 & - \\ 0 & - & 0 & + & 0 \end{bmatrix} \quad \mathrm{sgn}(U) = \begin{bmatrix} + & - & + & + & - \\ + & + & - & - & + \\ + & + & + & - & + \\ + & + & - & + & - \\ + & + & - & + & + \end{bmatrix}$$

The direct utility matrix is zero-sum in that for every donor there is a receiver of the flow. In ecological terms we think of a (+, −) relationship as consumption (predation) or exploitation, but more generally it represents zero-sum conservative transfer from one compartment to another. Matching compartments pairwise across the main diagonal gives the relationship type as shown in Table 4.1.

Notice first, that all the compartments are interrelated ultimately—there are no zero elements in the U matrix. Next, notice that while two of the neutral (0, 0) direct relations in D become either (+, −) exploitation or (−, +) altruism, two others become (+, +) mutualisms. Also, the proximate (−, +) relation in D directed from compartment 2 to 5 becomes (+, +) mutualism in the holistic U-matrix evaluation. In this, the presence of each compartment of a pair benefits the other. Lastly, note that overall the integral matrix has twice as many positive signs (12) as the proximate matrix (6), where each added ultimate + replaces either a proximate 0 or −; this illustrates the holistic

TABLE 4.1 Direct and Integral Relations for Cone Spring Ecosystem.

Direct	Integral
$(sd_{21}, sd_{12}) = (+, -) \Rightarrow$ agonism	$(su_{21}, su_{12}) = (+, -) \Rightarrow$ agonism
$(su_{31}, su_{13}) = (0, 0) \Rightarrow$ neutralism	$(su_{31}, su_{13}) = (+, +) \Rightarrow$ mutualism
$(su_{41}, su_{14}) = (0, 0) \Rightarrow$ neutralism	$(su_{41}, su_{14}) = (+, +) \Rightarrow$ mutualism
$(su_{51}, su_{15}) = (0, 0) \Rightarrow$ neutralism	$(su_{51}, su_{15}) = (+, -) \Rightarrow$ agonism
$(sd_{32}, sd_{23}) = (+, -) \Rightarrow$ agonism	$(su_{32}, su_{23}) = (+, -) \Rightarrow$ agonism
$(sd_{42}, sd_{24}) = (+, -) \Rightarrow$ agonism	$(su_{42}, su_{24}) = (+, -) \Rightarrow$ agonism
$(sd_{52}, sd_{25}) = (-, +) \Rightarrow$ altruism	$(su_{52}, su_{25}) = (+, +) \Rightarrow$ mutualism
$(sd_{43}, sd_{34}) = (+, -) \Rightarrow$ agonism	$(su_{43}, su_{34}) = (-, -) \Rightarrow$ competition
$(su_{53}, su_{35}) = (0, 0) \Rightarrow$ neutralism	$(su_{53}, su_{35}) = (-, +) \Rightarrow$ altruism
$(sd_{54}, sd_{45}) = (+, -) \Rightarrow$ agonism	$(su_{54}, su_{45}) = (+, -) \Rightarrow$ agonism

emergence of network mutualism in proximate to ultimate utility transitions, which is one of the "CHs" described in the next section. The reader is referred to other literature (Patten, 1991, 1992; Fath and Patten, 1998; Fath, 2006, Patten and Whipple, 2007; Tuomonen et al., 2014) for other examples of utility analysis calculations and interpretations.

4.7 THE CARDINAL HYPOTHESES OF NETWORK ENVIRON ANALYSIS

We conclude this chapter with a review of some ecological "Principles in waiting" derived from quantitative network properties inherent in NEA mathematics. In this, we will in effect be pursuing an exercise that is discovering ecology in mathematical models. There are 20 "CHs" (see Patten, 2016a for a more extended presentation than here) that arose from over 40 years of NEA development at the University of Georgia, USA. These hypotheses might well be said to circumscribe a general holistic theory of ecology whose baseline orientation is to energy—matter transactional flow and storage networks.

Grounding Hypotheses

The first two CHs are anchoring properties of network structure (pathways) and function (flows and storages). They are foundational to the entire hypothesis set and all other aspects of network organization.

CH-1: Network Pathway Proliferation

After conservative substance enters a system through its boundary, it is *transacted*, that is, conservatively transferred, between the living and nonliving compartments within the system, being variously transformed and reconfigured by work performed along the way. The substance that enters as input to a particular compartment always while in the system remains within the output environ of that, and only that, compartment. Thus, flows within output environs as within-system partition units (Patten, 1978) defined by different inputs become entangled within and between the tangible (empirical) components of the system (this is network enfolding, CH-9, another of the properties discussed later). Reciprocally, these same empirical flows running in output-referenced input environs become progressively untangled to appear as boundary outflows comprising the said system outputs.

In accordance with second-law requirements, a part (and eventually all) of this substance is continually dissipated back to the environment by the entropy-generating processes that do work and make the system function. At any point in time subsequent to initial introduction, remaining substance continues to be transported around the system, and as it does so it traces out virtual pathways that extend in length by one unit at each transfer step. Pathway numbers increase exponentially with this increasing pathway length, with the result that the interior of the system becomes a complex interconnected network, albeit virtual, in which all components communicate, indirectly if not directly, with all or almost all (depending on the connectivity structure) the others. This pathway proliferation is one of the sources of the essential holism that environ theory impresses onto the interiors of systems. Without the openness of semipermeable boundaries, pathways would neither begin nor end (except at the Big Bang and Big Crunch), and the interior networks initiating output environs and terminating input environs at boundary points of entry and exodus would never exist.

Ecological systems at all scales are, by their higher order, indirect ($m \geq 2$) pathways, more highly interconnected and interdependent than denoted by adjacent, first-order ($m = 1$) linkages alone. In ecosystems, in particular, the pathways of food chains hidden in food webs are much longer, energy cycling is the rule, and food web constituents are much more interrelated (network homogenization, CH-3) than usually described in empirical studies. These properties, demonstrated decades ago in NEA, still run generally counter to currently accepted ecological thought. Such is the cultural schism still in force between conventional ecology and the systems ecology espoused in this book.

CH-2: Network Nonlocality

As pathways extend, the amount of substance carried along at any given step is less than in the previous step due to dissipation. Therefore, pathways eventually end as they run out of originally introduced material. The rate of decay can be expressed as an exponential function, just as is the rate of pathway proliferation. Dissipation and pathway extension and growth in numbers are in conflict, but early in the transactional sequence following introduction the rate of the former exceeds that of the latter such that the total substance transferred between compartment pairs over the aggregate of pathways of a given length interconnecting them exceeds that of direct intercompartmental transfers. In other words, indirect pathways (those of lengths ≥ 2) deliver more substance from any compartment to any other than a direct empirical (adjacent) link between them. The influence carried by this transferred substance follows the substance itself in its being associated with pathways of particular lengths, and thus the conservative as well as nonconservative causes in the system can be said to be nonlocal. Indirect effects are dominant in realistically configured network systems, and this is especially true for complex systems, like ecosystems. The limit process that carries introduced conservative substance throughout the system to ultimate dissipation ensures that direct energy—matter links are quantitatively insignificant in comparison to the total. These links, provided by direct interactions such as feeding, serve only to structure the network; they make little contribution to intrasystem determination once this structuring is established (see network interior amplification, CH-8).

Dominant indirect effects in nature is a very different proposition from that espoused in mainstream ecology at the present time. It is only an hypothesis, but robust in the mathematics of steady-state environ analysis. Each extended pathway that collectively provides its basis begins with openness at the boundary—either reception of input followed by forward passage of material in output environs to ultimate dissipation or exhaustion from outputs preceded by the traceback of substance in input environs to its boundary points of original introduction. Network nonlocality underscores the essential holism of all reasonably well-connected transactional systems. Every component in ecosystems, large and sparse in adjacent linkages though these may be, are richly interconnected to a multitude of others by interactions at a network distance, only few of which have direct or adjacent (Fig. 4.2) links to the one in question. Indirect effects virtually expressed in concrete empirical reality are the glue of holistic network organization, and this is universal in the organization of nature.

Growth and Development Hypotheses

Four CHs describe aspects of network processes expressed in systemic growth and development. Growth is increase in system size and activity, development the increase in organization (Ulanowicz, 1995, p. 650). To organize is to move away from thermodynamic equilibrium. The first growth and development hypothesis (CH-3) concerns the closing of network organization by the elongating pathways of CH-1 to produce the indirect effects and holism of CH-2. The second (CH-4), a corollary of the first, places network growth and development within the ascendency framework of movement away from thermodynamic equilibrium. The last two (CH-5 and CH-6) are goal functions that contribute to nonlocality (CH-2) and also serve as generating properties for the utility hypotheses, *network synergism* (CH-13) and *mutualism* (CH-5), which find expression in the *Janus Enigma Hypothesis* (CH-16).

CH-3: Network Homogenization

One consequence of network nonlocality is the tendency for intermediate sources and sinks within systems to become blurred. That is, in the limit process that takes introduced energy and matter to boundary dissipation there is so much transactional intercompartmental mixing around over the long and high-number pathways that causality tends to become evenly spread over entire reachable networks. The result is all compartments in well-connected systems are about equally significant in generating and receiving influences to and from others. As a consequence, holism takes on the character of becoming more or less uniformly distributed in its universal expression. Beginning and ending at the open-system boundaries, the web of life based on local transactions of energy and matter tends to become quite homogeneous in its unseen, ultimate, intercomponent relationships (Patten et al., 1990; Fath and Patten, 1999).

Thus, by the matrix algebra behind this hypothesis, connected systems may tend to operate as much more closed networks of more evenly distributed flow-storage relationships than is generally appreciated from empirical observations. However, applied to real ecological systems, there are scale considerations to be taken into account. In very large and presumably sparse networks of actual ecosystems, a mole of nodes, say, with only 10^{-6} fractional connectivity, would produce a lot of indirect relationships but the network as a whole would still be a rarified universe, the majority of its bodies neither proximately nor remotely related. In such systems, there is the real question whether or not an introduced amount of propagating substance remains long enough in system storage and circulation to fill in all the blanks, even over evolutionary time, in correspondingly large and sparse adjacency and flow intensity matrices. In addition, nonuniform input patterns will tend to cause lopsided departures from any homogenization ideal. Obviously, many points of clarification remain to be realized.

This CH is a place, then, where the unreality of small-scale models may mislead about what is empirically achievable or expressed in ecosystems. Present models are stark ideals against the scales involved. They help formulate concepts and see relationships, but they do need to be tempered against what is empirically realizable. That is why all the CHs are considered hypotheses, not principles. There is little in observational experience to suggest that the elements making up ecological flows and stocks actually are uniformly distributed. Therefore, network homogenization might best be interpreted as a tendency expressed in graph algebra, but perhaps is not much realized in reality. Diversity, heterogeneity, and differentiation are the attributes of observable order, not uniformity, homogeneity, and sameness. The significance of homogenization as a mathematical property is therefore very much in need of further assessment as a real-world property.

CH-4: Network Aggradation

When energy or matter enters a system across its boundary, the system is moved further from thermodynamic equilibrium and to that extent can be said to *aggrade*, the opposite of dissipation (boundary exit) and degradation (energy quality reduction). Aggradation is negentropic, although entropy is still generated (e.g., as heat) and boundary-dissipated by interior aggrading processes. Environ theory appears to inform Schrödinger's *What-is-Life?* riddle (1944) of how negentropic development can proceed against the gradient of second-law degradation and dissipation. It shows a necessary condition for aggradation to be one single interior transaction within the system network—*simple adjacent electromagnetic connection!* Fig. 4.6 shows this in simple terms, letting increase in the TST (the sum of flows into or out of all compartments) relative to total boundary input or output (they both equal 10) be the aggradation measure. The linkage of $f_{21} = 5$ flow units from compartment one to two in Fig. 4.6B induces a throughflow of $T_2 = 15$ at compartment 2. The boundary contributions remain unchanged in both diagrams at total inputs and outputs equal 20, with the result that the TST/total cross-boundary input ($\sum z$) or output ($\sum y$) equals 1.0 for Fig. 4.6A but 1.25 for Fig. 4.6B. This is network aggradation, interpretable as further departure from equilibrium in Fig. 4.6B compared to Fig. 4.6A and resulting in a more complex system.

Given openness and sustained boundary input and output, there would appear to be no upper bound on this interior aggradation process. Thus, everything in nature that concerns differentiation and diversification of living and nonliving structures and processes, and transactional interactions between these both within and across scales, can be seen as incrementally contributing to network aggradation—movement away from equilibrium. Realizing that solar photons come in small quanta that can only power processes at similarly small scales, and the fact that scales increase bottom-up through interactive coupling, network aggradation would appear to provide, perhaps, an electromagnetic-coupling answer to Schödinger's durable "What is life?" question, Unbounded energy- and matter-based linkage following on boundary openness would be an elegant basis indeed for life in its thermodynamic dimensions—simple, and ubiquitous. Is a photon-by-photon accounting possible?

CH-5: Network Throughflow Maximization

Network aggradation processes generate maximum intrasystem throughflows at steady state. This can be taken as one of the growth-and-development "objectives" of self-organization. Throughflow reflects kinetic "activity" and performance of work, and these are the antithesis of the randomness and stasis associated with the maximum entropy condition. Patten (2016b) showed, employing a structured sequence of ecosystem models to simulate "building a biosphere", that networks of increasing connectivity contribute to maximum throughflow generation. When energy is the transfer currency, maximum throughflow is maximum power. Considering the degradation of order by entropy generation to be "time's arrow" (Blum, 1951), maximum power becomes "time's speed regulator" (Odum and Pinkerton, 1955), the basis for maximum network synergism in the Janus Hypothesis (CH-16). This confers combined organism−environment fitness in the place of traditional biological fitness, which generally entails environmental degradation in its acquisition. The interconnection of components by substance flows increases and becomes more complex as systems mature, and this becomes a determinant of mutually beneficial organism−environment relationships.

CH-6: Network Storage Maximization

Mass−energy storage as standing stocks is (compared to flows, which are virtual) the tangible expression of thermodynamic aggradation in systems growth and development. Aggradation processes generate maximum intrasystem storages at steady state, and this can be taken as another growth-and-development "objective" of aggradative self-organization. Storage reflects potential "activity" and performance of work, again the antithesis of randomness and stasis in the maximum entropy condition. Another element in network aggradation (CH-4) is therefore the maximization of standing stocks at steady state. If throughflow reflects kinetic antientropic activity, then storages represent the accumulated potential of natural capital, which also stands far from thermodynamic equilibrium. When energy is the transactional currency, the quantity maximized is energy density. This CH was championed by S. E. Jørgensen as a *maximum exergy storage* principle in numerous publications since its original introduction (Jørgensen and Mejer, 1979. It also serves (Patten, 2016a; see Fig. 8) as a storage alternative to maximum throughflow generation (CH-5) in the Janus Hypothesis (CH-16). In a recent CH (CH-17), Patten (2016a) showed how storage self-transfer subsequences along network pathways contribute most to the quantification of pathway transfer rates. Thus, paradoxically, at steady state the maximization of storages (non-transfers) also serves to maximize transfers (non-storages)—another of nature's network mysteries that become so obvious after the fact. We will look at this again further below in the description of CH-17.

Amplification Hypotheses

Like successful investments in economics, energy—matter received at system boundaries grows in significance in passing through the system toward its ultimate dissipation. More activity (throughflow) is supported and more natural capital (storage) produced than the face value of boundary inputs would seemingly allow. A simple illustration of the "networking" processes involved was briefly discussed earlier in connection with Fig. 4.6. These processes entail both boundary and interior contributions.

CH-7: Network Boundary Amplification

When a compartment within a system brings substance into the system from outside, the importing compartment is favored in development over others that do not do this. The reason is a technical property of both the throughflow- and storage-generating matrices of environ analysis known as *diagonal dominance*. The throughflow case is easiest to explain. Its generating matrix (N) multiplies the system input vector (z) to produce a throughflow vector (T) (Fig. 4.3, bottom middle panel) Elements (n_{ij}) of the generating matrix represent the number of times substance introduced at one compartment (j) will appear in another (i). First introduction by boundary input constitutes a first "hit" to the importing compartment. Non-importing (off-diagonal) compartments do not receive such first hits. In matrix multiplication of the generating matrix and input vector, importing compartments line up with their corresponding inputs such that first hits are recorded in diagonal positions; that is, input z_i to compartment i appears in the iith position of the generating matrix. This alignment produces the diagonal dominance. Off-diagonal elements represent contributions to i (in row i) from the other interior compartments ($j \neq i$), not across the boundary. These do not receive their first-hit from boundary input, but from other interior compartments, and so are correspondingly smaller in numerical value. Storage generation is similar. Elements (s_{ij}) of storage-generating matrices denote residence times in each ith compartment of substance derived from other jth compartments. Diagonal dominance in these generating matrices also associates longer residence times with boundary versus non-boundary inputs due to the first-hit phenomenon of the throughflow model, and longer residence times result in greater standing stocks.

Boundary amplification may offer explanations for many phenomena in ecosystems—edge effects, zonation, ecotones, invasive species, trophic levels, etc. Consider the latter as an example. The transfer levels of network unfolding (see section CH-10: Network Unfolding) are non-discrete due to the mixing around (CH-3) of energy and matter in the complex network of indefinitely extending pathways. This negates the Lindeman (1942) conception of discrete trophic levels.

Boundary amplification is a relatively new property in environ theory. It has the potential to explain the emergence of discrete trophic levels within complex reticular networks, and of course the more prior property behind this is system openness.

CH-8: Network Interior Amplification

It is sometimes observed in the environ mathematics of particular networks that substance introduced into one compartment at the boundary will appear more than once at another compartment, despite boundary dissipation in the interim. This is due to recycling, and it is easily seen how progressively diminishing fractions of a unit of introduced substance can cumulatively produce a sum over time in a limit process that exceeds the original amount. The second law cannot be defeated by this means, but energy cycling (Patten, 1985) following from open boundaries can compensate it and make it appear at least challenged in network organization. This is but one of numerous unexpected properties of networks contributed by cyclic interconnection and system openness.

The interior amplification property extends beyond cycling, however. The fact is that transactional digraphs and their isomorphic representations as transition matrices can be relationally partitioned into reflexive, symmetric, and transitive elements. Figs. 4.8A and B show this partitioning for, respectively, digraph and transition matrix depictions of three ecological compartment models. Let $i, j, k = 1, \ldots, n$ compartments in a system, and let $\mathbf{T}$ = "transfers (directly or indirectly) energy-matter to" be the canonical binary linkage relation of all transactional networks. Then:

- the reflexive elements ($j\ \mathbf{T}\ j$) are the digraph nodes, Fig. 4.8A, and the matrix diagonal entries, Fig. 4.8B;
- the left(L)-transitive elements ($j\ \mathbf{T}\ k$ and $k\ \mathbf{T}\ i \Rightarrow j\ \mathbf{T}\ i$) are the blue downward-directed flow arrows pointing away from (i.e., leaving(L)) sources in Fig. 4.8A, and the blue-colored lower triangle matrix entries in Fig. 4.8B;
- the right(R)-transitive elements are the red upward directed flow arrows pointing back (i.e., returning (R)) toward sources in Fig. 4.8A, and the red-colored upper triangle matrix entries in Fig. 4.8B; and
- the symmetric (cycle closing) elements ($j\ \mathbf{T}\ i \Rightarrow i\ \mathbf{T}\ j$) are identified as magenta-circled arc pairs in Fig. 4.8A and paired magenta ovals in Fig. 4.7B.

In NEA throughflow analysis, distribution matrices (N) map boundary input vectors (z) into throughflow vectors (T) (Fig. 4.3, bottom middle panel). TST is a kinetic measure of antientropic activity, hence network aggradation (CH-4). In NEA storage analysis, residence time matrices (S) map boundary input vectors (z) into standing stock vectors (x) (Fig. 4.3, bottom right panel). Diagonalizing z produces storage matrices ($X = S \cdot \mathrm{diag}(z)$) whose entries give the storage (x_{ij}) at each compartment i generated by each boundary input (z_j) at j. Fig. 4.8C shows, for the three models of Figs. 4.8A and B, the sums of values in the S and X matrices (labeled "sum_S_totl" and "sum_X_totl", respectively) and, in each case, their three partition submatrices. Amplification factors are of the form sum_S_totl/sum_S_refl and sum_X_totl/sum_X_refl. These amplification factors tell the story. Referring back to Section 4.2, where the trophic categories autotrophs (reflexive), consumers (transitive), and decomposers (symmetric) were aligned with the relational properties of networks, the following conclusions can be drawn from the Fig. 4.8C results:

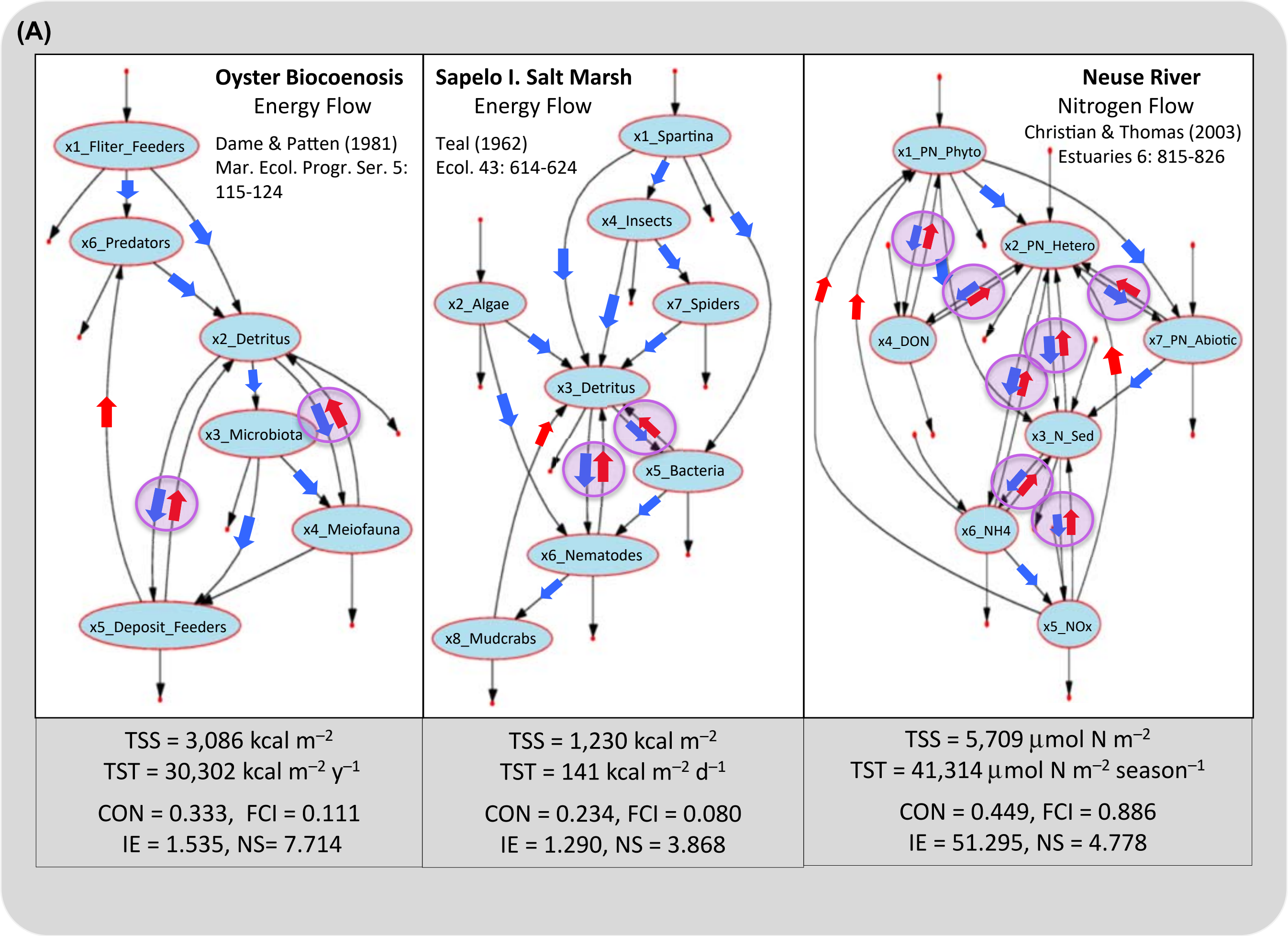
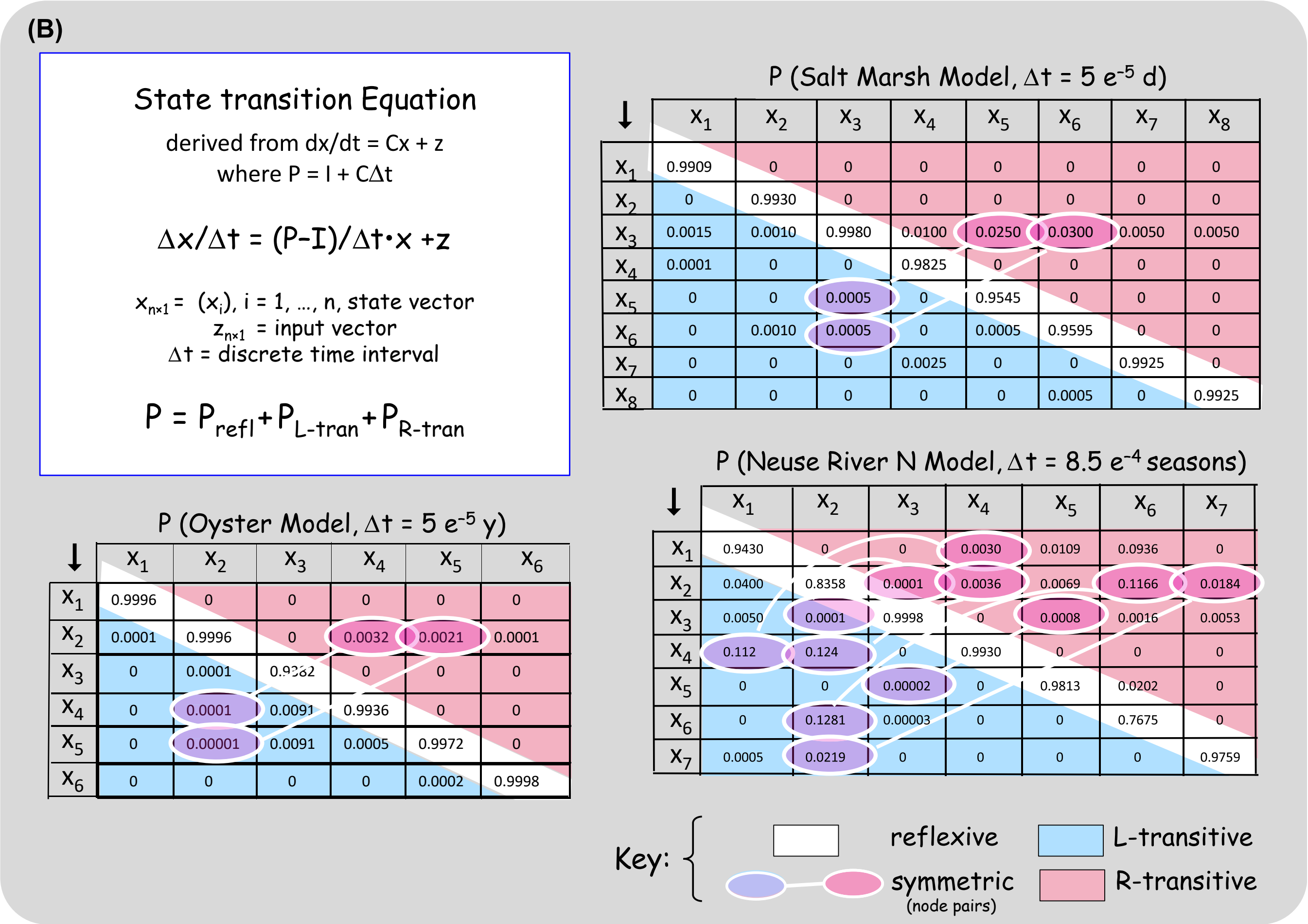


FIGURE 4.8A Relational partitioning of digraphs for three ecological compartment models, two for energy, the third for nitrogen. The nodes are the reflexive elements. Arcs marked with *blue arrows* (leaving, L) or directed downward away from sources are elements in L-transitivity. Arcs marked with *red arrows* (returning, R) directed upward toward sources are elements in R-transitivity. Arc pairs identified by *magenta circles* express symmetric relations. Total system storages (TSS), throughflows (TST), connectances (CON), Finn cycling indexes ($0 \le \mathrm{FCI} \le 1$), indirect effects indexes (IE), and network synergism indexes (NS) are shown at the bottom of each diagram.



State transition Equation

derived from $dx/dt = Cx + z$
where $P = I + C\Delta t$

$$\Delta x/\Delta t = (P-I)/\Delta t \cdot x + z$$

$x_{n\times1} = (x_i),\ i = 1, \ldots, n$, state vector
$z_{n\times1}$ = input vector
Δt = discrete time interval

$$P = P_{refl} + P_{L\text{-}tran} + P_{R\text{-}tran}$$

P (Salt Marsh Model, $\Delta t = 5\ e^{-5}$ d)

↓	x_1	x_2	x_3	x_4	x_5	x_6	x_7	x_8
x_1	0.9909	0	0	0	0	0	0	0
x_2	0	0.9930	0	0	0	0	0	0
x_3	0.0015	0.0010	0.9980	0.0100	0.0250	0.0300	0.0050	0.0050
x_4	0.0001	0	0	0.9825	0	0	0	0
x_5	0	0	0.0005	0	0.9545	0	0	0
x_6	0	0.0010	0.0005	0	0.0005	0.9595	0	0
x_7	0	0	0	0.0025	0	0	0.9925	0
x_8	0	0	0	0	0	0.0005	0	0.9925

P (Neuse River N Model, $\Delta t = 8.5\ e^{-4}$ seasons)

↓	x_1	x_2	x_3	x_4	x_5	x_6	x_7
x_1	0.9430	0	0	0.0030	0.0109	0.0936	0
x_2	0.0400	0.8358	0.0001	0.0036	0.0069	0.1166	0.0184
x_3	0.0050	0.0001	0.9998	0	0.0008	0.0016	0.0053
x_4	0.112	0.124	0	0.9930	0	0	0
x_5	0	0	0.00002	0	0.9813	0.0202	0
x_6	0	0.1281	0.00003	0	0	0.7675	0
x_7	0.0005	0.0219	0	0	0	0	0.9759

P (Oyster Model, $\Delta t = 5\ e^{-5}$ y)

↓	x_1	x_2	x_3	x_4	x_5	x_6
x_1	0.9996	0	0	0	0	0
x_2	0.0001	0.9996	0	0.0032	0.0021	0.0001
x_3	0	0.0001	0.9382	0	0	0
x_4	0	0.0001	0.0091	0.9936	0	0
x_5	0	0.00001	0.0091	0.0005	0.9972	0
x_6	0	0	0	0	0.0002	0.9998

FIGURE 4.8B Relational partitioning of transition probability matrices (P) corresponding to each of the three Fig. 4.8A models. The diagonal entries are the reflexive elements (P_{refl}), the *lower triangles* contain left-(or leaving-) transitivity elements ($P_{\text{L-tran}}$), and the *upper triangles* contain right-(or returning-) transitivity elements ($P_{\text{R-tran}}$). The *paired ovals* denote symmetric elements (P_{symm}).

- Reflexive compartments alone, acting in isolation from others, can generate considerable network aggradation. Ecologically, these can only be autotrophs.
- Transitive consumers, interchanging only between themselves without access to node storages, as reflected in NEA storage-free flow analysis of acyclic networks, have little capacity for sustained antientropic activity.
- Positive amplification factors, showing $sum\_S\_totl > sum\_S\_refl$ and $sum\_X\_totl > sum\_X\_refl$ (and in one model, >>), indicate not only the power of interactions to move and keep transactional systems far from equilibrium but also that this is the fundamental role of interactions (trophic and nontrophic) in bioenergetic phenomenology since, in the above results, interactions not involving standing stocks evidence little capacity on their own to generate antientropic development.

Several points of ecological interest follow from these results:

➢ First, reflexivity is the only obligatory (necessary) relational property to be associated with ecological compartments. Transitive and symmetric linkages enhance network aggradation, to be sure, so capacities to form these in adaptive radiation will be favored, but still they are facultative in evolutionary development. Compartmental reflexivity translates into universal self-interested behavior and irrepressible growth of biotic categories, and is also expressed in individualistic dynamics and high holding capacities (nontransfer probabilities) of both living and nonliving substance storage compartments (cells, organisms, sequestering deposits, etc.). The more kinds (n) of compartments there are in a system, the greater will tend to be, by reflexive processes alone ($X\_refl = S\_refl \cdot \text{diag}(z)$), the system's contribution (X_refl) to network aggradation.

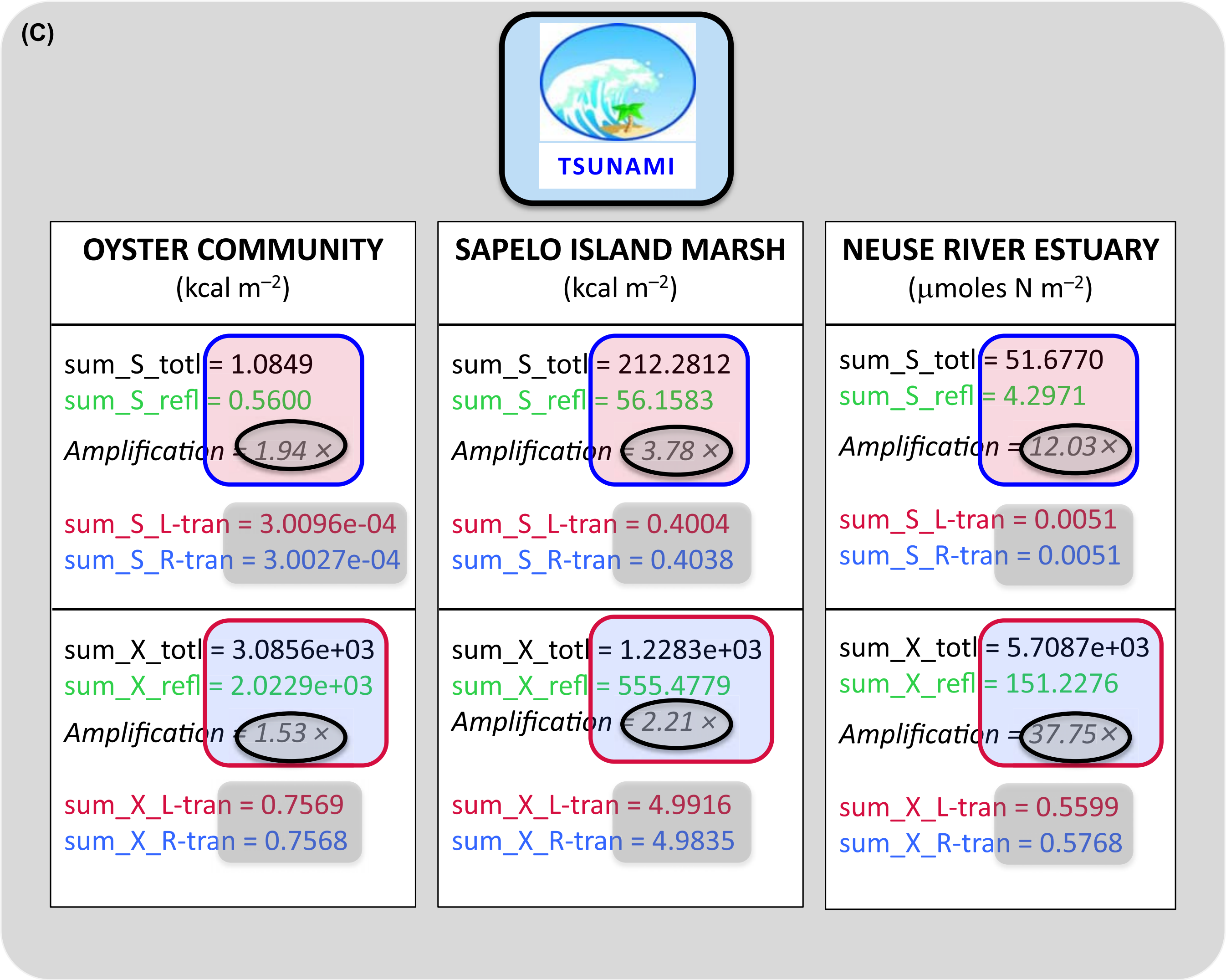


FIGURE 4.8C Network interior amplification, reflected in summations of elements in intensive storage, or residence time, matrices (*S*), and extensive storage matrices (*X*), as generated by the entire systems (*S*_totl, *X*_totl) and their partition subsystems (*S*_refl, *X*_refl; *S*_*L*-tran, *X*_*L*-tran; and *S*_*R*-tran, *X*_*R*-tran). Amplification factors in all cases are referenced to *S*_totl and *X*_totl.

➢ Second, the more compartments (n) in a system, the more opportunities ($n^2 - n$) there will be for pairwise transitive and symmetric linkages to form. Thus, in effect, all three relational categories call for increasing the number of nodes in transactional networks. Ecologically, increasing biodiversity is the major way to do this because biota are plastic whereas abiotic categories are more or less fixed. It is biota that ever expand to fill, change, and create new niches (opportunities) for life in the biosphere. Development begets development. Life, then, is the true engine of aggradative activity on the planetary surface, and biodiversity manifests the radiative tendency to generate and meet opportunity more than any other property. Conventional ecology holds that biodiversity is important and a good thing to promote and protect, but it has been unable to put forward any real scientific argument or evidence for this. In this present network property, interior amplification, there may lie the beginnings of a general ecological answer to the "why biodiversity" question.

Integrative Hypotheses

Stocks and flows are composite quantities in networks. Multiple inputs generate a like number of output environs, and all are mutually entwined to form the aggregate throughflows and storages that make up compartmental systems. Similarly, multiple outputs are generated from stocks and flows that contribute to a corresponding number of input environs. NEA unravels these environs from the compositions that form the wholes that are physically constituted systems. There is no mystery, only realization, in this as all systems are compositions formed from their components. What is different here is that what is being mixed together are virtual quantities—transactional networks representing tangled energy–matter webs. The four hypotheses of this section concern various aspects of composition, the synthesis of parts into wholes, and decomposition, the reduction of wholes into parts.

CH-9: Network Enfolding

This property refers to the incorporation of indirect energy and matter flows and storages into empirically observed and measured flows and storages. It is another property of coupled systems elucidated by environ mathematics, and it potentially touches many areas of ecology such as chemical stoichiometry, embodied energy ("emergy"), and ecological indicators. Ecologists observe and measure, for example, the chemical composition of organisms or bulk samples. For an entity to have a "composition" means it is a *composite*—made up of materials brought to it from wherever its incoming network reaches in the containing system—directly and indirectly. This has consequences for even a seemingly straightforward concept like a "direct" flow where, it turns out, "macroscopically" or "empirically direct" must be distinguished from "microscopically" or "analytically direct." To illustrate, referring back to Fig. 4.2, the flow f_{21} from compartment 1 to 2 is unambiguously direct. Macroscopically, the link and the process responsible for it (like eating) are direct, and microscopically so are the molecules (food) transferred because it is derived directly from the boundary input z_1. This latter directness is due to the fact that flow f_{21} represents the first transfer of boundary input from the compartment that received it to another; it is uncommingled with substance from other sources because, in this case, input z_2 cannot reach compartment 1. The situation is different in Fig. 4.3. The flow f_{21} in this model is still macroscopically adjacent to compartments 1 and 2 (i.e., empirically "direct"), but now it contains composited flow derived from all three inputs. These inputs, the throughflows and storages (not shown) they generate, and also the other three adjacent flows are all complexly enfolded into f_{21}. The enfolding is mutual, and in this case it is universal because all interior network elements are reachable from all the others. The entire system of Fig. 4.3 is thus (at steady state) a composite of itself, which is the ultimate expression of holism. Moreover, this composition property, network enfolding, is true for complex systems generally. If one can imagine empirically sampling this system, then f_{21} (and the other interior flows as well) strike the senses as direct. However, they are not, when referenced to origins, since they contain indirect flows from the other sources a few to (due to cycling) many times removed, and so are better considered as "adjacent", or perhaps just "observed." In environ mathematics, this embedding or entrainment of newly received inputs into the established flow stream of the system is reflected in infinite series, as previously illustrated in Fig. 4.4.

Let $f_{21}/T_1 = g_{21}$ define a throughflow-specific dimensionless flow intensity. The coefficient g_{21} is a probability, therefore its powers form a convergent infinite series: $(1 + g_{21} + g_{21}^{(2)} + \ldots + g_{21}^{(m)} + \ldots)$. The parenthesized superscripts denote coefficients derived from matrix, not scalar, multiplication. This power series maps the boundary input z_1 into the portion of throughflow at 2 contributed by this source: $T_{21} = (1 + g_{21} + g_{21}^{(2)} + \ldots + g_{21}^{(m)} + \ldots)z_1$. The first term of the series brings the input into the system: $1 \cdot z_1$. The second term represents the "direct" flow over the link of length 1: $g_{21}z_1$. All other terms represent indirect flows associated with pathways of all lengths 2, 3, …, m, … as $m \to \infty$. The throughflow component T_{21} accordingly contains a plethora of indirect flows: $(g_{21}^{(2)} + \ldots + g_{21}^{(m)} + \ldots)z_1$. This is one of three elements in the throughflow at compartment 2: $T_2 = T_{21} + T_{22} + T_{23}$. At compartment 1 the throughflow is similarly decomposable: $T_1 = T_{11} + T_{12} + T_{13}$, and at compartment 3: $T_3 = T_{31} + T_{32} + T_{33}$. Each term in these sums has a similar infinite series decomposition to that just given for T_{21}. With this, one can now appreciate there is more than meets the eye in the Fig. 4.3 network. The focal flow f_{21} in question has a decomposition into enfolded elements as follows:

$$f_{21} = g_{21}T_1 = g_{21}(T_{11} + T_{12} + T_{13})$$

$$= g_{21}\left[\left(1 + g_{11} + g_{11}^{(2)+\ldots+} g_{11}^{(m)+\ldots}\right)z_1 + \left(1 + g_{12} + g_{12}^{(2)+\ldots+} g_{12}^{(m)+\ldots}\right)z_2 + \left(1 + g_{13} + g_{13}^{(2)+\ldots+} g_{13}^{(m)+\ldots}\right)z_3\right].$$

This is what an ecologist measuring f_{21} would measure empirically and consider a "direct" flow. One can see, however, that the entire system is embodied in this measurement. This is network enfolding. It gives a strong message about the inherent holism one can expect to be expressed in natural systems and, as stated above, its broad realization is likely eventually to influence many areas of ecology.

CH-10: Network Unfolding

Ever since Raymond Lindeman (1942) pursued Charles Elton's original food cycles, but they came out unintendedly as sequential food chains instead, to which ecologists could better relate, mainstream empirical ecology (for example, food web theory, biogeochemical cycling) has had a difficult time returning to meaningful analysis of the concept of cycling. The preoccupation with chains prompted Higashi and Burns (Higashi et al., 1989) to develop a methodology for unfolding an arbitrary network into corresponding isomorphic "macrochains." Emanating from boundary points of input and arrayed pyramidally, these resemble the food pyramids of popular textbook depictions. Because the networks are cyclic, however, the macrochains differ from normal acyclic food chains in being indefinite in extent. Network unfolding refers to the indefinite proliferation of substance-transfer levels in ecosystems. The terminology "transfer pathways" and "transfer levels" is preferred to "food chains" and "trophic levels" because nontrophic as well as trophic processes are involved in any realistic ecosystem. Examples of nontrophic processes include import and export, anabolism and catabolism, egestion and excretion, diffusion and convection, sequestering, immobilization, and so on. Whipple subsequently modified the original unfolding methodology to discriminate the various trophic and nontrophic processes involved (Whipple and Patten, 1993; Whipple, 1998). The transfer levels so discriminated are nondiscrete in containing contributions from most, if not all, the compartments in a system, and also they continue to increase in accordance with continuation of the limit process that ultimately dissipates all the introduced substance from the system. Exchange across open borders is at the heart of network unfolding.

Fig. 4.9 illustrates how networks of arbitrary topology are recomposed to form pyramidal macrochains by the network unfolding algorithms. Labeling and vertical positioning of the stocks, flows, and outputs at each level (I, II, III, IV, …) denote that all these categories (except transfer level I in Fig. 4.9B) are composites. In reasonably well-connected networks, as in the real world, compartments (Fig. 4.9A) are made up of multiple, not single, transfer levels, and reciprocally, transfer levels are made up of multiple, not single, compartmental categories. Level structuring by diminishing quantities of undissipated substance as material moves down pathways in networks forms ecological pyramids ("macrochains") with distributed (in Fig. 4.9, multicolored) compartmental compositions at each level. This is shown to the right in Fig. 4.9B and C. The latter shows the information in Fig. 4.9B, obtained by Higashi et al. (1989) unfolding, with trophic (solid arrows) and nontrophic (broken arrows) transfers as discriminated by the Whipple (1998) algorithm. The level structuring in this case gives true trophic levels.

CH-11: Network Centrifugality and Centripetality

These two properties follow from the expression of network enfolding (CH-9) and unfolding (CH-10) in the divergent and convergent subsystems that constitute output and input environs, respectively. Ulanowicz (1986; see also this book, Chapter 6) called attention to centripetality in the ascendency framework of autocatalytic nodes in networks pulling resources from near and far corners of systems into themselves, not unlike vacuum cleaners sweeping particles into their storage containers and holding them for later disposition. In environ theory, *network centripetality* is manifested as afferent flows in input environs that are convergent on focal compartments and ultimately comprise the outputs from those compartments. That is, each input environ circumscribes the set of all incoming (centripetal) flows to each compartment that converge to become that compartment's boundary output. The dual, *network centrifugality*, is manifested as efferent flows in output environs that are divergent from focal compartments and are constituted from the inputs to those compartments. Each output environ encompasses the collection of outgoing (centrifugal) flows from each compartment that propagate and diverge from that compartment's boundary input. How network centrifugality comes to be expressed through individual particles passing though constituted systems is illustrated in Patten (2016a, fig. 11.1).

Centrifugality and centripetality are the searching and reaching, then combining and closing phenomena that make physical concreteness, and the next conjecture prescribing it, entirely possible.

CH-12: Network Topogenesis

This CH proposes that in transactional networks qualitative digraph topology on a global level is sufficient to quantify both system stocks and flows at the local level. If true, such a proposition would considerably alter the human worldview by showing how system-wide connectivity holistically determines from all over connected networks the quantitative properties of entities and processes in the small. Cross-scale bipolarity of causal determinism would find expression in the mutual reflection of small in large, and large in small. Right now, this hypothesis is far from proved, but it has promising directions.

Two methodologies designed to illustrate the reasoning behind it are, for flows *Link Tracking* (L_kT), and for standing stocks *Loop Tracking* (L_pT). Hill (1981), in his PhD dissertation, proposed in a concept he called "influence", that

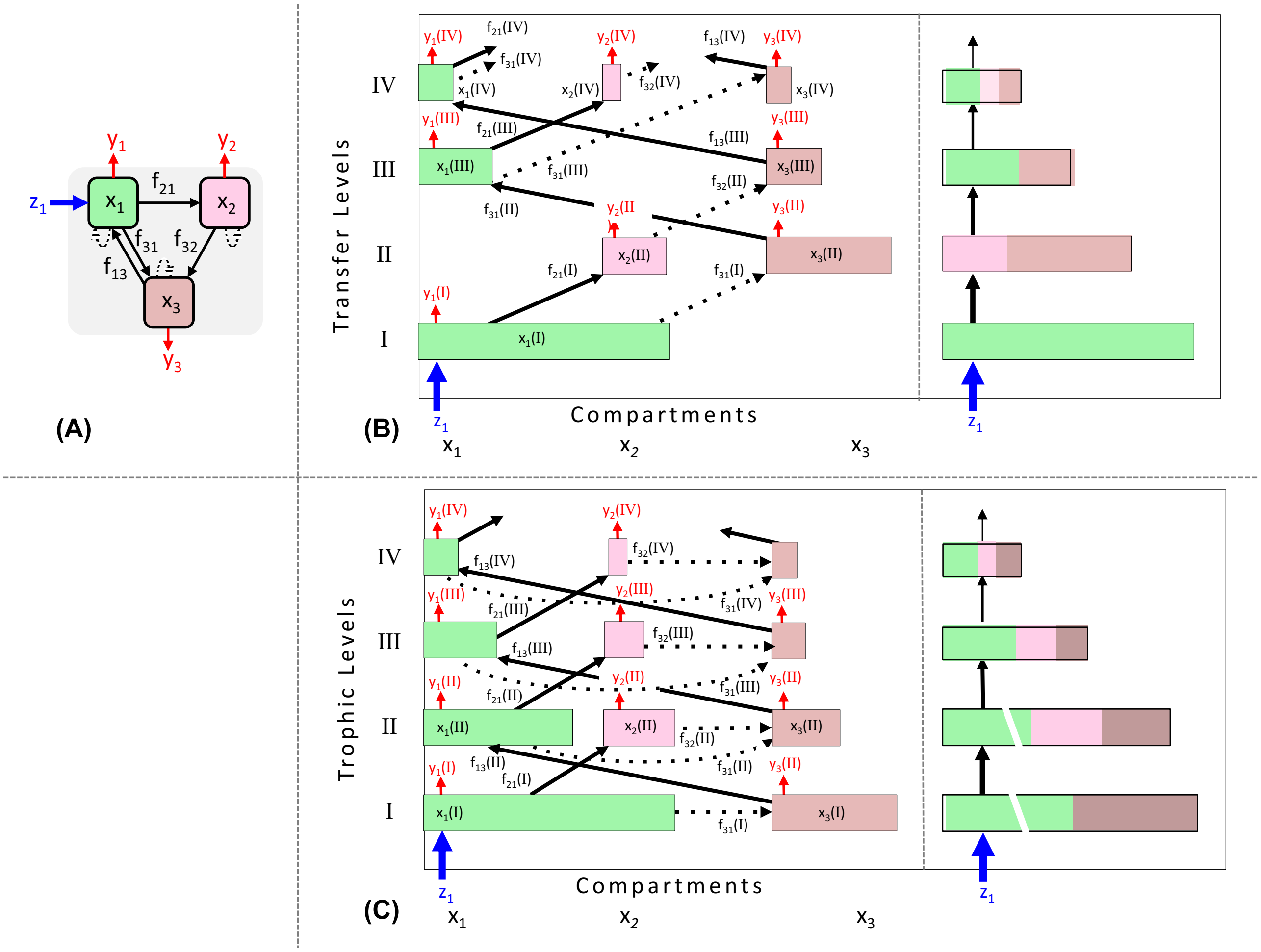


FIGURE 4.9 Illustration of network unfolding for the model (A) of Figs. 4.3 and 4.5 with only one input, z_1. For a food web orientation, the compartments can be interpreted as x_1 = Autotrophs and Mixotrophs, x_2 = Secondary Consumers, and x_3 = Detritus and Decomposers. (B) Graphic depiction of how network unfolding maps (left panel) the digraph in (A) into a pyramid of transfer levels (right panel). (C) Same as (B) but discriminating (left panel) trophic and nontrophic transfers to generate (right panel) a pyramid of true trophic levels. Multiple nontrophic processes can be so discriminated. In the left panels of (B) and (C), *solid arrows* denote trophic flows and *broken arrows* nontrophic. In the right panel pyramid diagrams, the *arrows* are composites of flows from/to corresponding levels in the left panels. Further description in text. Sources: *Redrawn and modified after Higashi et al. (1989, fig. 4, p. 250), and Whipple, S.J. 1998, fig. 2, p. 267).*

digraph structure contains all the information needed to determine stocks and flows of conserved quantities. He did not show this, but the idea has endured through years of NEA development. One paper on link-tracking flow generation has been published (Patten, 2015a). This method is briefly described in Patten (2016a, figs. 11.1—11.3). Storage generation by L_pT still eludes development as an operational methodology. This is described at length as a new property in Patten (2016a; figs. 12.1—12.5). L_pT is especially difficult computationally, and may actually be NP-complete (http://en.wikipedia.org/wiki/NP-complete) as expressed in networks of realistic scale and complexity. Computational intractability notwithstanding, both methodologies provide important insights into how digraph structure, a holistic property, determines or at least constrains, energy—matter movements in networks. If mechanistic reductionism explains network causality from below, then topogenic holism explains it from above. The two together comprise a dualistic explanatory system of bidirectional, bottom-up/top-down, centrifugal/centripetal (CH-11), within- and across-scale hierarchical organization.

L_kT takes the node—link adjacency structure of qualitative digraphs to be like a road system in providing channels of constraint for traffic flow. The difference is one is physical infrastructure and the other virtual. Just as road systems evolve to accommodate (and stimulate) more and more traffic flow, reflecting the growth-and-development imperatives of CH-4 and CH-5, such goal functions may be "topogenetically" imprinted in evolved pathways etched into landscapes by history (see section CH-17: Network Clockwork Stockworks). That is, they may constitute epigenetic inheritance systems at landscape scales. From the air, avenues, trails, and other pathway scars left from former generations of activity are clearly visible, and it is hard not to conclude they reflect (and this continues downscale) an inheritance system expressed in the present in ongoing landscape evolution. It is such history that current states encapsulate and leave behind in state-space formulations of system dynamics. CH-20 at the end of this section deals broadly with extragenetic inheritance at ecological scales.

L_pT is a corresponding prospective methodology to L_kT for storage generation. Just as L_kT formulates a matrix, $N_{L_kT} = \sum_{m=0,\infty} (G_{L_kT})^m$ that maps an input set into throughflows, $N_{L_kT} \cdot z = T_{L_kT}$ (Fig. 4.3, Storage Analysis column), the goal of L_pT is to find another matrix, $S_{L_pT} = \sum_{m=0,\infty} (P_{L_pT})^m \, \Delta t$, that can similarly map an input set into calculated node storages, $S_{L_pT} \cdot z = x_{L_pT}$ (Fig. 4.3, Storage Analysis column). This has been achieved in principle in Patten (2016a), but for realistic cases computational intractability impedes development of an operational methodology. From the rationale and results described below, it can be concluded with some certainty that storage information is in fact enfolded (CH-9) within qualitative node–link digraphs used to depict the structure of transactional networks. Numbered steps in Patten (2016a) explain the loop-tracking rationale, illustrated by the salt marsh energy model of Teal (1962; see Fig. 4.8), parameterized using a unit time step, $\Delta t = 1.0\ y$.

From the still very tentative developments that are L_kT and L_pT at the present time, the way does seem clear to begin seriously considering the Hill (1981) conjecture that qualitative digraphs are sufficient to determine the quantitative flow and storage properties of transactional networks. Clearly, more research of a fairly advanced mathematical nature is needed to definitively resolve this topogenic issue.

Relational Hypotheses

Energy–matter storage-and-flow networks are *transactional*, meaning the quantities they transfer are conservative and zero-sum. The elementary particles involved are countable and finite and cannot be in more than one place at a time. This means if one flow or storage element in a system gains or possesses (+) a particular particle at a moment in time, another flow or compartment must simultaneously lose or not contain (−) that particle. Adjacent transactions between compartment pairs are accordingly zero-sum. Binary relations are nonconservative interactions that form secondary relational networks as a direct consequence of transactional activity. For example, in Fig. 4.1 each flow link shown represents a primary transaction that entails a secondary trophic relation, which is consumptive (+, −) as defined by zero-sum passage of energy-matter particles to each consumer (+) from each consumed (−) compartment. The three zooplankton compartments are all competitors (−, −) in that each vies with the others for the finite conservative particles that comprise the phytoplankton compartment. The competition relation (−, −) is secondarily derived from the transaction-based consumptive relations (+, −) directed from phytoplankton to the zooplankton groups 1, 2, and 3. Considering the three signs +, −, 0, there are nine combinations of these taken two at a time (Patten and Whipple, 2007; Fath, 2007). Some of these were expressed earlier in Table 4.1 of the Cone Spring model example, Section "Network Example 2 – Cone Spring Ecosystem".

Three CHs will be discussed below under the relational heading; others also have relational characteristics superimposed on their primary transactions, and could very well also have been included here.

CH-13: Network Synergism

The quantitative methodology of environ theory lends itself to development of certain qualitative aspects of the environmental relation with organisms. Energy and matter are objective quantities, but when cast as resources they produce subjective consequences of having or not having them. A concept introduced in game theory (von Neumann and Morgenstern, 1944, 1947) to describe the usefulness of outcomes or payoffs in games is *utility*. Environ mathematics implements this concept to bridge the gap between objective energy and matter and their subjective value as resources. Utility measures the relative *value* of absolute quantities; it is subjective information extracted from and added onto objective facts (Patten, 1991, 1992). A *zero-sum game* is one in which a winner gains exactly what the loser loses. As stated earlier, each conservative transaction in ecosystems is zero-sum, but its relative benefit to the gainer and loss to the loser may be different.

Network synergism is the emergence by network propagation of boundary inputs to interior throughflows and storages, of positive > negative utilities (benefits > costs) in system organization. Fath (1998b; also in Fath and Patten, 1998b; appendix) proved this property is always expressed in transactional networks due to the diagonally dominant, reflexive, positive self-mutualism terms in the integral utility matrix, *U*. Network synergism concerns how nonzero-sum interactions arise in conservative flow–storage networks whose proximate transactional linkages are zero-sum (Fath and Patten, 1998). Nonzero-sum interactions tend to be positive such that benefit/cost ratios, which equal one in direct transactions, tend in absolute value to exceed one when nonlocal indirect effects are taken into account. Such network synergism involves huge numbers of pathways (CH-1), dominant indirect effects (CH-2), and an indefinite transfer-level structure that unfolds as a limit process (CH-10)—all features of utility generation (Fig. 4.4) that reflect holistic organization in ecosystems and the ecosphere. Once again, without open boundaries there would be no interior networks, no transactional or relational interactions, and thus no nonzero-sum benefits to components. Life in networks is worth living, it can be said, because the key property of openness as a necessary condition has made all subsequent properties derived from it possible.

If *network nonlocality* (dominant indirect effects, CH-2) is the first principle of environ system theory, then *network synergism* is a good choice for second because this converts the Darwinian struggle-for-existence world of conflict, competition, and strife that has dominated ecological thought for over a century into a more benign place of habitation for living organisms. The zero-sum struggles of local levels of organization are still there, but in nature's hidden extended networks these are transformed to form a more accommodating world of positive, nonzero-sum, system-wide benefits for all. Network synergism is the endpoint of an ecological *Janus Enigma Hypothesis*, CH-16 (Patten, 2016b), which starts by conferring proximate fitness to organisms at the expense of degraded environments, but then goes on to fashion out of network indirect effects ultimate, cost-exceeding fitnesses for both. Further observations about the ecological significance of network synergism will be deferred until after the description later in this section of its corollary hypothesis, network mutualism.

CH-14: Network Interaction Typing

If causal determination in nature is bipolar, then it is reasonable to consider how top-down holism might contribute to the determination of ecological interaction types such as competition, predation, mutualism, etc., which are usually considered locally and mechanistically defined. Patten and Whipple (2007) and Fath (2007) investigated this problem and showed there were two ways interaction types could be determined by networks. In *structural determination* the magnitudes of network flows have no influence. Interaction types are determined strictly by digraph structure. This kind of determination is limited to simple and elementary graph types. With increasing complexity, network flows become determining. Thus, quantitative information is needed, and this was referred to by these authors as *parametric determination.* Patten (2016b) showed that integral utility matrices (U) on which these determination categories are based contain throughflows arrayed in various (complex) algebraic configurations, with or without additional single flows not contained in throughflows. Tuominan et al. (2014) showed that those networks without leftover single flows are structurally determined while those with such flows are parametrically determined. This and other developments discussed at length in Patten (2016a; Section 3.5.3) demonstrate there is much still to be learned about the role of digraph structure and function in the determination of ecological interaction types, both directly and also indirectly at near and far network distances. Understanding holistic determinism requires that such studies be undertaken in the near or far future.

CH-15: Network Mutualism

Under Darwinism, the ecological worldview is one of organisms gnashing and clawing their way to the top of the "struggle-for-existence" heap. Yet nature observed is a pretty serene and settled place where life for the most part seems supported and good for most organisms over most of their existence times. The struggle is there, to be sure, but seems softened by more success than failure much of the time. Life starts and ends in moments, but goes on agreeably for longer periods in between.

Network mutualism is a qualitative extension of CH-13 (Patten, 1991, 1992) that speaks to "agreeably." Every pair of compartments in a transactional network experiences positive (+), negative (−), or neutral (0) *relations* derived from the transactions that directly and indirectly connect them. Ordered pairs of these three signs are nine in number and each pair reflects a qualitative interaction type. For example, the most common types of ecological interactions are $(+,-)$ = predation, $(-,-)$ = competition, $(+,+)$ = mutualism, and $(0,0)$ = neutralism. Since the signs of benefits and costs in network synergism are + and −, respectively, the shift to $|\text{benefit/cost}|$ ratios > 1 in CH-13 carries with it a shift to positive interaction types. This is network mutualism, and it indicates the benefits that automatically accrue to living organisms by their being coupled into transactive networks. Network synergism and mutualism together make nature a beneficial place conducive to agreeable life. This is quite different from seeing life only as a "struggle for existence"; this is locally and episodically true, but not globally. The built-in positive properties of networks expressed in network synergism and mutualism operate to reduce the struggle.

CH-16: Network Janus Enigma Hypothesis

Fig. 4.10 diagrams the Janus hypothesis, which will be abbreviated JH/e in the subsequent discussion. The upper section broadly reflects local and mechanistic relationships (the Janus "first look"). The lower section represents more global and systemic relationships ("second look"). The upper section concludes with enhanced biological fitness (Fitness-I), but at the cost of a degraded environment from which the resources to do the thermodynamic work to produce desired departure-from-equilibrium outcomes were drawn. Biota and the biosphere aggrade (CH-4), and environmental life support degrades, in the dialectical resolution of antientropic versus entropic forces. The lower section realizes both biological and environmental fitness (Fitness-II). Biota and environment both aggrade, and the processes by which this occurs are inherent in the mathematics and logic behind transactional network organization. There is a long way to go to full understanding.

Let us take a closer look—we will follow the diagram (Fig. 4.10). The background second law is on the left, pulling everything down to randomized, gradientless, static equilibrium. Everything to the right fights against this. The ABCs in the Aggradation Nexus are some of the processes involved, all emergent from and functioning within the graph structure that, in CH-12, is held to sufficiently determine them. The energy–matter outcome of all the processing is a dual maximization—of kinetic activity on the one hand, registered in TST (CH-5), and of kinetic potential on the other, registered as the natural capital of total system storage (TSS; CH-6). The upper, first-look line is manifested by binary transactions between adjacent standing-stock compartment pairs, exchanges that are conservative and zero-sum, and transmit temporally and spatially immediate cause and effect. The lower, second-look line

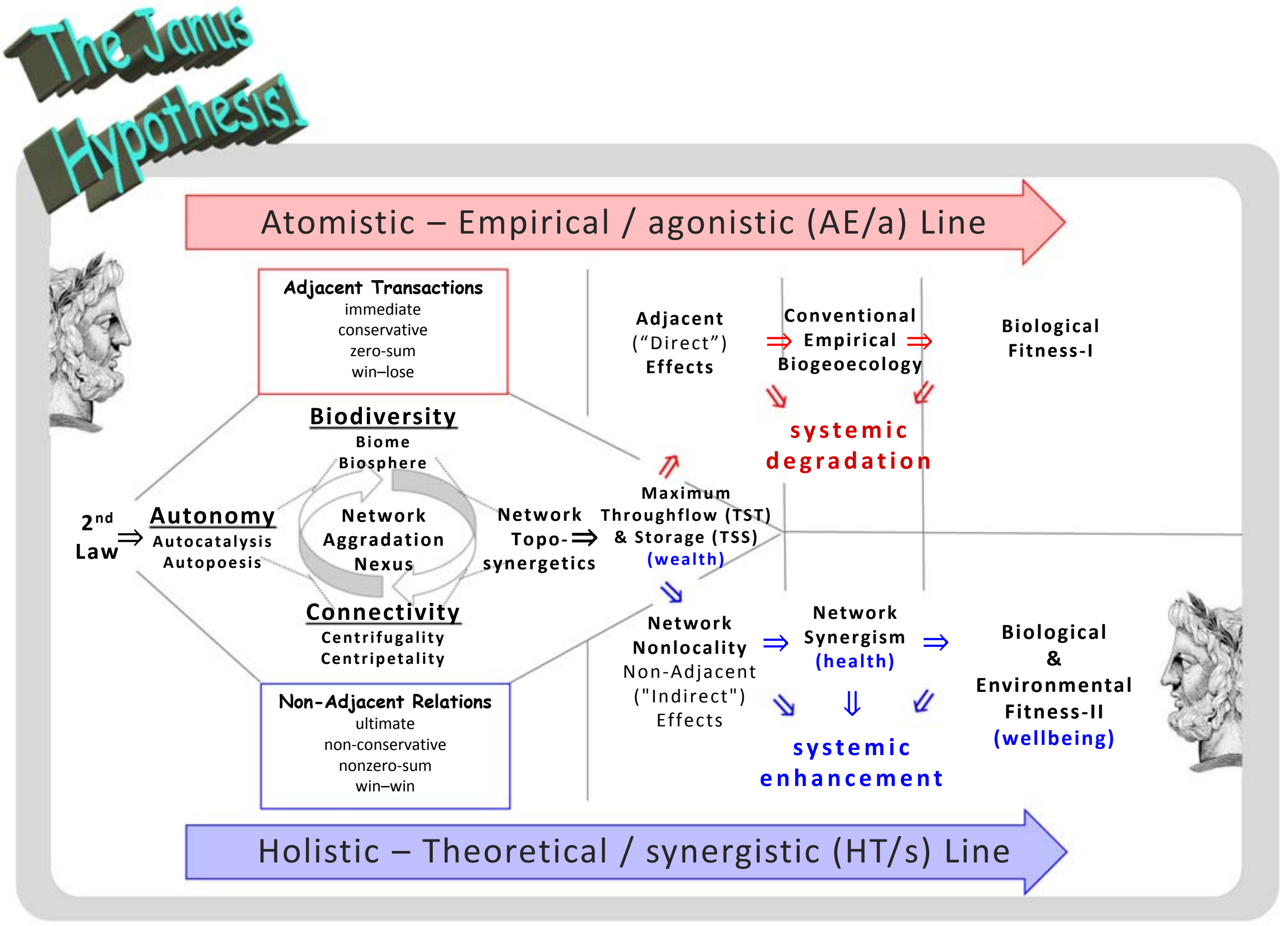
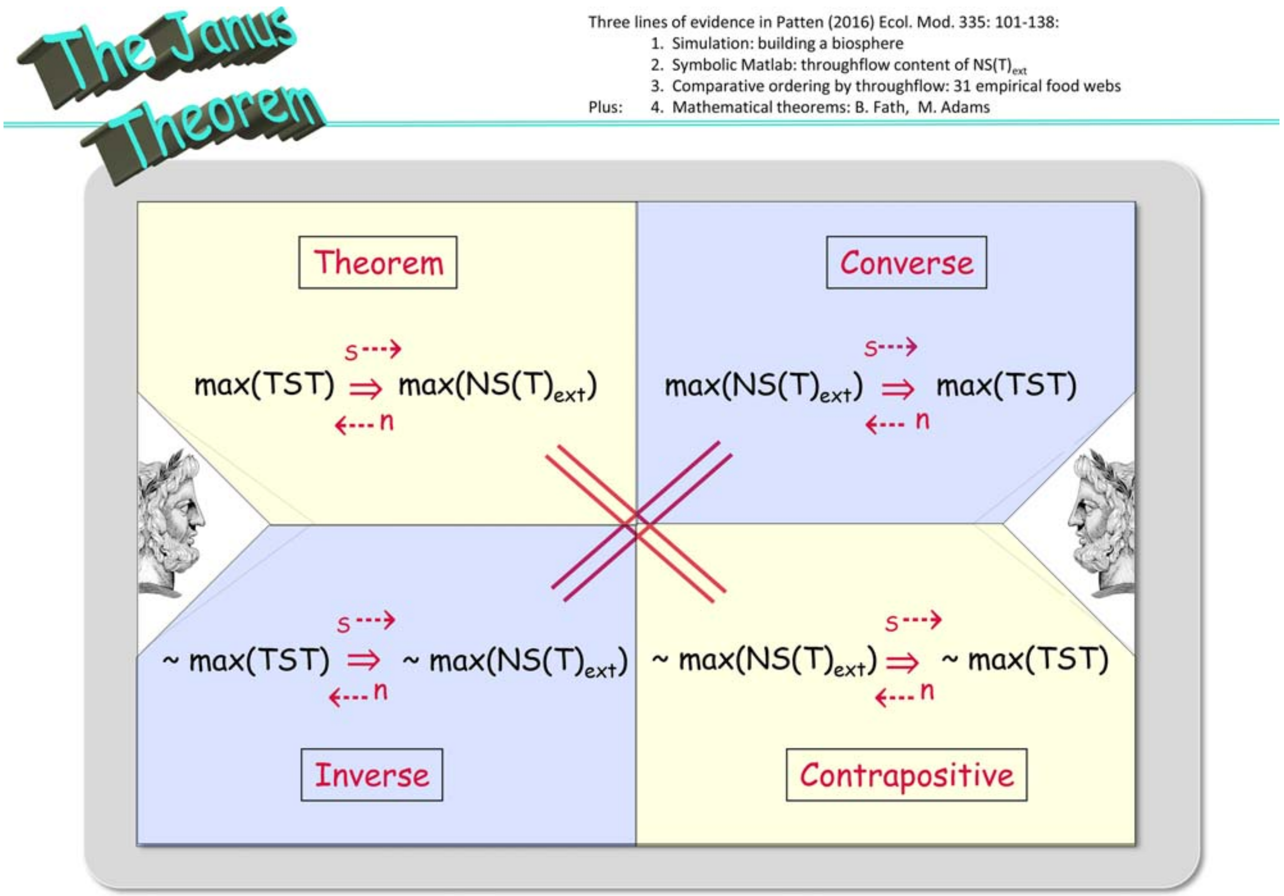


FIGURE 4.10 The *Janus Enigma Hypothesis*—maximizing fitness for life in the geobiosphere. This diagram interrelates all the elements of the Janus Hypothesis. The upper section represents proximate, generally observable and unmeasurable, empirical processes of mechanistic causality that lead to biological fitness, but at a cost of degraded life support. The lower section represents higher level processes, generally carried out by largely inaccessible, and therefore generally (because distributed) unobservable and unmeasurable empirical processes of holistic causation. The antientropic Network Aggradation Nexus contains three core processes ("ABCs"), and several related subsidiary processes, implicated in movement away from thermodynamic equilibrium. Further discussion in text. Source: *Modified after Patten (2016), fig. 1, p. 103.*

involves reticulated, relational sequences of transactions transmitted directly and indirectly between compartment pairs. These relations are nonconservative and nonzero-sum and transmit ultimate causes and effects. The key property that makes the lower line dominant over the upper is network nonlocality—dominance of indirect effects (CH-2). Three biologically and ecologically significant goal functions follow on this last one logically and sequentially from one another in the JH/e: max(indirect $>$ direct effects; CH-2) $\Rightarrow$ max(TST, TSS; CH-5, -6) $\Rightarrow$ max(network synergism; CH-13) $\Rightarrow$ max(Fitness-I and -II; CH-20). To use a common and somewhat overworked metaphor of the present period, in this Janus Hypothes is a perfect storm of individually improbable relationships comes together automatically as a built-in property of transactional network organization, and this makes salubrious life possible and ubiquitous throughout the planetary biosphere.

The JH/e logic is summarized for the throughflow-based formulation in Fig. 4.11. Let D and $U = (I - D)^{-1}$ be intensive (dimensionless), direct (D), and integral (U) utility matrices, respectively (ref. Fig. 4.4; also Section "Network Example 2 – Cone Spring Ecosystem"). Let $Y = U \cdot T$ be extensive (throughflow-weighted) utility. Then, a useful measure of *extensive network synergism* is $\mathrm{NS}_{\mathrm{ext}} = \sum(U \cdot T)$. With these notations, the symbols in Fig. 4.11 can be interpreted. For example, the Janus Theorem states that maximizing TST (or TSS for the storage-based formulation) is sufficient (s) to maximize $\mathrm{NS}_{\mathrm{ext}}$, and the latter is necessary (n) to maximize the former. The Theorem and Contrapositive are logical equivalents, denoted by the large diagonally oriented equal sign (\\), and similarly, the Converse and Inverse are logical equivalents (//). As summarized in the upper right box, Patten (2016b) gave three lines of supporting evidence for the JH/e: (1) TST and $\mathrm{NS}_{\mathrm{ext}}$ both increased proportionally in a sequence of simple compartment models with equal boundary inputs and progressively more complex connectivity; (2) U


Three lines of evidence in Patten (2016) Ecol. Mod. 335: 101-138:
1. Simulation: building a biosphere
2. Symbolic Matlab: throughflow content of $\mathrm{NS(T)}_{\mathrm{ext}}$
3. Comparative ordering by throughflow: 31 empirical food webs

Plus: 4. Mathematical theorems: B. Fath, M. Adams

FIGURE 4.11 Logic-of-propositions structuring (*if* LHS *then* RHS) of the throughflow-based Janus Hypothesis. Each proposition has a truth-value, either true or false. The left-hand (*if*) sides state sufficient conditions (s) for the right (*then*) sides to follow. The right-hand sides are necessary conditions (n) for the left sides. The theorem and contrapositive are logical equivalents (denoted by the two diagonal equals (=) signs); prove one and the other is proved also. The converse and inverse are also logically equivalent. The symbol ($\sim$) denotes negation; $\sim$LHS $\Rightarrow$ $\sim$RHS means "*not* LHS implies *not* RHS." If both LHS $\Rightarrow$ RHS and RHS $\Rightarrow$ LHS, this may be written LHS $\Leftrightarrow$ RHS, and stated LHS *iff* RHS, where *iff* means "if and only if." The storage-based formulation has the same logical structure.

matrices were shown to contain algebraic arrays of throughflows that, when increased, would also increase NS_{ext}; and (3) positive correspondences of TSS and NS_{ext} pairings along an increasing sequence of values were demonstrated for 31 pastoral food webs in Ukraine. Since these results were published, mathematician M. Adams (2017; see Patten, 2019) has obtained an algebraic proof of the JH/e converse. A similar proof of the primal theorem is still being sought; whether the outcome is true or false, the ecological implications will be interesting.

The enigma problem in the JH/e lies in the converse, or more specifically the inverse which is logically equivalent and thus also implied in M. Adams' proof. The inverse states that if TST (also TSS, in a parallel storage formulation of network synergism)—Fig. 4.10) is not maximized in network organization, then neither is NS_{ext}. This means, as stated in the converse, that maximizing TST (or also presumably TSS, though this proof is still pending) is necessary to maximize NS_{ext}, hence systemic Fitness-II. In evolutionary selection, networks that fail to meet this prescription will tend to be reshaped in ecosystemic and biospheric dynamics until the condition is satisfied. Thus, a dilemma and possible danger confronts humanity. Nature is objective and unforgiving. If one configuration of organisms can achieve max(NS_{ext}) better than another in a landscape or biome setting, evolutionary selection will favor the former, and if *Homo sapiens* is, by its own actions or not, in the latter group, it will not fare well. All organisms, humans included, are inherently local problem-solving entities. The sensory-motor apparatus of biota shaped in evolutionary dynamics is geared to the identification and solution of local problems associated with the immediate needs of making a living—obtaining food, shelter, mates, etc.; protecting against disasters, pathogens, and other threats. Distal conditioning phenomena in time and space may be known and understood, but in competition with immediate needs, they lack sufficient urgency to prompt the evolution of a cognitive sensitivity to indirectness (CH-2). Such adaptation may be underway now in humanity, however, as the globe shrinks and the spheres of technology-driven human activity expand.

Autonomy and Self-Organization Hypotheses

CH-17: Network Clockwork Stockworks

This hypothesis seems as strange and counterintuitive as its alliterative name when first confronted, but when understood it makes good ecological sense. Referring to Figs. 4.8A–C, the "standing stockworks' of CH-8 manifesting compartment reflexivity alone were shown to possess considerable capacity to produce standing stocks. The transitive (and also symmetric) links that language usually associates with the "net" in networks have little such stock-generating ability on their own. When "stockworks" (reflexive) and "networks" (transitive, symmetric) combine, however, Ch-8's amplification of stock-generation over reflexive generation by itself occurs. The reason is all about how standing stocks contribute to pathway proliferation, and to the pathways generated. This is developed and exemplified at length in Patten (2016a, figs. 12.2–12.6).

Standing stocks determine the dynamics and other properties of conservative substance movements in ecosystems and the biosphere. Reflexively based "clockwork standing stockworks", to which transitive and symmetric "networks" of interconnection add profoundly (CH-8) but do not anchor, are the order of the day in living concrete nature. Empirical ecology has a key part of the truth completely right—nature, as perceived, is all compartmental standing stocks. But it misses the vital virtual part: nature's invisible *net*works are all about standing stocks too—their extensions into the world around them, even as their substance marks time in the clockwork stockworks of place.

CH-18: Network Environ Autonomy

Fig. 4.5 illustrated the partition property of both output and input environs for a simple compartmental system. Autonomy goes with this—each of the six environs enjoys this property by the fact that every conservative element within it is completely confined to or circumscribed by it, and the environ whole is generated by or referenced to a unique input or output relationship at the system-level boundary. One of the richer NEA consequences of boundary openness, therefore, is the extension of reflexive, symmetric, centripetal "selves" that are compartments into the broader transitive and centrifugal surrounds that environ theory seeks to identify, quantify, and subject to comparative analysis. Input and output environs converge inward and diverge outward from their defining entities, and in a sense reflect and project, respectively, the unique individuality of the latter in and into the world at large. Ownership of this "projection" by the defining compartments is never released, however. They and their paired environs retain a unity that can never be disassembled, but can be decomposed by mathematical analysis. Moreover, not only are the compartments themselves, particularly the living ones, unique, but so also are the environs they generate and encompass. A careful reading of the consequences of organisms as open systems having environments that uniquely attach to them is that not only are the organisms autonomous in their innate reflexivity in standing stockworks, but so also are their environs in their innate transitivity and symmetricity as extended networks, although of necessity more diffusely so.

It was Estonian physiologist Jacob von Uexküll (1926) who first put forward a view of the organism−environment relationship that is not very far from the one environ theory affords. Uexküll's organisms had an incoming "world-as-sensed" and an outgoing "world-of-action", corresponding to input and output environs, respectively. He held that the world-of-action wrapped around to the world-as-sensed via "function-circles" of the organisms to produce an organism−environment complex that was a continuous whole, the true functional unit of nature that decidedly was not the organism alone in isolation. However, Uexküll acknowledged the impossibility of tracing pathways of influence through the general environment from outputs back to inputs, and to that extent the theoretical autonomy he held for his organism−environment complexes was operationally, though not conceptually, compromised.

The stocks and flows of each output or input environ within a system have their own unique structural and dynamic characteristics from those defined by the same substance running in different environs. Every environ is unique. For those of the Sapelo Island salt-marsh energy model (Fig. 4.6A), this uniqueness is registered structurally in the enumerated pathways of Fig. 4.12A, generated by the mth path-length (and for storage analysis, time-passage $m\Delta t$) powers of the adjacency matrices, $A(0)$ and $A(1)$. Functional uniqueness is generated in pathway progressions of link transfer probabilities, expressed by mth powers of corresponding matrices G, G' converging to N, N' for throughflows, and P, P' leading to S, S' for storages.

Environs are boundary defined, and the first reason for their differences is that different energy−matter entry or exit points, respectively, for output and input environs, define different pathway sets (structure) over which introduced substance travels. These necessarily impose differing link-transfer probability sequences along the pathways, and this generates different dynamics (function). Referring to Fig. 4.12A, each jth column in the matrices shows the numbers of pathways of lengths $m = 1, 2, \ldots, 5$ and 100 propagated in output environs E_j to all eight compartments by inputs (z_j) to compartments j. Columnwise comparisons in each mth matrix show clearly that different input entry points generate different numbers of pathways (and, by inference, corresponding flows) of each given length. Similarly, each ith row in the matrices shows the numbers of pathways of lengths $m = 1, 2, \ldots, 5$ and 100 that lead back through input environs E_i' to all $j = 1, 2, \ldots, 8$ compartments contributing to outputs (y_i). The differing numbers of environ pathways determine different pathway identities, each involving a unique link-transfer sequence and mth-order probabilities associated with these.

Ignoring input environs for present purposes (the same considerations apply), Figs. 4.12B and C show first-order $P(0)^m$ and $P(1)^m$ matrices corresponding to $A(0)^m$ and $A(1)^m$, $m = 1, 2, \ldots, 5$, in Fig. 4.12A. Each jth column in the $P(\bullet)^m$ matrices shows transition probabilities associated with corresponding numbers of pathways, $A(\bullet)^m$, of lengths $m = 1, 2, \ldots, 5$ in each jth output environ, E_j. Each ith row in the $P(\bullet)^m$ matrices shows transition probabilities generated by the numbers of length m pathways (of lengths $m = 1, 2, \ldots, 5$ and 100) that lead back through output environs E_i' to all $j = 1, 2, \ldots, 8$ compartments from outputs (y_i).

Fig. 4.12D shows how structure and function combine to produce composite flows to throughflows and storages in transactional networks. Pathways are of two types. Those without self-loops ($j \rightarrow k \rightarrow \ldots \rightarrow i$) are termed *paths*; they carry flows to throughflows in throughflow analysis. Pathways with self-loops ($j \rightarrow \ldots \rightarrow \{k \rightarrow k \rightarrow \ldots k\} \rightarrow \ldots \rightarrow i$) are called *walks*; they carry flows to storages in storage analysis. Paths of lengths $m = 0, 1, 2, \ldots$ are enumerated by matrices $A(0)^m$, and they generate corresponding flow transfer probabilities $P(0)^m$. Walks of lengths $m = 0, 1, 2, \ldots$ are enumerated by matrices $A(1)^m$, and they generate corresponding storage transfer probabilities $P(1)^m$. Fig. 4.12D details four examples, the color-highlighted pathways and probabilities in Figs. 4.12A−C, of how composite mth-order transfer probabilities are generated over each set of length m paths and walks. Paths are subsets of walks, and therefore are included in the walk counts and probability values. In each section of Fig. 4.12D, the boxed and color-coded sums of matrix powers on the left, $P(0)_{ij}^{(m)}$ and $P(1)_{ij}^{(m)}$, equal the sums of products of link probabilities, $P(0)_{ij}$ and $P(1)_{ij}$, shown parenthetically beneath the links $j \rightarrow i$ that comprise each pathway. The main points illustrated are enumerated in the figure legend; they bear repeating here: (1) Each path and walk is unique. (2) Each such pathway is uniquely quantified by products of their individual link probabilities, which may be transfer probabilities, p_{ij} ($j \neq i$), associated with transfer links, $j \rightarrow i$, or self-looping transfer delay probabilities, p_{jj}, associated with storage links, $j \rightarrow j$. (3) Storage, by introducing transport delay, materially increases the number of transfer pathways between each (i, j) compartment pair. (4) The storage self-looping ($j \rightarrow j$) link contributions, p_{jj}, to the products of aggregate link transfer probabilities along each walk are always greater than link transfer ($j \rightarrow i$) contributions, p_{ij} ($j \neq i$); storage is the dominant component of transactional transfers in nature's interconnected networks, justifying the term "clockwork stockworks" used in CH-17 to refer to transactional networks. And finally, (5) the identified relationships are valid for all pathways of all lengths m that indefinitely extend to complete dissipation

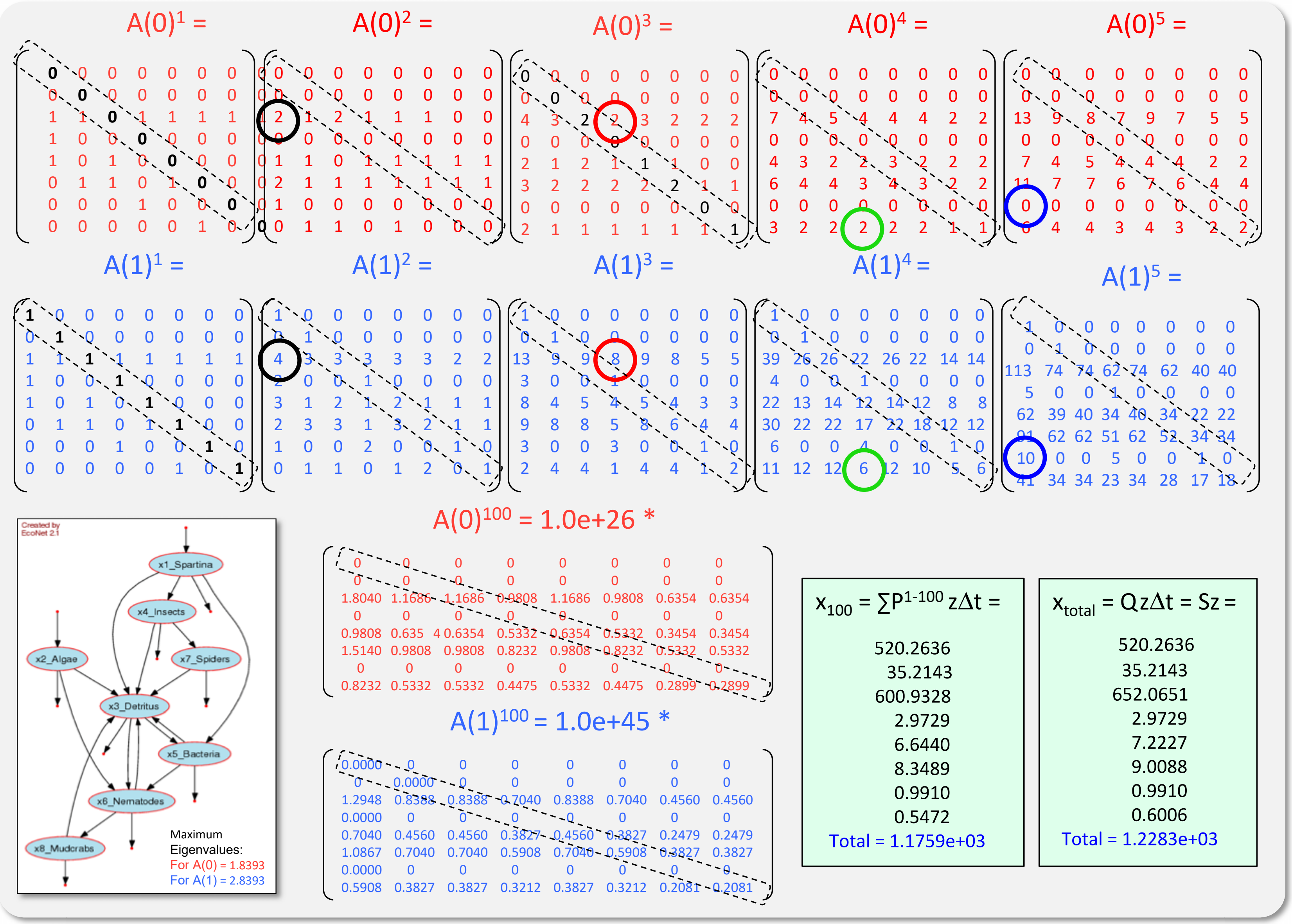
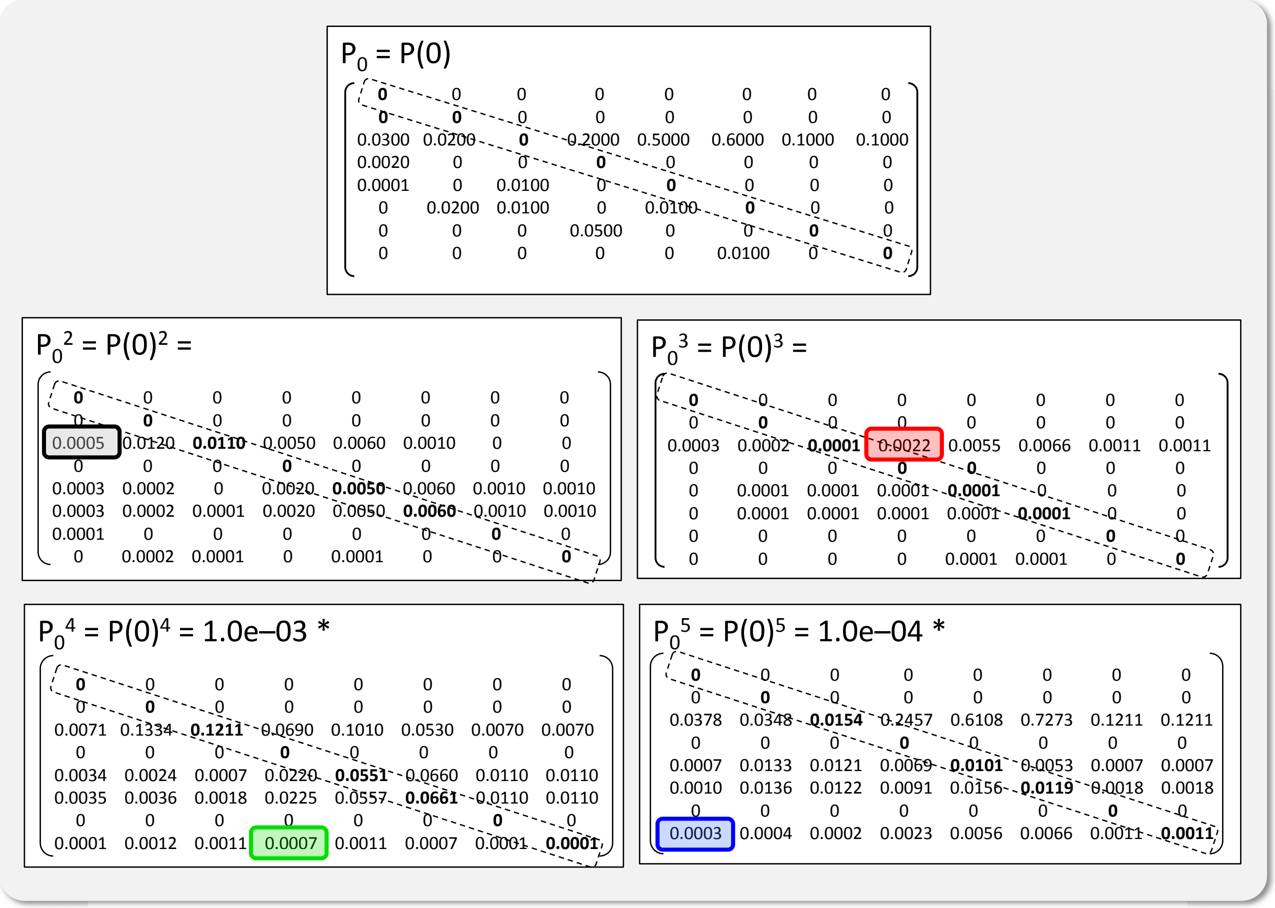


FIGURE 4.12A Powers, $m = 1, \ldots, 5$, and 100, of structure matrices for the Teal (1962) salt marsh energy model of Fig. 4.8A. The digraph is shown again at the lower left for convenient reference. Adjacency matrices without storage self-loops have zero entries on the principal diagonals, and are denoted $A(0)$; those with self-loops have unit diagonal entries and are denoted $A(1)$. Pathways lacking self-loop link sequences are called *paths*, and those with such sequences are *walks*. Paths of lengths m are enumerated by powers $A(0)^m$, and walks of lengths m by $A(1)^m$. Maximum eigenvalues of the $A(0)$ and $A(1)$ matrices define the rates of pathway growth in numbers with length; these are shown adjacent to the digraph at the lower left. The circled entries identify selected pairs of entries (same colors) for comparison without, in $A(0)^m$, and with, in $A(1)^m$, self-looping storage subsequences along the pathways. Diagonal elements are circumscribed to assist orientation. Note that despite astronomical numbers of walks in $A(1)^{100}$, total storage is not yet fully accounted for by all walks of lengths $m \leq 100$. This is shown by $x_{total} > x_{100}$ in the green boxes to the lower right. Network nonlocality (CH-2) and its concomitant holistic causality, are enormous realities in the natural world, and they do not even begin to be recognized, much less accounted for, in contemporary ecology. Source: *Patten (2016a; fig. A4).*



$$P_0 = P(0)$$

$$\begin{pmatrix}
\mathbf{0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\mathbf{0} & \mathbf{0} & 0 & 0 & 0 & 0 & 0 & 0 \\
0.0300 & 0.0200 & \mathbf{0} & 0.2000 & 0.5000 & 0.6000 & 0.1000 & 0.1000 \\
0.0020 & 0 & 0 & \mathbf{0} & 0 & 0 & 0 & 0 \\
0.0001 & 0 & 0.0100 & 0 & \mathbf{0} & 0 & 0 & 0 \\
0 & 0.0200 & 0.0100 & 0 & 0.0100 & \mathbf{0} & 0 & 0 \\
0 & 0 & 0 & 0.0500 & 0 & 0 & \mathbf{0} & 0 \\
0 & 0 & 0 & 0 & 0 & 0.0100 & 0 & \mathbf{0}
\end{pmatrix}$$

$$P_0^2 = P(0)^2 = \begin{pmatrix}
\mathbf{0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \mathbf{0} & 0 & 0 & 0 & 0 & 0 & 0 \\
\boxed{0.0005} & 0.0120 & \mathbf{0.0110} & 0.0050 & 0.0060 & 0.0010 & 0 & 0 \\
0 & 0 & 0 & \mathbf{0} & 0 & 0 & 0 & 0 \\
0.0003 & 0.0002 & 0 & 0.0020 & \mathbf{0.0050} & 0.0060 & 0.0010 & 0.0010 \\
0.0003 & 0.0002 & 0.0001 & 0.0020 & 0.0050 & \mathbf{0.0060} & 0.0010 & 0.0010 \\
0.0001 & 0 & 0 & 0 & 0 & 0 & \mathbf{0} & 0 \\
0 & 0.0002 & 0.0001 & 0 & 0.0001 & 0 & 0 & \mathbf{0}
\end{pmatrix}$$

$$P_0^3 = P(0)^3 = \begin{pmatrix}
\mathbf{0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \mathbf{0} & 0 & 0 & 0 & 0 & 0 & 0 \\
0.0003 & 0.0002 & \mathbf{0.0001} & \boxed{0.0022} & 0.0055 & 0.0066 & 0.0011 & 0.0011 \\
0 & 0 & 0 & \mathbf{0} & \mathbf{0} & 0 & 0 & 0 \\
0 & 0.0001 & 0.0001 & 0.0001 & \mathbf{0.0001} & 0 & 0 & 0 \\
0 & 0.0001 & 0.0001 & 0.0001 & 0.0001 & \mathbf{0.0001} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \mathbf{0} & 0 \\
0 & 0 & 0 & 0 & 0.0001 & 0.0001 & 0 & \mathbf{0}
\end{pmatrix}$$

$$P_0^4 = P(0)^4 = 1.0\mathrm{e}{-}03 * \begin{pmatrix}
\mathbf{0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \mathbf{0} & 0 & 0 & 0 & 0 & 0 & 0 \\
0.0071 & 0.1334 & \mathbf{0.1211} & 0.0690 & 0.1010 & 0.0530 & 0.0070 & 0.0070 \\
0 & 0 & 0 & \mathbf{0} & 0 & 0 & 0 & 0 \\
0.0034 & 0.0024 & 0.0007 & 0.0220 & \mathbf{0.0551} & 0.0660 & 0.0110 & 0.0110 \\
0.0035 & 0.0036 & 0.0018 & 0.0225 & 0.0557 & \mathbf{0.0661} & 0.0110 & 0.0110 \\
0 & 0 & 0 & 0 & 0 & 0 & \mathbf{0} & 0 \\
0.0001 & 0.0012 & 0.0011 & \boxed{0.0007} & 0.0011 & 0.0007 & 0.0001 & \mathbf{0.0001}
\end{pmatrix}$$

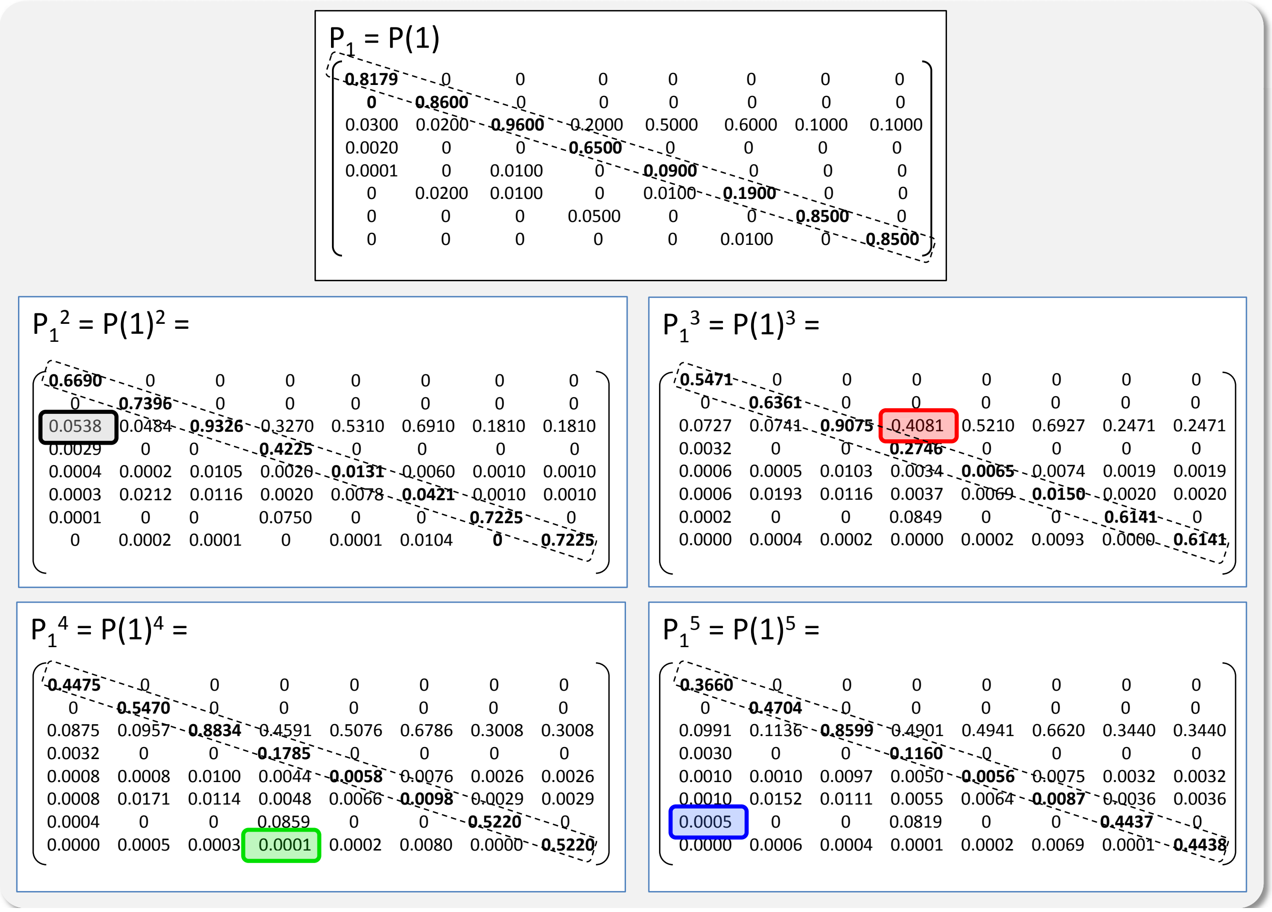
$$P_0^5 = P(0)^5 = 1.0\mathrm{e}{-}04 * \begin{pmatrix}
\mathbf{0} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \mathbf{0} & 0 & 0 & 0 & 0 & 0 & 0 \\
0.0378 & 0.0348 & \mathbf{0.0154} & 0.2457 & 0.6108 & 0.7273 & 0.1211 & 0.1211 \\
0 & 0 & 0 & \mathbf{0} & 0 & 0 & 0 & 0 \\
0.0007 & 0.0133 & 0.0121 & 0.0069 & \mathbf{0.0101} & 0.0053 & 0.0007 & 0.0007 \\
0.0010 & 0.0136 & 0.0122 & 0.0091 & 0.0156 & \mathbf{0.0119} & 0.0018 & 0.0018 \\
0 & 0 & 0 & 0 & 0 & 0 & \mathbf{0} & 0 \\
\boxed{0.0003} & 0.0004 & 0.0002 & 0.0023 & 0.0056 & 0.0066 & 0.0011 & \mathbf{0.0011}
\end{pmatrix}$$

FIGURE 4.12B Powers, $P_0^m = P(0)^m$ ($m = 2, \ldots, 5$), of the first order ($m = 1$) link-transfer probability matrix $P_0 = P(0)$, where the zeros denote zero diagonal elements. Selected entries in each matrix are identified by boxes color coded to correspond to entries in the Fig. 4.12A adjacency matrices, $A(0)^m$. Diagonal elements are circumscribed for convenient inspection. Note the quick appearance in the power sequence of nonzero diagonal entries. These are not self-loops ($m = 1$), denoting storage, but rather cycles of higher order ($m > 1$). Source: *Patten (2015c; fig. A7).*

as $m \to \infty$ in the process of interconnecting (i, j) compartment pairs in accordance with the given constraints of digraph structure. The general conclusion to be drawn from these observations is that each output and input environ in a system is structurally (pathways) and functionally (transfer probabilities) unique, and environ autonomy (CH-18) follows from this in at least two ways.

First, the status of environs as boundary-defined interior partition elements of stocks and flows in compartmental systems confers autonomy by definition because no substance running in any one environ of a given orientation also runs in another. There is no energy—matter mixing between environs. They are space-time extensions of their concrete defining nodes, distributed and virtual in their fundamental openness such as to make the said nodes more like puppets dancing to nature's tune on its hidden strings, and less like punctate beings, sessile or motile, divorced from the greater stocks and flows of planetary movement.

Second, there is the structural and functional autonomy described in earlier paragraphs above that reflects where (for output environs) substance enters and (for input environs) exits a system. These structural and functional differences confer behavioral autonomy, and this extends to substances of each particular kind in one environ versus that of the same kind in other environs. Energy and matter of different kinds behave differently in each unique environ, caused by a substance's intrinsic properties and propensities for interaction expressed from different points of entry or exit into or from a system. There is more. Boundaries are not permanent barriers to substance flow; they vary both objectively and also by the purposes and choices of observers. Environs of fixed-boundary systems are unique and autonomous, but against variable boundaries they become themselves puppetlike in responding to the dynamics of boundary establishment and disestablishment. Add to this the final perspective of scale—boundaries circumscribing levels of organization—and the full scope and multiscalar nature of nested environs coming into and out of existence by virtue of boundary dynamics in hierarchical organization begins to be realized.



$$P_1 = P(1)$$

$$\begin{pmatrix}
\mathbf{0.8179} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\mathbf{0} & \mathbf{0.8600} & 0 & 0 & 0 & 0 & 0 & 0 \\
0.0300 & 0.0200 & \mathbf{0.9600} & 0.2000 & 0.5000 & 0.6000 & 0.1000 & 0.1000 \\
0.0020 & 0 & 0 & \mathbf{0.6500} & 0 & 0 & 0 & 0 \\
0.0001 & 0 & 0.0100 & 0 & \mathbf{0.0900} & 0 & 0 & 0 \\
0 & 0.0200 & 0.0100 & 0 & 0.0100 & \mathbf{0.1900} & 0 & 0 \\
0 & 0 & 0 & 0.0500 & 0 & 0 & \mathbf{0.8500} & 0 \\
0 & 0 & 0 & 0 & 0 & 0.0100 & 0 & \mathbf{0.8500}
\end{pmatrix}$$

$$P_1^2 = P(1)^2 =$$

$$\begin{pmatrix}
\mathbf{0.6690} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \mathbf{0.7396} & 0 & 0 & 0 & 0 & 0 & 0 \\
\boxed{0.0538} & 0.0484 & \mathbf{0.9326} & 0.3270 & 0.5310 & 0.6910 & 0.1810 & 0.1810 \\
0.0029 & 0 & 0 & \mathbf{0.4225} & 0 & 0 & 0 & 0 \\
0.0004 & 0.0002 & 0.0105 & 0.0020 & \mathbf{0.0131} & 0.0060 & 0.0010 & 0.0010 \\
0.0003 & 0.0212 & 0.0116 & 0.0020 & 0.0078 & \mathbf{0.0421} & 0.0010 & 0.0010 \\
0.0001 & 0 & 0 & 0.0750 & 0 & 0 & \mathbf{0.7225} & 0 \\
0 & 0.0002 & 0.0001 & 0 & 0.0001 & 0.0104 & \mathbf{0} & \mathbf{0.7225}
\end{pmatrix}$$

$$P_1^3 = P(1)^3 =$$

$$\begin{pmatrix}
\mathbf{0.5471} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \mathbf{0.6361} & 0 & 0 & 0 & 0 & 0 & 0 \\
0.0727 & 0.0741 & \mathbf{0.9075} & \boxed{0.4081} & 0.5210 & 0.6927 & 0.2471 & 0.2471 \\
0.0032 & 0 & 0 & \mathbf{0.2746} & 0 & 0 & 0 & 0 \\
0.0006 & 0.0005 & 0.0103 & 0.0034 & \mathbf{0.0065} & 0.0074 & 0.0019 & 0.0019 \\
0.0006 & 0.0193 & 0.0116 & 0.0037 & 0.0069 & \mathbf{0.0150} & 0.0020 & 0.0020 \\
0.0002 & 0 & 0 & 0.0849 & 0 & 0 & \mathbf{0.6141} & 0 \\
0.0000 & 0.0004 & 0.0002 & 0.0000 & 0.0002 & 0.0093 & 0.0000 & \mathbf{0.6141}
\end{pmatrix}$$

$$P_1^4 = P(1)^4 =$$

$$\begin{pmatrix}
\mathbf{0.4475} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \mathbf{0.5470} & 0 & 0 & 0 & 0 & 0 & 0 \\
0.0875 & 0.0957 & \mathbf{0.8834} & 0.4591 & 0.5076 & 0.6786 & 0.3008 & 0.3008 \\
0.0032 & 0 & 0 & \mathbf{0.1785} & 0 & 0 & 0 & 0 \\
0.0008 & 0.0008 & 0.0100 & 0.0044 & \mathbf{0.0058} & 0.0076 & 0.0026 & 0.0026 \\
0.0008 & 0.0171 & 0.0114 & 0.0048 & 0.0066 & \mathbf{0.0098} & 0.0029 & 0.0029 \\
0.0004 & 0 & 0 & 0.0859 & 0 & 0 & \mathbf{0.5220} & 0 \\
0.0000 & 0.0005 & 0.0003 & \boxed{0.0001} & 0.0002 & 0.0080 & 0.0000 & \mathbf{0.5220}
\end{pmatrix}$$

$$P_1^5 = P(1)^5 =$$

$$\begin{pmatrix}
\mathbf{0.3660} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \mathbf{0.4704} & 0 & 0 & 0 & 0 & 0 & 0 \\
0.0991 & 0.1136 & \mathbf{0.8599} & 0.4901 & 0.4941 & 0.6620 & 0.3440 & 0.3440 \\
0.0030 & 0 & 0 & \mathbf{0.1160} & 0 & 0 & 0 & 0 \\
0.0010 & 0.0010 & 0.0097 & 0.0050 & \mathbf{0.0056} & 0.0075 & 0.0032 & 0.0032 \\
0.0010 & 0.0152 & 0.0111 & 0.0055 & 0.0064 & \mathbf{0.0087} & 0.0036 & 0.0036 \\
\boxed{0.0005} & 0 & 0 & 0.0819 & 0 & 0 & \mathbf{0.4437} & 0 \\
0.0000 & 0.0006 & 0.0004 & 0.0001 & 0.0002 & 0.0069 & 0.0001 & \mathbf{0.4438}
\end{pmatrix}$$

FIGURE 4.12C Powers, $P_1^m = P(1)^m$ ($m = 2, \ldots, 5$), of the first order ($m = 1$) link-transfer probability matrix $P_1 = P(1)$, where the ones denote unit diagonal elements in the corresponding adjacency matrices, $A(1)^m$, in Fig. 4.12A. Selected entries in each matrix are identified by boxes color coded to correspond to entries in Fig. 4.12A adjacency matrices, $A(1)^m$. Diagonal elements are circumscribed for convenient inspection. Source: *Patten (2015c; fig. A6).*

Here is a question—if an established boundary disappears, and the environs it allows definition fade with it, does the implicit environ order remain to be expressed again should the boundary reappear? In other words, do systems and their pathways once established persist aphysically through time, available to be reinvented physically whenever the circumstances that allow this come together? A question like this has metaphysical overtones that take inquiry to a new level. Environs are reminiscent of quantum physicist David Bohm's (1980) concept of *implicate order*, which holds that order, once established in the flow-stream that is reality, becomes permanently imprinted in that flow-stream. Reality has memory—even though state-space theory teaches that unique histories are carried into present states, which then combine with inputs to uniquely generate futures, the pasts in the present states are implicitly carried forward into these futures. That metaphysical considerations can enter ecology in the latter's theoretical pursuit of environment as a concept is surprising. It does, perhaps, help explain why mainline ecological science resists the call to holism lest it be drawn into realms of thought and empirical intractability that cultural wisdom senses will not contribute to hard ecological understanding, the kind that can be "taken to the field."

The picture that emerges overall, then, is that environs—partition elements in aggregate networks—have integrity as constituted though diffuse units, and are indeed by the partition and dynamic-difference properties fully autonomous yet node-contingent within the systems they occupy. No substance is ever exchanged between any two environs. Also, all measures of them that environ theory has so far allowed have never revealed two environs the same in any of their characteristics. Every environ is unique. A given compartmental element in one environ will have, for a fixed unit of boundary input or output, different flow, throughflow, storage, turnover, and output attributes from the same element in other environs. Substance flow and storage packets associated with the same

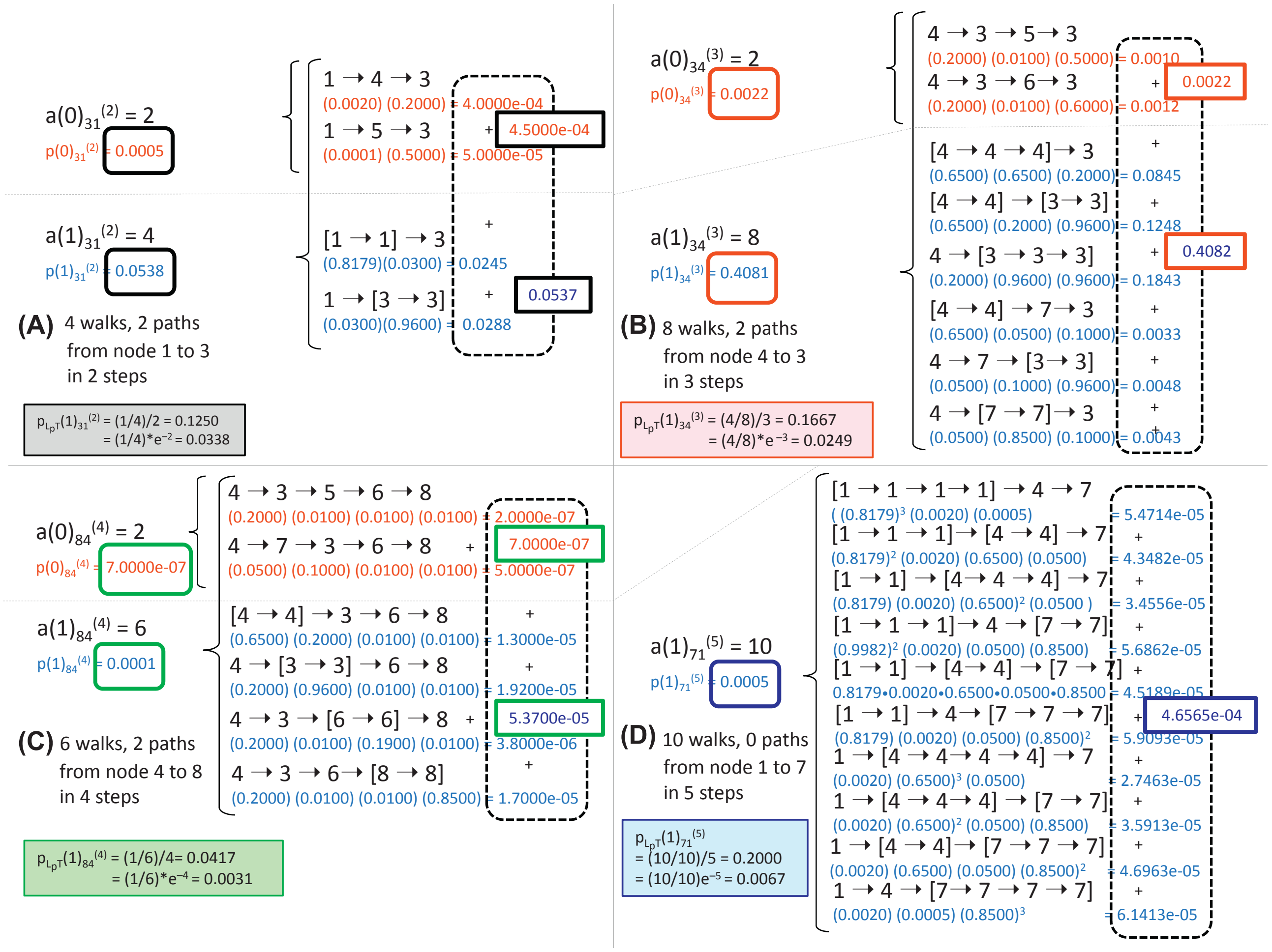


FIGURE 4.12D Details of the circled paths, $A(0)^m$, and walks, $A(1)^m$, of lengths $m = 2, 3, 4$, and 5 as color-highlighted in Figs. 2.12A–C. Paths are subsets of walks, and so are included in the walk counts and probability values. In each section, the boxed and color coded sums of matrix powers on the left, $P(0)_{ij}^{(m)}$ and $P(1)_{ij}^{(m)}$, equal the sums of products of link probabilities, $P(0)_{ij}$ and $P(1)_{ij}$, shown parenthetically beneath the links $j \rightarrow i$ that comprise each pathway (path or walk). The main points illustrated are: (1) Each path and walk is unique. (2) Each such pathway is uniquely quantified by products of their individual link probabilities, which may be transfer probabilities, p_{ij} $(j \neq i)$, associated with transfer links, $j \rightarrow i$, or self-looping transfer delay probabilities, p_{jj}, associated with storage links, $j \rightarrow j$. (3) Storage, by introducing transport delay, materially increases the number of transfer pathways between each (i, j) compartment pair. (4) The storage self-looping $(j \rightarrow j)$ link contributions, p_{jj}, to the products of aggregate link transfer probabilities along each walk are always greater than link transfer $(j \rightarrow i)$ contributions, p_{ij} $(j \neq i)$; storage is the dominant component of transactional transfers in nature's interconnected networks, justifying the term "clockwork stockworks" used in CH-17 to refer to transactional networks. Finally, (5) the identified relationships are valid for all pathways of all lengths m that indefinitely extend to complete dissipation as $m \rightarrow \infty$ in the process of interconnecting (i, j) compartment pairs in accordance with the given constraints of digraph structure. Source: *Patten (2016a; fig. 12.5, p. 75).*

compartments in different environs are different. Uexküll may have been more correct than he realized when he wrapped his worlds-of-action around to his worlds-as-sensed via his functions-circles of the organism, and said that the entire existence of the organism is imperilled should these function circles (implicate order?) be interrupted. Concrete organisms and their virtual environ pairs have a continuity of being that is undeniable, and from the considerations outlined above it is concluded the environs are in several ways autonomous network elements in the economy of nature.

Holism Hypotheses

All the CHs of this chapter are in some sense or other expressions of holism. NEA is fundamentally an approach to holistic systems analysis that occupies places in inquiry where reductionistic empiricism cannot go. The remaining two hypotheses have system-wide reaches and implications that qualify them as expressly reflecting systemic holism, perhaps somewhat more overtly than some of the others.

CH-19: Network Distributed Control

Ecologists from the beginnings of the subject have always been concerned with issues of control—allogenic or autogenic—at physiological, population, community, and ecosystem levels of organization. The subject permeates the discipline in many forms. There are no obvious discrete controllers in ecosystems, though there are concepts like "key industry organisms" and "keystone species" that are suggestive of such possibilities. In general, in view of the nonlocality property (CH-2), control in ecosystems would have to be considered as realized by dominantly indirect means. This is the postulate of distributed control, and as with indirectness itself it has origins in boundary openness (Schramski et al., 2006).

Distributed control means decentralized regulation of system components by direct and dominant indirect (CH-2) effects carried by conservative substance transfers propagated and progressively dissipated over network distances. The numbers of pathways manifesting this control are enormous, e.g., the paths ($A(0)^{100} \approx 10^{26}$) and walks ($A(1)^{100} \approx 10^{45}$) of length $m = 100$ in the Teal (1962) salt marsh model (Fig. 4.12A). The transferred substances may represent resources that facilitate the processes of recipients, or toxins that limit said processes. Component j in a system is defined as controlling another, i, if j facilitates or inhibits i more than i facilitates or inhibits j. This CH holds that (1) distributed, diffuse, indirect, decentralized, remote, etc. control is the dominant regulatory force operating throughout nature's living networks; (2) this control is manifested by long pathways (CH-1) and dominant network indirect effects (CH-2); and (3) the resultant combination of forces is what keeps ecosystems functioning coherently, near-linearly (Patten, 1975, 1983, 1997, 2013, 2014), and stably, resisting and recovering from perturbations, and tracking and adapting to planetary change—at times biotically induced—through bio-geo-physico-chemical evolutionary time.

Such concepts, with their implied linearity, quasi-linearity, and linearization around operating planetary trajectories, lend themselves to investigation by the methodologies of linear algebraic environ analyses. In the throughflow analysis of environ theory (Fig. 4.3), compartment j controls i if the throughflow at i generated by j is greater than the reverse, that is $n_{ij}z_j > n_{ji}z_i$, or in matrix format, $Nz > (N')^{\mathrm{T}}y$. Similarly, in the storage methodology (Fig. 4.3), compartment j controls i if the standing stock at i generated by j is greater than the opposite, that is $s_{ij}z_j > s_{ji}z_i$, or in matrix terms, $Sz > (S')^{\mathrm{T}}y$. Schramski (2006) extensively developed the Patten (1978b) distributed control concept by elaborating and applying what he called *control difference* (CD) and *control ratio* (CR) measures.

The need for cross-scale consistency in bipolar causality would have it that lower levels of organization must participate as equally as upper scales in distributed control relationships. Mechanistic lower scales must mesh consistently with upper-scale holism. Therefore, distributed control must be manifested through an incredibly complex scale-spanning network of transactional interchange. Darwin (1859, pp. 122, 123), for his time, had uncanny naturalistic insight into the nature of the systemic processes involved. Speaking of evolutionary improvement through natural selection, he gave hint to an understanding of distributed control: "This improvement inevitably leads to the gradual advancement of organisation of the greater number of living beings throughout the world. But … if all organic beings thus tend to rise in the scale, how is it that throughout the world a multitude of the lowest forms still exist … ? Why have not the more highly developed forms everywhere supplanted and exterminated the lower?" He gave a systems answer (p. 125), fashioned at a time that knew little about microbiological saprovory and its ecological need in biogeochemical nutrient regeneration: " … under very simple conditions of life a high organisation would be of no service … ." In the economy of nature, in any age, the same basic functions of organizing energy and material resources exist to be performed. Any ecosystem order, simple or complex, must produce protoplasm and degrade it. Commitment to tracking a particular planetary order at a particular time means that a given set of organisms must be systemically coevolved to mutually consistently perform these tasks. If an ecosystem order is simple, then control requirements will be simple and so also the organisms required to carry it out. Darwin understood the unity of the entire organization, but not in supporting network terms, and certainly not including implicate order whose preservation through time (if true) would have precluded the following hypothetical experiment: " … if under nearly similar climate the eocene inhabitants of the world could be put into competition with the existing inhabitants [they couldn't, because their world that gave rise to them could not be duplicated in present time], the former would be beaten and exterminated by the latter … ." The animals in any zoo could never be a match for their wild counterparts coadapted and coevolved with the distributed-controlling environments that produced them.

CH-20: Network Ecogenetic Coevolution

The "Modern Synthesis" of biological evolution describes the process in terms of two fundamental phenomena—transgenerational descent, and its modification over time. It recognizes one kind of descent, genetic, and one modifying process, natural selection. Ecologically, selection steers genetic descent nonrandomly toward adaptive, planet-tracking, fitness-maximizing biotic configurations in the biosphere. Other modifying processes, such as genetic drift and mutation, act at random. Thus, genetic fitness becomes a matter of genes contributed by ancestral organisms to descendants via germ-line inheritance expressed exclusively in "vertical gene transfer." The dogma separates this "germ track" from a corresponding body or "soma track" of supposedly nonheritable, mortal phenotypes by an impenetrable "Weismann barrier" (Weismann, 1885). In the post-Watson−Crick era of the second half of the 20th century, this barrier came to mean unidirectional DNA → RNA → protein coding. It ensures that "nothing that happens to the soma can be communicated to the germ cells and their nuclei" (Mayr, 1982, p. 700). This is *genetic determinism*—the doctrine that the structure and function of organisms are exclusively determined by genes protected from outside influences.

The doctrine has always been questioned, but it is now under serious revision involving a greater role for environment. Numerous mechanisms for environmental control of gene expression have long been recognized (e.g., Klipp et al., 2005). Recently, gene-sequencing technology (genomics) is increasingly revealing the introduction of environmentally selected genetic material into the soma and genomes of macrobiota by commensal and parasitic microorganisms—viruses, archaea, bacteria, and fungi. Internet sources estimate that 8% of the human genome has viral origins. The number of bacterial species in our bodies is more than ten thousand, and by most estimates they well outnumber and comprise several percent at least of the mass of human cells. Moreover, the microbes are arrayed in *microbiomes*, endogenous communities of ultimately exogenous origins with differentiated functions complementing host-organism functions. "Ultimately exogenous" means they got there by, not vertical, but "horizontal gene transfer" (e.g., Quammen, 2018) through the open door of the Weismann barrier their breaching renders obsolete. The breakdown of verticality opens another door to a serious consideration of "environmental inheritance" which, in a wider view of planetary biogeoecology, is the only kind that makes sense in a biosphere that must track and adapt to environmental change as its most basic task in enduring the exigencies and ensuring the contingencies of sustainable life.

Environment is underplayed in conventional evolutionary theory, where it appears only as a general agent in natural selection. The environment of environ theory is two-sided, and both sides can be seen to possess potentially heritable elements, enough to support the hypothesis that environment and genomes both code for phenotypes, one from inside, the other from outside the organism. The never-published term *envirotype* was coined more than 25 years ago to convey this idea (Patten, *Holoecology*, in prep.), and so "holoevolution" (CH-20) came to postulate joint and balanced contributions to mortal phenotypes from two evolutionary, potentially immortal, lines of inheritance. These are the conventional genotype, engaged in bottom-up coding within the cell, and a corresponding external envirotype, effectively manifesting in natural selection top-down coding from without. The envirotype is a third element lurking, but never identified, in geneticist R. C. Lewontin's (2000) "triple-helix" account of evolution which, without that author's actually saying so, distinctly explored the possibility that biogenic elements of environment constituted a bona fide biological inheritance system in its own right. Both input and output environs contribute to the heritable qualities of these envirotypes, as follows:

- *Input-environ-based inheritance.* We can begin with the cell, and then mentally extrapolate outward through higher levels of organization to the organism and beyond. Each level, including that of the whole ecosystem, can be understood to have its own mechanisms of receiving environmental information, generating responses to this, and retaining (inheriting) through natural selection the ability to continue responses that prove beneficial to survival. Consider a cell receiving an energy- or matter-based signal from a near or distant source in its input environ. Biologist B. Lipton (www.brucelipton.com/newbiology.php) presents a scenario that effectively breaches the Weismann barrier and allows transmission of environmental data directly to the genome. Openness is at the heart of this process because the "cellular brain," as Lipton refers to it, is not located deep inside the cytoplasm or nucleus, but at the cell boundary. It is the cell membrane, or plasmalemma, a crystalline bilayer of proteins and phospholipids that includes a set of "integral membrane proteins" (IMPs) that serve as receptors and effectors. Receptor proteins respond to incoming molecules, or equally electromagnetic energy fields, by changing shape. This enables them to bond with specific effector proteins (enzymes, cytoskeletal elements, or transporters of electrons, protons, ions, or other chemical categories) that carry out behavior. If the requisite effector proteins are not already present in the cytoplasm, the IMP perception units activate expression of appropriate genes in the nucleus to produce new ones. Such genes introduced into the DNA → RNA → protein sequence in the process remain behind to be copied, enabling the response to be repeated if adaptive, or ultimately fall obsolete and become consigned to the genomic set of inactive "junk" genes. Correct activations lead to life-enhancing behaviors, incorrect ones to maladaptation and death. Cellular adaptability thus becomes encoded in response to environmental inputs into new genes that encode new proteins, enabling survival in changing, but history-laden, environments. From the environ perspective, receptor molecules respond to signals transmitted in input environs, and effector molecules transmit the consequences to output environs. This initiates the second phase of environmental inheritance.

- *Output-environ-based inheritance.* When cells or other living entities act on their environments the latter are changed as a result. This is "niche construction" (Odling-Smee et al., 1996). Its essence is that it alters the machinery of natural selection because selection is, in the first instance, a manifestation of input environs. To the extent, however, that output environs generated by responses of their defining entities wrap around and become elements in those entities' input environs, the process becomes heritable, and epiphenomena such as autoevolution (Lima de Faria, 1988) emerge as distinct possibilities. Metazoan organization as "symbiogenic" aggregates of protozoan antecedents (Margulis, 1981, 1991) is an example. This is based on wrap-around feedback in which unicellular input- and output-environ overlaps are established in multicellular organization and achieve integration and identity. Organized cell communities possess self-similar IMP receptors responsive to the signal content of hormones and other intercellular regulatory macromolecules. This requires that output-environ elements become input-environ elements. Membrane proteins convert adjacent environmental signals into cellular "awareness," expressed as changes in protein configurations. The movements occasioned by these changes represent useful kinetic energy that does the work of achieving further departure from thermodynamic equilibrium, which multicellular organization represents compared to unicells. This is the essence of all antientropic growth and development extending to ecosystems and the ecosphere. Each level has mechanisms peculiar to it for implementing environment-based inheritance and perpetuating through time all forms of life that are operational genotype—phenotype—envirotype complexes. Organisms and their cells below, and communities and ecosystems above, can be said to inherit both their contained genes and attached environments from ancestral forms, and to the extent that these environments manifest holism, the great panoply of life spread over the globe at all levels of organization can be seen as evolving jointly, altogether, in the ecosphere—"holoevolution."

4.8 CONCLUSIONS

As evident throughout this chapter, ecosystems are networks of interacting biota and abiota. Rigorous methodological tools such an ENA and NEA have been developed to deal with this. Reactionary clinging to a culture of old science will not change the realities to which the new science of this book is trying to open some doors, at least ever so slightly. As more and more applications of systems and network analyses arise, it is important to remember the common methodological roots of the approaches. In fact, because of its basic assumption about objects connected together as part of a larger system, which is used in several disciplines, the most promising application of network analysis may be as a platform for integrated environmental assessment models to address sustainability issues of combined human and natural systems.

CHAPTER

5

Ecosystems as Self-organizing Hierarchies

> All sciences are now under the obligation to prepare the ground for the future task of the philosopher, which is to solve the problem of value, to determine the true hierarchy of values. ***Friedrich Nietzsche.***

Ecologists often seem to take the existence of a hierarchical organization of nature for granted, and the reasons to this judgment are many (Rowe, 1961). First of all, looking at reality through a sequence of subordinate levels matches with our normal ways of doing science within the realms of biology, in a more or less reductionist manner, seeking explanations and identifying causes of phenomena predominantly at lower levels. With respect to this reductionistic viewpoint, the purpose of applying hierarchy theory is to move us closer to nature and not the opposite as feared by some authors (e.g., Guidetti et al., 2014). Such an open, comprehensive, and improved understanding of nature can be easily based on the linkage of some simple terms, elements, and concepts. In short, a hierarchy can be characterized as a partly ordered set with asymmetric relationships inside the whole entity (Allen and Starr, 1982; O'Neill et al., 1986, Allen and Hoekstra, 1992; Wu, 2013; Allen, 2001,[1] Eldredge et al., 2016). These interactions connect different levels of organization, which can be distinguished by their spatial and temporal characteristics. Due to those basic differences of typical extents and frequencies, hierarchies are developing as emergent properties of self-organized ecosystem dynamics (Nielsen and Müller, 2000). Within such development, the overall system is enfolding hierarchical constraints, limiting the degrees of freedom of lower hierarchical levels and potentials, derived from the lower levels' constitutions.

As a first example for such a well-known hierarchical distinction, we may view the existence of an organism as a result of its ability to find food, its ingestion, metabolism, growth, reproduction, and further factors which may be reduced to physiology, later to biochemistry, and ultimately to mere physicochemical reactions. Such an intuitive view may for sure be advantageous in reducing and organizing complexity and analyzing the particular set of hierarchies that we later will identify as having physical embeddedness, i.e., that the lower levels are successively surrounded by upper levels, as a central core feature. This represents a more holistic view by making use of at least a conceptual modeling approach for the embeddedness where it may also be a virtual construct, e.g., where the individual members of a population are not strictly confined by a distinct physical boundary and that allows for the analysis of ecosystems. It is also inclusive as it recognizes the relative success of reductionistic strategies and allows for the use of data from all levels. Thus, hierarchical viewpoints are suitable for unifying holistic and reductionistic approaches (Jørgensen, 2012). Meanwhile, when it comes to current discussions on environmental issues, we are moving toward the upper end of the hierarchy where the systems are composed of many organisms of many kinds, eventually belonging to any possible functional group of species, being it evolutionary primitive or a highly advanced species; monocellular or multicellular; bacteria, algae, or cormophytes; protozoans, invertebrates, and vertebrates; and maybe even humanoids. Systems come to include many of these organism types, with highly varying temporal and spatial scales, and as a consequence, the distinction into clear physical boundaries becomes obscure or is totally lost. One solution will be to define and design what we are going to work with so our conceptualization is fitting the actual specific conditions of the ecosystem in the best possible manner. In other words, our system analysis is case specific; and thus, our resulting ecosystem may take almost any form that relates to the real system under consideration as it mostly depends on a problem-oriented perspective. The systems as well as their boundaries are dependent on the problem to be solved; they are defined by the observer with respect to the questions on hand.

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[1] http://web.archive.org/web/20011218001638/http://isss.org/hierarchy.htm.

https://doi.org/10.1016/B978-0-444-63757-4.00005-X

Taking the whole together, we observe (at least) two distinct types of hierarchies, the series of embedded systems (also often referred to as nested systems) together with a series of nonembedded systems that must be constructed from relevant elements (Fig. 5.1).

To make things simple and considering the knowledge we have gained about ecosystems over the recent decades, the latter type seems to be the more relevant one for the analysis of ecological problems and ecosystems. As seen from the figure above, the obvious embeddedness reaches up to the organism level and therefore its elucidation is mainly concerned with the subdisciplines of autecology or ecophysiology. Both of them deal with mostly internal aspects of the organisms and the close relations to their respective environments, at most with the predatory processes of either "to eat" or "being eaten." That is, most often papers deal with energetics of the life cycles of representatives of a given species—taking the surroundings, the complex environment in which they are truly embedded, as a "black box" for granted and representing relatively stable conditions (continuous repetition of seasonal cycles as a Lagrangian stability).

The other type of the disciplinary hierarchy deals exactly with attempts of describing and characterizing the surroundings (Umwelt) in which the organisms are embedded because organisms or collections of species are never on their own. They mostly enter in herbivorous or prey—predator relations leading to sets of Lotka—Volterra relationships that may or may not be linked in a (Lindeman) trophic chain. But, at present we know that attempting to understand the behavior of natural systems from fundamental views of two-species prey—predator relationship or linear food chains is far too simple to make the full picture. Species interactions take the full set of species involved to capture at least a part of the prevailing complexity. Furthermore, the species and their functional groups are organized as networks where they may interact with several levels at the same time in space, and these networks may not

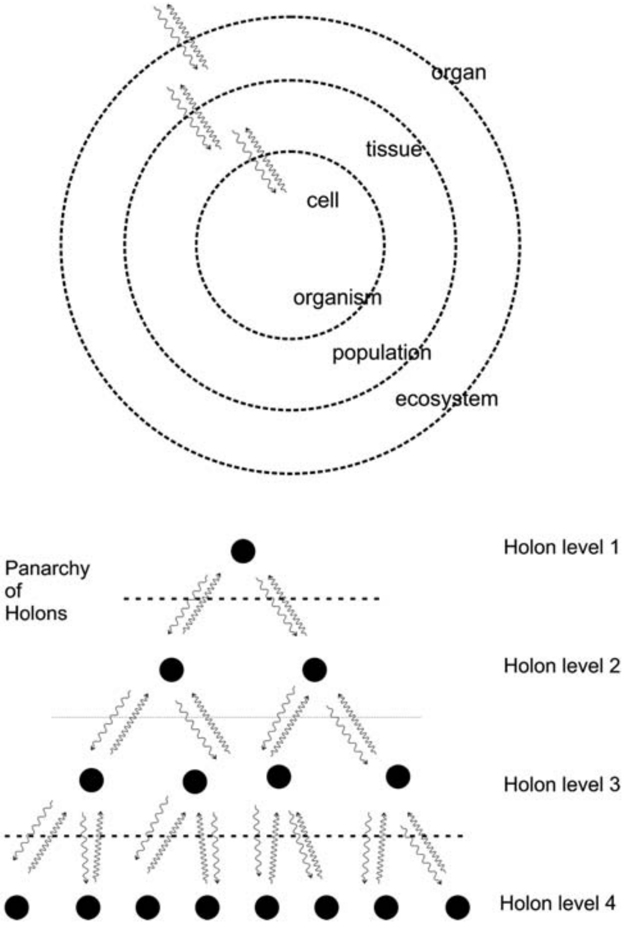

FIGURE 5.1 Examples of the two principal types of hierarchy found in the literature—the one of embeddedness—the upper part being real, physical embeddedness where an organism is having organs, tissues, and cells as continuously internalized levels, whereas organisms make up the population which in turn make up the ecosystem with no distinct physical bound, and the second representing a mere ranking of levels and processes.

necessarily be constant in time. These circumstances are clearly demonstrated in the previous chapter dealing with ecosystems as connected, complex networks. Also, in addition to the feeding interactions, the organism is dependent on and connected with its environment for all other aspects that allow it to continue as a living, self-organizing, aggrading, and dissipating system: the air, the soil, the water, the temperature, the chemical gradients, etc. The environment provides the conditions that sustain life (which the organism itself is part of, provides feedback to). We have found it useful to distinguish between discrete life (an organism) and sustained life (the ecosystemic processes) (Fiscus and Fath, 2019).

5.1 HISTORY OF HIERARCHY CONCEPTS IN ECOLOGY

Applying those demanded holistic attitudes, hierarchy theory as such was formulated during the late 20th century presumingly as part of the appearance of the general systems theory of von Bertalanffy (1968). Authors like Koestler (1967), Weiss (1971), Pattee (1973), and Simon (1962) can be addressed as pioneers of the hierarchical systems view. Although the view has become somewhat inherent in biological thinking, a real breakthrough in ecology seems to have come in the late 1970s where the first papers dealing with hierarchies in ecology emerged following the statistics of the Web of Science (WOS). Since then, the number of papers published in the area has grown markedly. Using WOS for a quick investigation in the area reveals that around 350 and 650 papers per year (2017 data) were published in the area when a combined search of the term hierarchy is coupled to ecosystems or ecology, respectively.

The stronger representation of papers containing the term hierarchy during recent decades is likely to be tightly coupled with the recognition of the extremely high level of complexity exhibited by ecosystems. This has led to an increased attention of the problems that arise both when doing research and management on these systems. Ecosystems and their counterparts, socioecological systems, have been widely recognized as belonging to a special class of middle numbered systems (Allen and Starr, 1982), self-organizing holarchic open (SOHO) systems (Kay et al., 1999), or complex adaptive systems (CAS) (Holland, 1992). To these features, the property of hierarchical (self-) organization, and emergent properties should definitely be added (Müller and Nielsen, 2000; Nielsen and Müller, 2000). Hierarchical thinking therefore represents a core issue in interpreting and understanding biological systems in a holistic manner (Farnsworth et al., 2017; Wu, 2013).

5.2 HIERARCHIES INHERENT IN BIOLOGY

Hierarchical concepts have been penetrating scientific thinking ever since the ancient Greeks and are often taken as a tacit background to the things we are doing as ecologist, the way we practice our research (Bizzarri et al., 2013). We often forget that the very way we see species organized—in a ranking in accordance to evolutionary systematics—implicitly contains an inherent idea that something, here typically a certain species or a functional group, is somehow more important, more advanced, more complex, more organized, or more central than others; and therefore, valued differently.

Traditionally, outcomes of these concepts are phylogenetic or evolutionary trees, which place primitive organisms at the base of the scheme and when climbing up it splits into branches of species being more and more advanced, mostly with increasing complexity (see Fig. 5.2). We demonstrate such a view in our practices as humans, ecologist, and managers. We tend to prioritize and protect species closer to ourselves or at least animals we believe possess the ability to present feelings, thinking, or any type of cognition in a mirror of ourselves.

Another core point implicit in the above reflection is the idea that some organisms or species are more sophisticated or complex than others. This idea also lies behind the launch of the concept of exergy and emergy in the late 1970s. As an extension, in exergy analyses the level of complexity was hypothesized to be reflected in the size of the genome (Jørgensen et al., 1995) or subsets hereof (Fonseca et al., 2000) for a relative weighting of the complexity level. Clearly, organisms such as chordates are more complex than protozoans, and such a view is even reflected in our ideas about the food chain where higher level (advanced) organisms are usually feeding on lower levels, simple organisms. Meanwhile, many conceptualizations of ecosystem food chains are often neglecting the simplest forms, bacteria that really make up a fundamental and essential part of the ecosystem function by ensuring the circulation of nutrients within the system and from a functional perspective share a role of consumers (Steffan et al., 2015). Meanwhile, the recent way of presenting the organisms in the cladistic trees presents the organisms in a manner

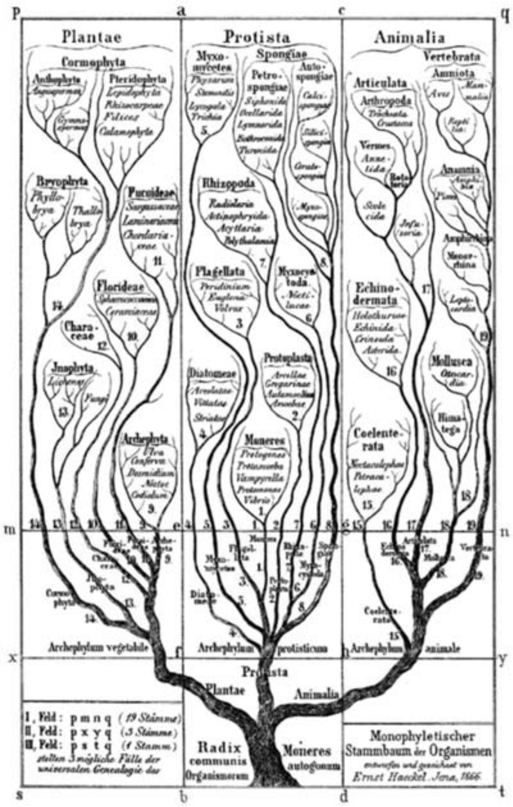

FIGURE 5.2 Phylogenetic tree where the branches terminate at various levels believed to indicate a hierarchical position in accordance to a hypothetical and constructed level of evolutionary level of complexity.

that is more "fair" as it places all species or phylogenetic groups at the top. This ought to remind us that when viewed from a functional angle all representatives in the ecosystems count equal as each performs an essential function in the system, i.e., makes the system exist.

O'Neill et al. (1986) make this mix of observations the starting point of one of the earliest books dedicated to hierarchical understanding of ecosystems. This treatment begins by pointing out the apparent gap in our understanding of systems of seemingly either static—focusing on elements such as species or populations—or dynamic, which covers a more process-oriented entrance to the analysis. As in many cases of complex systems, for such an analysis to be successful it is not a question of "either or" but rather "both and," i.e., we need a more holistic approach and the authors point at the hierarchical approach to be the optimal concept needed in the future to increment or complete our understanding of biological systems. Such ideas actually represent a predecessor of postmodern science (Funtowicz and Ravetz, 1993) in ecology. This implementation of the hierarchy theory in ecology has had a tremendous impact and has been expanded on by many other contributors like Allen and Hoekstra (1992), Müller (1992), Hari and Müller (2000), Gardner et al. (2001), or Salthe (1985). Meanwhile, it can be argued that hierarchical thinking was present in systems theory much earlier (Gayer, 1969; Drack and Pouvreau, 2015).

As with the phylogenetic example, many texts on reductionism and holism in biology take a very distinct hierarchical approach to understand such systems. We know traditionally from the first scholarly studies in biology that organisms are composed of organs consisting of tissues, cells organelles, macromolecules, etc.—all of which are getting consistently smaller and smaller—the smaller, being embedded in the above/previous level. Such an illustration is shown in Fig. 5.1 and Table 5.1. What is most characteristic is that within the sequence of levels each level is typically separated by physical boundaries that are most often of a membrane-like character. The cell membrane separates the cell from its environment or adjacent cells, other membranes are separating the organelles from the cell sap and so on. Moving in the other direction, tissues and organs are most often delineated by another set of membranes until the final boundary with yet another cell layer, in the human/mammalian case our skin.

Whereas, the evolutionary tree certainly expresses a ranking of the organisms more or less in accordance with the time it has taken to evolve (see Jacob, 1977) that very organism type, another question that appears is how to describe

TABLE 5.1 Examples of the Distinction Between Scalar, Control, and Nonnested Hierarchies as Opposed to an Understanding Which Involves a Physical Embedding of the (Sub-)systems.

Nonnested Hierarchies	Nested Hierarchies
Examples: The military command hierarchy; food webs	Examples: The army consisting of soldiers of all ranks; taxonomic systems
Not suitable for exploration	Suitable for exploration
Same criteria (or measurement units) pressing across all levels	Different criteria (or measurement units) at different levels
Comparison between hierarchies is more feasible	Comparison between hierarchies is less feasible
System-level understanding cannot be obtained by knowledge of parts	System-level understanding can be obtained by knowledge of parts

After Wu (2013)

such a hierarchy? We may talk about a scalar hierarchy to a certain extent as organisms tend to be larger and take up more space the higher they are placed in the hierarchy. When organizing the ranking in another way, for instance, expressed in the food chain or other ecophysiological process bundles, we may even talk about a control hierarchy. At least, we frequently did so earlier when ecosystems were considered to be regulated by predation and the whole series of levels was considered to be what is usually referred to as "top-down regulated." Meanwhile, it has been shown on several occasions that the lower levels also play very important roles in shaping the function and flow of the ecosystem. For instance, the capture of solar radiation by primary producers has a prominent role and is responsible for the whole energetic input into the system from which all other activities are made possible. Further recycling and retention of matter, such as nutrients, is carried out by bacteria or very simple organisms mostly in sediments or soils. Both the latter are placed at the lowest levels of the hierarchy, but nevertheless lead to the fact that bottom-up control must be applied in order to get a full view of the regulatory mechanisms. When dealing with embedded systems we may correspondingly talk about outside—inward regulations versus an inward—outside perspective. For further discussions on this, the reader may refer to Nielsen and Ulanowicz (2000), Nielsen (2007, 2016), and Salthe (1985).

5.3 CLASSICAL HIERARCHIES IN TIME AND SPACE

While the above hierarchies in biological thinking remained relatively unarticulated, it became more and more apparent that systems thinking from physics penetrated into the biological sciences, most likely with the introduction of a more holistic view as applied, for instance, through the works of E.P. and H.T. Odum, making it easier to observe the importance of spatial and temporal patterns.

A central role in this evolution has been played by Arthur Koestler who introduced the concept of the holons, units that were continuously embedded in each other: every level consists of a set of smaller parts, which in turn consisted of even smaller parts, and so on. Each level thus contains a "Janus-faced," dualist—not to say dialectic property of having relations with other levels in both upward and downward directions. The relationships to ecology became apparent when B.C. Patten declared ecosystems to be understood as holons—or environs as they were named—in what must be seen as a seminal paper in this connection (Patten, 1978).

Following the view of Koestler, hierarchies are normally observed in a vertical manner (cf. above) as illustrated in Fig. 5.3. The view fits well with the physically embedded system. Meanwhile, this seems not to play as large a role as one might expect although all boundaries are more or less virtual or mental having been constructed by human thinking. This is due to the fact that we most often tend to construct these types of hierarchies when used for either research or management, regulation purposes in a manner where the upper layer tends to be inclusive, i.e., including lower level elements.

One major observation was that time and space scales are often linked so that larger systems are coupled with a longer time scale and at the same time are embedding or including smaller and smaller systems with successively smaller and smaller time scales. The various time scales influence the way the systems communicate. Communication between levels takes place so that the upper level communicates with signals of lower frequency than the lower level and that the lower level communicates upwards with signals of a higher frequency. Signaling here can take place by the exchange of energy, matter, or information. The upper levels tend to dampen and level out or filter

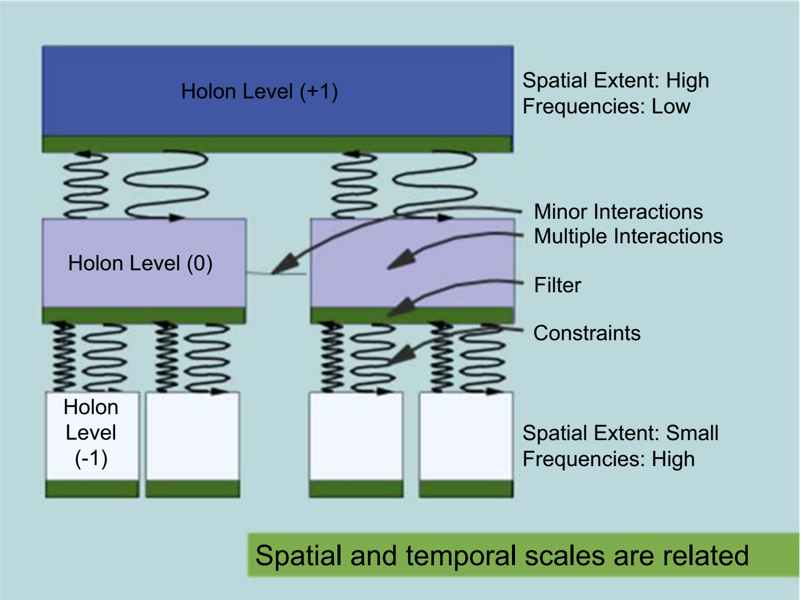

FIGURE 5.3 Basic features of ecosystem hierarchies, following Müller (1992).

the signals from the lower levels. They do not necessarily react on them and are thus acting as constraints on the lower levels because these cannot filter the signals from above. Interactions may also take place between components at the same level—in a horizontal signal transfer at the same spatiotemporal level—where frequencies also may differ and constrain each other. Following the ideas of ontic openness (Chapter 3), we have a guarantee that internal competition and adaptation between the holons at each level will take place in this manner.

The consequences of the hierarchical structure from Fig. 5.3 may be illustrated by Fig. 5.4, which shows some hypothetical relations between different functional holons: due to broad extent processes the geological and geomorphological conditions of an ecosystem have been set by extremely long-term processes. For instance, the Holocene glaciation dynamics have been determining the actual shapes of several landscape types. The subsequent geomorphological processes have been operating since 10,000 years and are producing slow changes for very large regional

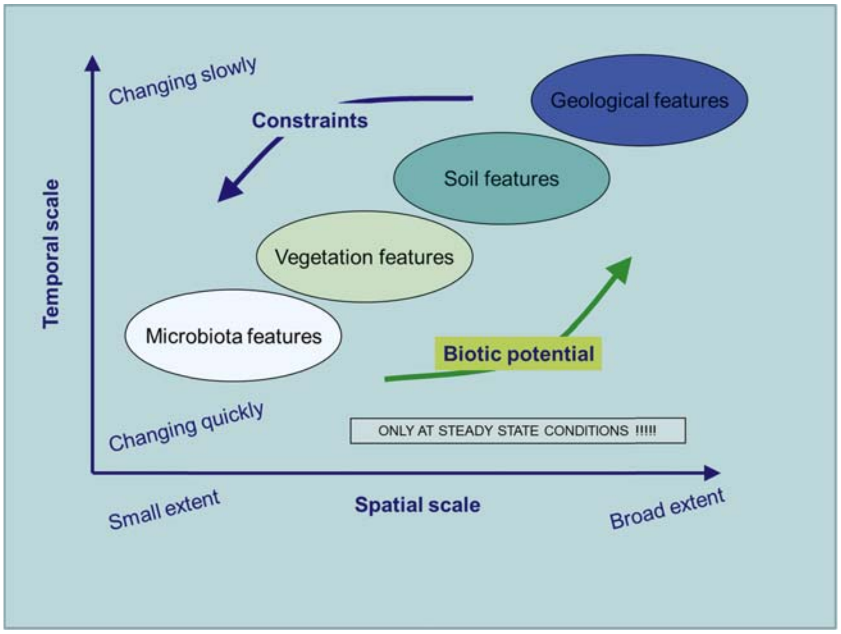

FIGURE 5.4 Exemplary consequences of spatiotemporal hierarchies for ecosystem structures and functions.

entities. Due to these (slow and large) features, many soil characteristics are determined, only certain soil development processes can become active, and therefore the geological structure is constraining the soil development, reducing the degrees of freedom of soil evolution. Due to the resulting pedological structures, only certain vegetation will have the potential to grow, and due to this specific plant cover, the developing freedom of the fauna is also reduced. Finally, the faunistic and floristic conditions determine the potentials of the microflora. The different holons are in fact reducing the degrees of freedom in a top-down hierarchy. In the other direction, the direct effects are low. For instance, soils may only impact the extremely long-term changing geological features. Thus, the bottom-up direction is characterized by biotic or abiotic potentials. Their changes are mostly filtered or dampened by the upper level as long as the system is operating under steady-state conditions. In situations of instabilities, this hierarchy is broken and the future development can be determined by the very actual lower level situations as well.

Evolution at a larger scale is possible when mismatches between lower levels and upper levels become too large (O'Neill et al., 1986). In such a case, e.g., when the prevailing biotic potential cannot follow the dynamics of climatic constraints, the scaling mismatch will eventually lead to a breakdown of the system, and a new constellation or configuration will emerge either by bifurcation or jump-wise in a form following the pattern of punctuated equilibria. Such a behavior is most likely linked with the fact that all holon levels are in fact ontically open (see also Chapter 8 on disturbance and decay).

5.4 HIERARCHICAL FEATURES: BOUNDARIES, GRADIENTS, AND CONSTRAINTS

One fundamental property essential to form a hierarchy—a necessary condition—is the establishment of a physical or conceptual boundary. Boundaries make it possible to distinguish holons and the holons' levels from one or another. The levels do not perform the same functions and they allow for strong differences between themselves. The importance of such boundaries and their recognition, is e.g., discussed by Yarrow and Salthe (2008).

Within the boundaries, the differences are in fact the gradients that make the whole series of systems and subsystems tick, or in other words the gradients make things move between holons, they create potentials, make the system function, make it alive. Also, these gradients can be assigned to different hierarchical levels. A simple example is the sequence of carbon gradients in an ecosystems, reaching from extremely slowly developing soil carbon fractions over long-living tree biomasses, bushes to perennial or annual herbs, animals with different life spans and microbes which have a generation time of hours. These temporal characteristics of the carbon pools can be correlated with their spatial extents and thus be documented in a hierarchy similar to the one shown in Fig. 5.4. The accounted pools provide the potentials for flows between them; thus, gradients can be understood as the bases for all ecosystem processes. They can easily follow the gradient profiles from places with high concentrations to regions with low amounts of matter, energy, information, or organisms. Thereby certain resistances are regulating the speed of the reactions. On the other hand, they can also work with slow frequencies, accumulating the pools as a long-term process. Between both directions of gradient creation and degradation typical equilibria exist in different ecosystem types (see Müller, 1998).

Consequently, the relations between the various levels, their very functions, become constrainers of at least the adjacent levels. In fact, it is not too hard to imagine the relations constraining the whole system when considering the complexity of the ecosystem network, e.g., thermodynamic constrains imposed on upper levels (Nielsen, 2009). A process such as photosynthesis even when normally considered to be placed at lower levels of the hierarchy is a major regulator to the upper levels by determining what is fed upwards into the systems functioning as a significant element of the system's net primary production and its overall biological potential. The herbivores clearly are limiting biomass but also acting as stimulators of primary production. Likewise, in a situation of nutrient limitation, the role of dead organic material and recirculation becomes evident as a constraint.

Boundary Issues

In an evolutionary perspective, the separation of systems from their respective surroundings represents an essential event that allows many features of the system to emerge and must be seen as a necessary condition. This is maybe not valid for the self-organizational process alone as self-organization may appear without boundaries such as autocatalytic cycling or hypercyclic organization. But, when a separation occurs it allows for the growth of the system, although this property can really not be separated by the existence of growth and dissipation.

In the case of physical boundaries, a clear material and energetic relationship exists as matter or energy has to arrive from somewhere and dissipation needs to end up somewhere outside the system. Usually, for matter or energy, this is an outside—inward relation, whereas in the traditional views, information flows are supplied from the inside, i.e., the genetic apparatus. The new science of biosemiotics is putting a new perspective on this (Emmeche and Hoffmeyer, 1991, Nielsen, 2007, 2016).

Adding the perspective that systems may interact via hierarchies which are not necessarily physically embedded complicates our understanding of the systems. We need to understand the processes at new levels and new manners as physical embeddedness stops with organisms. The inclusion of more species in a population or in communities makes it possible at first to understand higher systems' performances as collective behavior, i.e., what happens is only a result of actions and reactions at lower levels, e.g., at the individual level, such as is known from the Gleasonian individualistic perspective on ecology/ecosystems. Many examples on emergent properties of ecosystems serve to illustrate that this is definitely not the full story.

Meanwhile, adding the hierarchical perspective to parts of the ecological systems that are not necessarily embedded is of high value to ecosystem studies. For instance, Kolasa (2014) recommends a hierarchical entrance to boundary studies to be essential for understanding ecosystems. In particular, it may assist in "(1) categorizing types, (2) deciding what is and what is not a boundary, (3) fruitful resolution, (4) approaching, complex, nested systems, and (5) deciding criteria to use about a particular boundary type." Eventually, this approach includes boundaries of both embedded (nested) and virtually embedded systems. Finally, when discussing delineations, besides easily visible physical borders as skin or cuticula, virtual or case-specific boundaries can exist. That is especially the case when we move to scales situated above the organism level. Here, home ranges of organisms can play a role, watersheds as containments of certain hydrological flow directions, or ecosystem complexes that can be characterized by soft borders like ecotones. At these scales, the selection and determination of borders is a task of the observer with respect to his very specific field of problems.

Thermodynamic Gradients

As remarked above, living systems in general are existing and carrying out their activities due to gradients, differences in concentrations over their boundaries, made possible exactly due to the establishment of that very boundary. To fulfill the thermodynamic demands, a gradient is not enough since the system also needs to be thermodynamically open, i.e., allowing the passage of both energy and matter as well as information over its boundaries. Of course, the respective flows can also be understood as transfers within a spatiotemporal hierarchy.

The two ecosystem indicators derived from thermodynamics—emergy and exergy—represent measures that are clearly based on a hierarchical interpretation of the systems. Emergy expresses the hierarchical ranking of the levels by their respective transformations of energy levels (such as trophic levels) that originated with solar radiation, whereas exergy correspondingly is using the relative information content of the genome to do this, leading to the eco-exergy as described in Chapter 2.

Constraint

The outside of an ecosystem—being it a physical surrounding in case of embedded, nested systems, or neighboring systems—acts as a constrainer to the development of the system. We may in many cases relate these constraints to what is imported or imposed as forcing functions on the system mostly of either matter or energy—but also the possibility to export may, in some cases, be quite important. Hence, it is closely related to the gradient relationships between the systems.

At the same time, the system may be constrained from the inside, for instance, by limitations in genetic or physiological capabilities. In this context, it is important to note that the system of constraints is a self-organized consequence of successional development (see Müller, 1998; Nielsen and Müller, 2000). If this can be carried out in an undisturbed manner, then the developing ecosystem creates its internal hierarchy on its own without artificial pressures from the outside. The hierarchy emerges as a consequence of complexification. Furthermore, the strength of the hierarchical constraints—the functional top-down limitations of developmental degrees of freedom—is a basic precondition for the metastability of the ecological systems (see Chapter 8).

The constraining process gets an extra dimension through the hierarchical view of higher levels normally having not only larger spatial scales but also longer temporal scales symbolized by the fact that signaling in the system is taking place with longer wavelengths. It is believed that the difference in time scale and lower frequency acts to dampen and level out the signals from lower levels and that this dampening acts as a constraint but also as a means for stability on the system.

Emergence

The three factors mentioned above, (1) the boundaries separating the systems from the environment, (2) the gradients between the systems, and (3) the constraints, shape properties that are not necessarily predictable from the basic system knowledge. The respective phenomenon is often referred to as emergence, and the respective systems possess emergent properties. In fact, emergence is said to imply a hierarchy (Gignoux et al., 2017), or hierarchy is a precondition for emergence. Nielsen and Müller (2000) have defined emergence as "the consequence of interactions between the parts of a system, which can create new properties of the whole. These new properties cannot be foreseen from the knowledge about the parts alone." This means that in self-organized dynamics, each hierarchical level has at its disposal certain features which cannot be found nor foreseen at the lower levels. These features arise from the interactions of the parts. Therefore, self-organization automatically leads to hierarchical structures, and one quality of the respective interactions is the constraints that appear to be self-imposed by the entity.

The lack of predictability caused by the phenomenon of emergence is truly annoying to our chances of doing proper management but seems to be penetrating the whole world of biological hierarchies (Ponge, 2005). If properties are truly emergent but not recognized as such or not well understood, then how do we ensure that we preserve them? In all cases, the uncertainties induced by such phenomena are really pointing back to the precautionary principle. We really have to understand emergent properties much better in order to manage the environment. We must learn how to work with them and induce them in ways that are consistent to the benefits of ecosystems and humans.

Odum's classic 1977 article suggested using emergent properties as a research target of ecosystem development (Odum, 1977). This idea has been realized, for instance, within some indicator systems that use ecological orientors (see Chapter 10).

5.5 UNDERSTANDING HIERARCHICAL FUNCTION

The usage of hierarchical understanding and interpretation of the various holon levels may be exercised from two quite different entrance points. The first one is primarily used for structuring our knowledge and organizing our work on ecosystem performance in an attempt to deal with focal units of the system (ontological perspective). The second approach is directed toward the question how do the units behave on their own or as interacting with members of the same or other holon levels (phenomenological perspective).

Hierarchical Interpretations Above the Organism level

As mentioned above, the organization of organisms is at first represented by the individuals combined into collections called populations with no actual physical boundary and where a dominant part of the function is made up by the sum of individual organisms. Here, no major temporal or spatial scale variation exists within the population.

Another hierarchical interpretation commonly used in ecology is that of the scalar hierarchic organization into the trophic hierarchy, food chains, and trophic networks. The scales differ with types of organisms—as larger animals generally eat smaller ones (with the exception of big herbivorous mammals)—and hence the body size often is related to the trophic function and position. In principle, this should lead to the possibility of using an allometric approach to interpretation, description, and modeling—an obvious idea but it maybe not as trivial as it sounds (Ritterskamp et al., 2016). Additionally, besides body size, life span, and trophic positions, the typical expansion of the home range of organisms linked with the duration of community processes can be considered as a means of scale distinction. And, of course several abiotic holons can be defined by the observer, which have certain spatial and temporal specialities.

As an example, hierarchical responses in lakes have been hypothesized to be composed of immediate, short-term responses on fast reacting, lower levels of the system, while long-term reactions are exhibited by the upper levels of the system (Wagner and Adrian, 2009). Carpenter (1989) has used a hierarchy approach to distinguish different levels of eutrophication processes (Fig. 5.5, right side). The author distinguishes four groups at different spatial and temporal scales, whereby the higher levels limit the degrees of freedom of the lower ones. On the highest spatio-temporal level, we can find the edaphic potential. It is as a property of the corresponding watershed, characterized by the ecophysiological potentials of the terrestrial ecosystems, the long-term land-use structure and the agricultural intensity. These are factors that change slowly. At this scale, the nutrient input into the lake is regulated. In the aquatic system, the nutrient inputs can be amplified by mobilization from the sediment. Relatively fast changing factors such as temperature, light, and oxygen concentrations are forcing functions for the colonization of the water

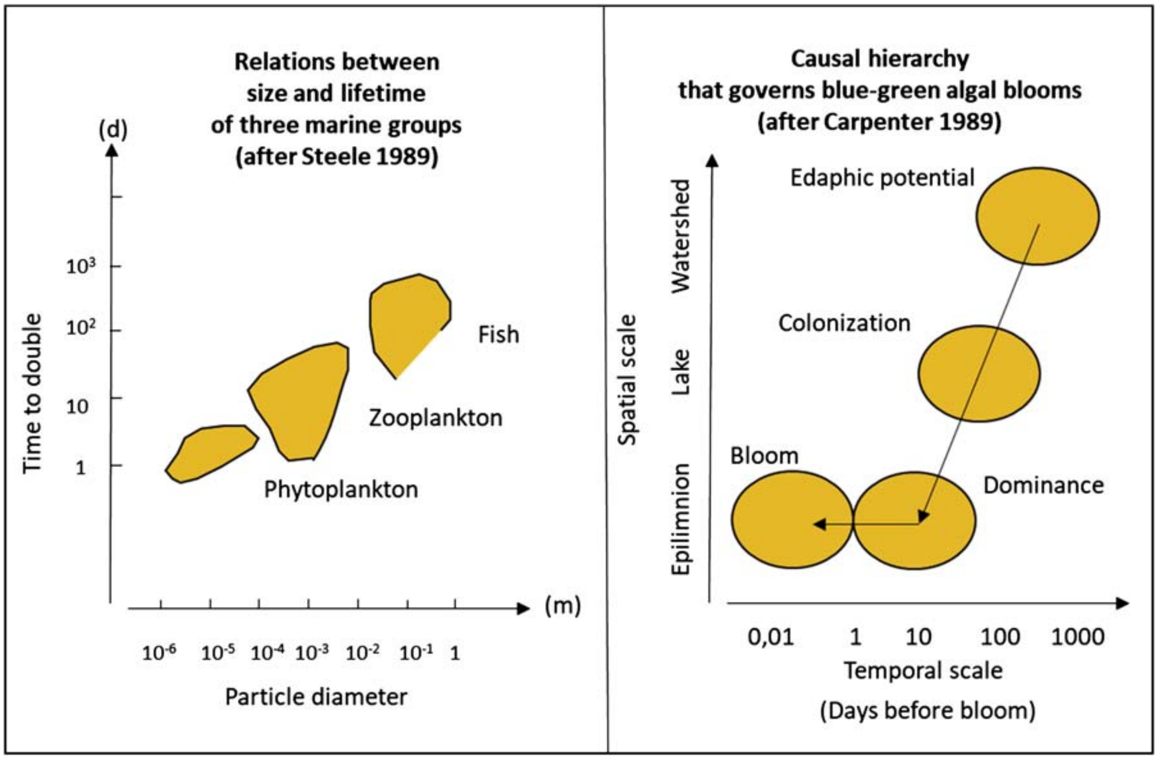

FIGURE 5.5 Two examples of structural and functional hierarchies referring to aquatic ecosystems. *After Steele (1989), Carpenter (1989), and Müller, E., 1992. Hierarchical approaches to ecosystem theory. Ecol. Model. 63, 215–242.*

column by phytoplankton. The next level of analysis is the community structure of the epilimnion. In very short process sequences, blue-green algae reach dominance, regulated by the N/P ratio, the pH, and the herbivorous structure. Finally, blooms that take place in phases with low mixing are influenced by light conditions and available CO_2 concentrations with the highest frequencies of change. Thus, the described sequence of processes demonstrates hierarchical determinations in systems beyond the organism level.

A structural—hierarchical viewpoint concerning aquatic ecosystems has been discussed by Steele (1989): On the left-hand side of Fig. 5.5, correlations between the size of nekton, herbivorous zooplankton, and phytoplankton in pelagic marine environments, and the lifetimes of these groups are illustrated. The size of the organisms' home ranges and the degrees of dispersion are related by this correlation, and consequently nutrition can be regarded as a scale transition.

Population—Community Level

A population may be described as a collection of individuals which all belong to the same species. In ecology, it is considered to have its own subdiscipline of population ecology. Likely to be one of the oldest ecological disciplines, it deals with a wide range of subtopics related to the survival of populations, demographics, growth and survival, age distributions, intra- and interspecific competition, dispersion of organisms, migratory behavior, and how all of it relates to environmental issues such as conservation and biodiversity.

In a hierarchical context, this means that the time scale of the dominant population processes is more or less the same for all participants. Thus, we deal with relations within horizontal holon levels. This is particularly accentuated for systems where several populations interact as they compete for the same resources as, for instance, in the case of phytoplankton populations. Samples rarely consist of one species only and eventually represent a mix of what must be seen as a set of competing holons each waiting to take over as a consequence of interactions between internal and external constraints.

The interaction would be much the same for all sublevels composing the structure of the several to many communities of the ecosystem.

Ecosystems—Patches and Mosaics

Populations, communities, and societies come to interact through their respective trophic interactions and relations as described in the previous sections. As a result of the interacting processes, in many cases, assemblages are observed to take on complex patterns expressed as mixes of uniform distributions of populations or even communities. The phenomenon of spatial distribution is known as patch, mosaics, or biocoenotic relations. To each of these, adjacent science branches exist that are dealing with the changes and dynamics of such distributions. In a hierarchical context the relationships may still be described as horizontal but at another level of hierarchy.

We are now reaching a level of complexity where our present conceptualization and our modeling efforts are challenged and found insufficient in fully explaining empirical observations made, i.e., the actual phenomenology of ecosystems most likely to be due to emergent properties (e.g., Fox, 2006). Much of this partly seems to confirm or explain the findings of B.C. Patten et al. through their theoretical works on ecosystem networks coming up with new phenomena such as network synergism, amplification, and aggradation (see Chapters 4).

Hierarchical interpretations seem to be particularly abundant in a few areas such as riverine or stream ecosystems (Thorp et al., 2006; Cisielka and Bailey, 2007) or terrestrial systems (Bardgett et al., 2005).

One major importance is that while an ecosystem might be found constant at a larger scale, the patches and resulting mosaics may in itself be dynamic. Thus, the ecosystem is still in balance, but a dynamic one, where changes are exhibited in components that are horizontally combined at a lower level. This has been suggested to represent a new paradigm of patch dynamics, mosaic cycles, and stratified stabilities in ecology (Wu and Loucks, 1995).

Landscapes Sensu Lato

The hierarchical approach to ecosystems seems to have gained much popularity in investigations of larger systems that are actually more likely to represent several ecosystems and definitely more than one population or trophic level.

In fact, we may identify different landscapes and regions which are more unified by physico-geographical conditions rather than belonging to the same ecosystem types. These areas may be defined by belonging to a type of sheds—for instance, a water- or sea-shed, where linkage is made up by physical flow patterns of water, or air-sheds where major inputs may be driven by atmospheric relationships.

Landscapes in general, probably due to the large space and time scale perspective, have many possibilities to include many hierarchical views, such as those of subsystems being embedded or enclosed in, sharing a space and making up horizontal hierarchies, and exhibiting the importance of constraints at or between any of the levels chosen (Szabo and Meszena, 2006). Consequently, in landscape ecology, a broad field of literature has been developed around the problem of scales and scaling (e.g., Levin, 1992; Blöschl and Sivapalan, 1995; O'Neill, 1996, Wu and Li, 2006).

Thus, in particular watersheds—systems of larger rivers and smaller streams have received much attention and have been found to exhibit patterns that demonstrate the value of the hierarchical approach for analyzing size dependencies, trophic relations, or even emergent properties, and issues such as top-down versus bottom-up regulation as well (Lowe et al., 2006; Parsons and Thoms, 2007).

Oceanic ecosystems may be analyzed for their spatial patterns over regional scales—corresponding to landscapes—although they may be characterized better as being seascapes (Kavanaugh et al., 2014). The authors applied a "hierarchical patch mosaic paradigm" in order to compare the pelagic systems of the North Pacific and their result may be a bit surprising showing that seasonality is playing a minor importance in determining function at all levels. Similar studies have been carried for marine coastal areas and related to their wetland environments (Schaeffer-Novelli et al., 2005).

Regional Scales

The community structure of rocky intertidal communities has been analyzed with the aim to reveal whether real macroscale processes would dominate the development of this type of ecosystem or if it would be dominated by factors that originate from meso- or local scale (Menge et al., 2015). Over a wide spatial scale—from 100 km to 100 m they came up with the conclusion that while environmental factors dominated at meta-ecosystem level where the "normal" ecological processes would play a more important role at the lower levels.

As we are widening the scope in this analysis, finally several attempts should be mentioned to assign any ecological structures and processes to spatial and temporal scales (e.g., Di Castri and Hadley, 1988; Gunderson and Holling, 2002; Gunderson et al., 2017; Lampitt et al., 2010). One example is depicted in Fig. 5.6. These hierarchical schemes can be found with reference to vegetation dynamics, climate change, landscape processes, or resilience assessments.

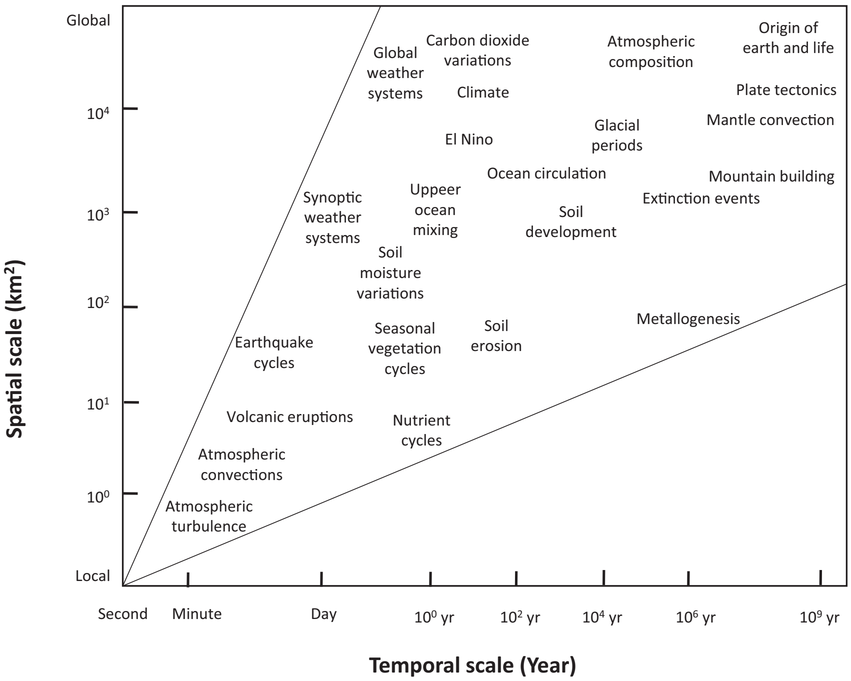

FIGURE 5.6 Spatiotemporal scales of ecological processes within a space−time correspondence arrangement. *From Wu (2013)*

They are also often used to assign different environmental decision-making processes to different levels of the administrative hierarchy, thus they demonstrate one path of linkage between ecological and human systems.

5.6 MANAGING ECOSYSTEMS AS HIERARCHIES

The messages of hierarchy theory to the management of ecosystems are clear although not always pleasant. On a scientific level, it often requires additional views and work as it requires data that are not always existing. Second, it requires one to focus not only at the focal level but also on at least the two adjacent levels to both sides—upward and downward—of the hierarchy.

This means that ecosystem studies potentially must take place over a wide range of hierarchies and therefore get increasingly complex. In addition, it also has the consequence that ecosystem studies are inherently multidisciplinary as it takes "local" experts at each level to analyze what exactly is going on and what might be the causal mechanism(s) leading to observed ecosystem behavior.

In short, scientists must be strongly focused, but so must managers and policy makers. The overall goal of a responsible and adequate ecosystem management must include almost all levels, which in the end is not an easy task both due to temporal and economical conditions. Meanwhile, an approach founded in hierarchy theory might be able to assist in pointing out proper and relevant target areas both for the management and the production of the underlying understanding of such management as well.

One consequence of the theory is to realize the significant role of constraints: if there is a problem appearing at the focal level (n), then the reasons might be originating in level (n + 1) as well as in (n − 1); thus, both have to be analyzed. Concerning the respective measure for improvement, also both directions might be possible. While a modification in (n − 1) is related to changes in the system's potentials, a measure at the level (n + 1) is directed toward the system of constraints. Therefore, if management is based on strengthening the ecosystem's self-organization processes, a modification of the constraints at (n + 1) gives the focal and lower levels the chances to develop in an orientor-based direction, capable of optimizing several emergent ecosystem properties.

Furthermore, it is essential to realize the correct working scale in management. Fig. 5.7 tries to demonstrate these conditions using eutrophication processes as examples for a hierarchical distinction of the indication and management process. The object of this case study is a nested hierarchy, consisting of an ecosystem, which is part of a landscape, which is part of a watershed, which is part of a whole region. The figures consider some elements of the DPSIR

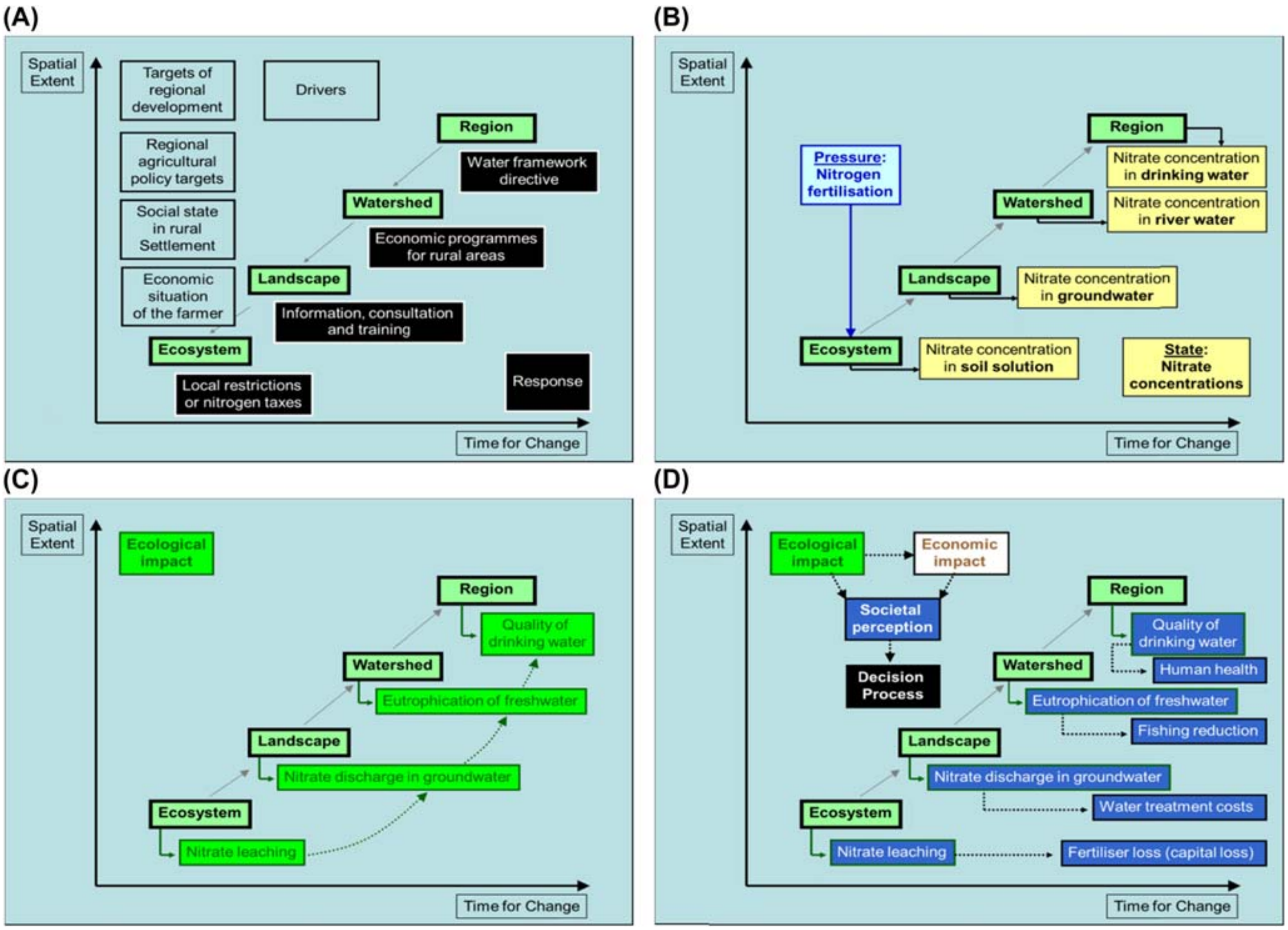

FIGURE 5.7 Hierarchical example of eutrophication processes regarding the DPSIR approach.

management approach (see Burkhard and Müller, 2008). Starting with part (B), we see the pressure (developments in release of substances, physical and biological agents, the use of resources, and the use of land by human activities) of our series, that is nitrogen fertilization, which takes place at the ecosystem level, e.g., of an arable field. The high local nutrient load leads to high nitrogen concentrations in the groundwater (landscape scale), in the river water (catchment scale), and the danger of NO_3 accumulations in the drinking water at the regional scale. This pressure provokes changes in the ecosystem state (changes in quantifiable and qualitative physical, biological, and chemical conditions in a defined area). In the next step (C) certain impacts become visible, which modify the systems' capacities to provide ecosystem services and which therefore will have economic impacts (D). Also, these processes are different at different scales. When these disturbances are realized by society, there will be a responding decision process (A) which will include a change of the drivers (A), the social, demographic, and economic developments in the society and corresponding changes in lifestyles, overall levels of consumption and production patterns as well as motivations for specific land-use strategies. These dynamics can be accompanied by political measures, which also differ from scale to scale. The example shows that implementation of hierarchical views is important when managing for ecosystem conservation in what is considered a "regional and historical context" (Rodzilksy et al., 2001). Furthermore, it becomes obvious that in fact the specific measures are only suitable at different scales. Therefore, the manager has to be aware not only of her or his own situation but also of the detailed scale of the management object.

In order to manage at the scales beyond the ecosystem level, awareness is needed of properties such as self-organization and emergent properties that act together and affecting the properties of the system's resilience (Peterson, 2000). These ecosystem characteristics are strongly dependent on the hierarchical functioning of systems (see Chapter 8), creating a feedback of hierarchy that begets more hierarchy. Several authors ascribe the metastability of ecosystems to the functioning of their internal system of constraints (see e.g., Müller, 1992; Gundersson and Holling, 2002). This means that a strong determination by activities at higher levels will make the system more robust for changes and will increase the system's overall ability for filtering and dampening external disturbances. Therefore, the strength of hierarchical constraints is a basic indicator for stability. Whenever bigger changes appear, the prevailing hierarchy is broken and the system will move to a new scheme of self-organized constraints.

The concept of panarchy may offer an opportunity to deal with the plethora of scales ever present in ecosystem functioning (Gunderson et al., 2017). This point additionally stresses the importance of the precautionary principle to be considered and respected even more when doing planning and management in future. The panarchy approach, occurring in both natural and social systems, has been applied to management of government agencies in Auad et al. (2018).

An hierarchical understanding has been implemented in an attempt to carry out a more holistic way of introducing mitigation and the resilience concept as strategies in the "Canadian boreal biome" (Fenton, 2016). According to this author, management can be done in a mitigation hierarchy in which "impacts on ecosystems are avoided, mitigated, restored, or compensated." Meanwhile, the strategies still need to be fully integrated and merged properly with the hierarchical concept. Another attempt to apply hierarchy, and particularly panarchy, to management was introduced by Auad et al. 2018 when looking at the United States Department of Energy, Bureau of Energy Ocean Management.

Fishery management may be one area where an extended and hierarchical understanding of the ecosystem is highly needed in order to improve ecosystem health in the future. Usually fishery management is carried out at organism, species, or population level (e.g., Apollonio, 2015) that is managing for the regulation and protection at only one level. One thing might be that the exact trophic position of a particular species might not be exactly known—but another is that the fish species in general belong to quite different levels in the trophic chain or rather network (Zacharias and Roff, 2000). Similar investigations and findings have been done on (semi-)terrestrial systems (Palik et al, 2000). Therefore, it is necessary to consider the entire ecosystem of interactions when managing for sustainable fisheries.

All in all, our management efforts for preserving biodiversity in general must be done with a hierarchical perspective in mind. Careful planning that considers both the structure of the food web together with its function is of utmost importance in preserving stable ecosystems (Thompson et al., 2012; Borelli et al., 2015). A management approach that only considers preservation of a single species, even rare, sensitive or keystone ones, may lead to total failure not considering the qualitative perspectives ensured by applying a hierarchic approach. The US Environmental Protection Agency's Endangered Species Act (1973), set a strong precedent for an ecosystem approach in the legal language:

> The purposes of this Act are to provide a means whereby the ecosystems upon which endangered species and threatened species depend may be conserved, to provide a program for the conservation of such endangered species and threatened species. ***ESA; 16 U S C. § 1531 et seq.***

However, implementation of the ecosystem approach takes time, money, patience, and regulatory means that are rarely aligned in the species' favor. Only 54 of the 1661 species listed have recovered to the point of being delisted. It is also important to keep in mind that during this time population growth, and subsequently habitat loss, has continued putting pressure on the health of the species and their ecosystems.

Finally, we might make the remark that recently the traditional features of hierarchical functioning have been broken concerning human—environmental systems. The previously observed strong relation between space and time, events concerning big spatial areas usually are rare and related to slow developments, has been shown in several examples in most ecological systems. But, when we turn to human—environmental systems, it becomes more and more obvious that traditional space—time correlations have been broken. Humans can produce changes so fast that natural systems hardly can follow. The fast traveling behavior, the speed of technical innovations, or the rapid information exchange over large distances via the Internet is forming new conditions for hierarchical structurations. Distances are decreasing and frequencies are increasing in the modern human comprehension of the world; and therefore, new circumstances for hierarchical ordinations must be found. The respective activities must be guided by the perception that we humans are depending on nature and ecosystems, their services, and their integrity. Thus, if we look for Nietzsche's hierarchy of values (see initial quotation of the chapter), then a high valuation of hierarchical performances in ecosystems will be a good basis for argumentation.

CHAPTER

6

Ecosystems Have Directionality

From the way the grass bends, one can know the direction of the wind. ***Chinese Quotation***

All nature is but art unknown to thee;
All chance, direction which thou canst not see;
All discord, harmony not understood;
All partial evil, universal good;
And, spite of pride, in erring reasons spite,
One truth is clear, Whatever IS, is RIGHT. ***Alexander Pope, 1773***

6.1 SINCE THE BEGINNINGS OF ECOLOGY

Ecosystems have directionality! This is an extraordinary statement, although the reader might at first wonder why. After all, one observes directional behavior everywhere: A billiard ball, when struck by another ball, will take off in a prescribed direction. Sunflowers turn their heads to face the sun. Copepods migrate up and down in the water column on a diurnal basis. Yet, despite these obvious examples, scientists have increasingly been trained to regard instances of directionality in nature as having no real basis—epiphenomenal illusions that distract one from an underlying static, isotropic reality.

Before embarking on how ecological direction differs from directionality observed elsewhere, it is worthwhile describing the ecological notion of succession (Odum and Odum, 1959). The classical example in American ecology pertains to successive vegetational communities (Cowles, 1899) and their associated heterotrophs (Shelford, 1913)—research conducted on the shores of Lake Michigan. Both Cowles and Shelford had built upon the work of the Danish botanist, Warming (1909). Prevailing winds blowing against a shore will deposit sand in wavelike fashion. The most recent dunes have emerged closest to the lake itself, while progressively older and higher dunes occur as one proceeds inland. The assumption here, much like the famed ergodic assumption in thermodynamics, is that this spatial series of biotic communities represents the temporal evolution of a single ecosystem. The younger, presumably less mature community consisted of beach grasses and cottonwood. This “sere” was followed by a jack pine forest, a xeric black oak forest, an Oak and hickory moist forest, and the entire progression was thought to “climax” as a Beech-maple forest. You cannot have one without the others. The invertebrate and vertebrate communities were observed to segregate more or less among the vegetational zones, although there was more overlap among the mobile heterotrophs than among the sessile vegetation.

Other examples of succession involve new islands that emerge from the sea, usually as the result of volcanic activity. One particular ecosystem that was followed in detail is the sudden emergence in 1963 of the approximately 2.8 km^2 island, Surtsey, some 33 km south of the large island of Iceland in the North Atlantic. Fig. 6.1 depicts the rise in the number of plant species found on the island. (Other measures of succession on Surtsey will be given below.)

6.2 THE CHALLENGE FROM THERMODYNAMICS

Now one might well ask how the directionality of these ecosystems differs in any qualitative way from, say the billiard ball mentioned in the opening paragraph of this chapter? For one, the direction of the billiard ball is a

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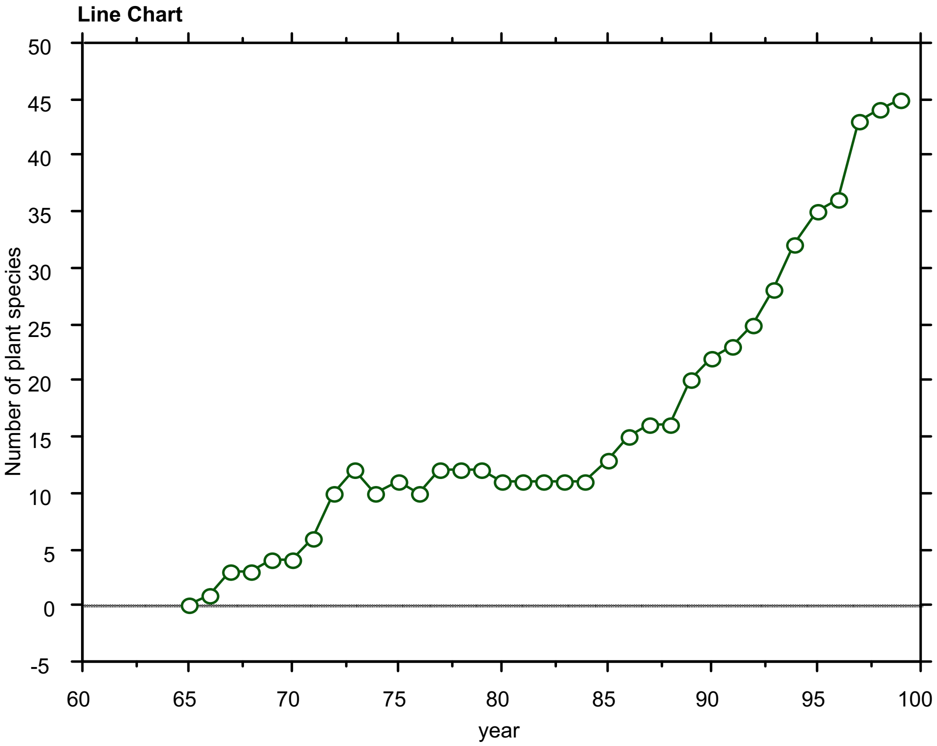

FIGURE 6.1 Increase over time in the number of plant species found on the newly created island of Surtsey.

consequence of the collision with the other ball, the Newtonian law of momentum and the Newtonian-like law of elasticity. The ball itself remains essentially unchanged after the encounter. Furthermore, if the ball is highly elastic, the encounter is considered reversible. That is, if one takes a motion picture of the colliding balls and the movie is shown to a subject with the projector operating in both the forward and reverse modes, the subject is incapable of distinguishing the original take from its reverse. Reversibility is a key attribute of all Newtonian systems, and until the mid-1960s all Newtonian laws were considered strictly reversible. Early in the 20th century, Noether (1918) demonstrated how the property of reversibility was fully equivalent to that of conservation, i.e., all reversible systems are conservative. There is no fundamental change in them, either before or after the event in question.

This pair of fundamental assumptions about how objects behaved set the stage for the first challenge to the Newtonian worldview. In 1820, Carnot (1824) had been observing the performance of early steam engines in pumping water out of mines. He observed how the energy content (caloric) of the steam used to run the engines could never be fully converted into work. Some of it was always lost forever. This meant that the process in question was irreversible. One could not reverse the process, bringing together the work done by the engine with the dispersed heat and create steam of the quality originally used to run the engine. See also the discussion of the second law of thermodynamics in Chapter 2.

But the steam, the engine, and the water were all material things, made up of very small particles, according to the atomic hypothesis that had recently been formulated. Elementary particles should obey Newton's laws, which always gave rise to reversible behaviors. Whence, then, the irreversibility? This was a conundrum that for a while placed the atomic hypothesis in jeopardy. The enigma occupied the best minds in physics over the next half century. How it was "resolved" demonstrates volumes about common attitudes toward scientific belief.

von Boltzmann (1872) considered the elements of what was called an "ideal gas" (i.e., a gas made up of point masses that did not interact with each other) to obey Newton's laws of motion. He then assumed that the distribution of the momenta of the atoms was normally random. This meant that nearby to any configuration of atoms there were always more equivalent distributions (having same mass and momentum) that were more evenly distributed than there were configurations that were less evenly distributed. Any random walk through the distributions would, therefore, be biased in the direction of the most probable distribution (the maximum of the normal distribution). Ergo, without violating conservation of mass or momentum at the microlevel, the system at the macrolevel was biased to move in the direction of the most even distribution.

This was a most elegant *model*, later improved upon by Gibbs (1902). It is worth noting, however, that the resolution was a model that was applicable to nature under an exceedingly narrow set of conditions. Nevertheless, it was accepted as validation of the atomic hypothesis and Newtonian reversibility *everywhere*, and it put an end to the controversy. This rush to consensus was, of course, the very antithesis of what later would be exposited as logical positivism—the notion that laws cannot be verified, only falsified. Laws should be the subject of constant and continual scrutiny; and scientists should always strive to falsify existing laws. But when conservation, reversibility, and atomism were being challenged, the response of the community of scholars was precisely the *opposite*—discussion was terminated on the basis of a single model that pertained to conditions that, in relation to the full set of conditions in the universe, amounted to "a set of measure zero"!

Such inconsistencies notwithstanding, the second law does indeed provide a direction for time and introduces history into science. The second law serves as a very significant constraint on the activities of living systems and imparts an undeniable directionality to biology (Schneider and Sagan, 2005).

6.3 DECONSTRUCTING DIRECTIONALITY?

Events in biology have been somewhat the reverse of those in physics. Whereas, physics began with directionless laws and was confronted with exceptions, biologists had originally thought that phylogeny took a progressive direction over the eons, culminating in the appearance of humankind at the apex of the natural order—the so-called "natural chain of being." Evolutionary biologists, however, have sought to disabuse other biologists of such directional notions (Gould, 1994). At each turn in its history, a biotic system is subject to random, isotropic influences. What looks in retrospect like a progression has been merely the accumulation of the results of chance influences. Complexity simply accrues until such time as a chance catastrophe prunes the collection back to a drastically simpler composition.

We thus encounter a strong bias at work within the community of scientists to deny the existence of bias in nature (a statement which makes sense only because humanity has been postulated to remain outside the realm of the natural). Physicists and (perhaps by virtue of "physics envy") evolutionary theorists appear keen to deny the existence of direction anywhere in the universe, preferring instead a changeless Eleatic worldview. It is against this background that the notion of direction in ecology takes on such importance.

Directionality, in the form of ecological succession, has been a key phenomenon in ecology from its inception (Clements, 1916). By ecological succession is meant "the *orderly* process of community change" (Odum and Odum, 1959) whereby communities replace one another in a given area. Odum and Odum (1959) do not equivocate in saying, "The remarkable thing about ecological succession is that it is directional." In those situations where the process is well known, the community at any given time may be recognized and future changes predicted. That is, succession as a phenomenon appears to be reproducible to a degree.

Of course, it was not long after the ideas of community succession came into play that the opinion arose that its purported direction was illusory. Gleason (1917) portrayed succession in plant communities as random associations of whatever plant species happened to immigrate into the area. Others have pointed out that "seres" of ecological communities almost always differ in terms of the species observed (Cowles, 1899). The ecosystem ecologist takes refuge in the idea that the functional structure nonetheless remains predictable (Sheley, 2002).

The question thus arises as to whether ecological succession is orderly in any sense of the word, and, if so, what are the agencies behind such order? We begin by noting that the directionality of ecosystems is of a different ilk from those mentioned in the opening of this chapter. With regard to all three of those examples, the direction of the system in question was determined by sources *exterior* to the system—by the colliding billiard ball in the first instance, and by the sun as perceived by the sunflower and copepod. It will be argued below, however, that the directionality of an ecosystem derives from an agency active *within* the system itself. Surely, external events do impact the system direction by providing constraints, but any one event is usually incremental in effect. On rare occasions an external event can radically alter the direction and the constitution of the system itself (Prigogine, 1978, Tiezzi , 2006), but this change is every bit as much a consequence of the system configuration as it is of the external event (Ulanowicz, 2009). The direction an ecosystem takes is both internal and constitutional. Most change seen elsewhere is neither.

6.4 AGENCIES IMPARTING DIRECTIONALITY

It remains to identify the agency behind any directionality that ecosystems might exhibit. Our natural inclination is such a search would be to look for agencies that conform to our notions of "lawful" behaviors. But such a scope could be too narrow. It would behoove us to broaden our perspective and attempt to generalize the notion of "law" and consider as well the category of "process." A process resembles a law in that it consists of rule-like behaviors, whereas a law always has a determinate outcome, a process is guided more by its interactions with aleatoric events.

The indeterminacy of such action is perhaps well illustrated by the artificial example of Polya's Urn (Eggenberger and Polya, 1923). Polya's process consists of picking from an urn containing red and blue balls. The process starts with one red ball and one blue ball. The urn is shaken and a ball is drawn at random. If it is a red ball, then the ball is returned to the urn with yet another red ball; if a blue ball is picked, then it likewise is returned with another blue ball. The question then arises whether the ratio of red to blue balls approaches a fixed value. It is rather easy to demonstrate that the law of large number takes over and that after a sufficient number of draws, the ratio changes only within bounds that progressively shrink as the process continues. Say the final ratio is 0.3879175. The second question that arises is whether that ratio is unique? If the urn is emptied and the process repeated, then will the ratio once again converge to 0.3879175? The answer is no. The second time it might converge to 0.81037572. It is rather easy to show in Monte Carlo fashion that the final ratios of many successive runs of Polya's process are uniformly distributed over the interval from 0 to 1.

One sees in Polya's Urn how direction can evolve out of a stochastic background. The key within the process is the feedback that is occurring between the history of draws and the current one. Hence, in looking for the origins of directionality in real systems, we turn to consider feedback within living systems. Feedback, after all, has played a central role in much of what is known as the theory of "self-organization" (e.g., Eigen, 1971; Maturano and Varela, 1980; DeAngelis et al., 1986; Haken, 1988; Kauffman, 1995). Central to control and directionality in cybernetic systems is the concept of the causal loop. A causal loop, or circuit is any concatenation of causal connections whereby the last member of the pathway is a partial cause of the first. Primarily because of the ubiquity of material recycling in ecosystems, causal loops have long been recognized by ecologists (Hutchinson, 1948).

It was the late polymath, Bateson (1972) who observed that "a causal circuit will cause a non-random response to a random event at that position in the circuit at which the random event occurred." But why is this so? To answer this last question, let us confine further discussion to a subset of causal circuits that are called autocatalytic[1] (Ulanowicz, 1997). Henceforth, autocatalysis will be considered any manifestation of a positive feedback loop whereby the direct effect of every link on its downstream neighbor is positive. Without loss of generality, let us focus our attention on a serial, circular conjunction of three processes—A, B, and C (Fig. 6.2). Any increase in A is likely to induce a corresponding increase in B, which in turn elicits an increase in C, and whence back to A.[2]

A didactic example of autocatalysis in ecology is the community that builds around the aquatic macrophyte, *Utricularia* (Ulanowicz, 1995). All members of the genus *Utricularia* are carnivorous plants. Scattered along its feather-like stems and leaves are small bladders, called utricles (Fig. 6.3A). Each utricle has a few hairlike triggers at its terminal end, which, when touched by a feeding zooplankter, opens the end of the bladder, and the animal is sucked into the utricle by a negative osmotic pressure that the plant had maintained inside the bladder. In nature the

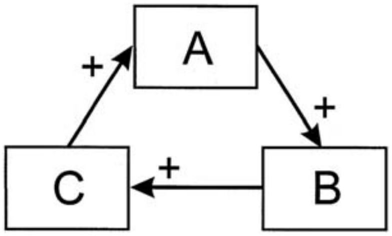

FIGURE 6.2 Simple autocatalytic configuration of three species.

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[1] This focus is not made to the exclusion of other forms of positive feedback, nor is it meant to displace the very necessary role of negative feedback, which play a vital role in the regulation systems processes (Chapter 7).

[2] The emphasis in this chapter is upon positive feedback and especially autocatalysis. It should be mentioned in passing that negative feedback also plays significant roles in complex ecosystem dynamics (Chapter 8), especially as an agency of regulation and control.

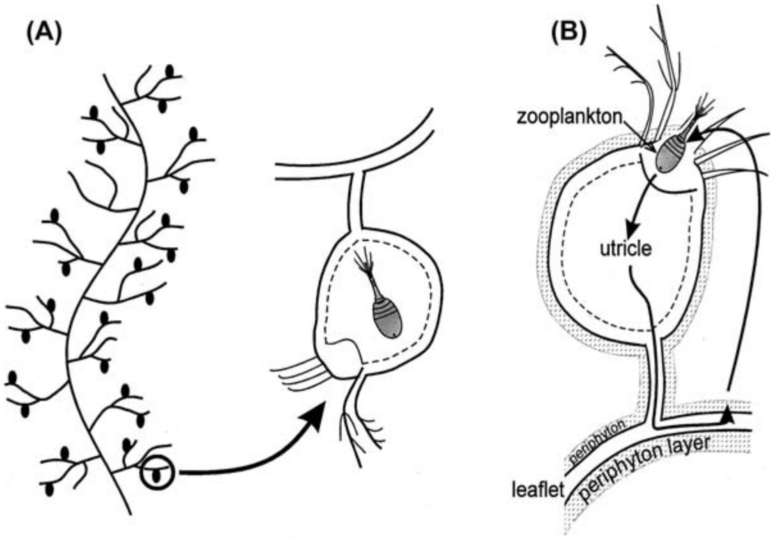

FIGURE 6.3 The *Utricularia* system. (A) View of the macrophyte with detail of a utricle. (B) The three-flow autocatalytic configuration of processes driving the *Utricularia* system.

surface of *Utricularia* plants is always host to a film of algal growth known as periphyton. This periphyton in turn serves as food for any number of species of small zooplankton. The autocatalytic cycle is closed when the *Utricularia* captures and absorbs many of the zooplankton (Fig. 6.3B).

In chemistry, where reactants are simple and fixed, autocatalysis behaves just like any other mechanism. As soon as one must contend with organic macromolecules and their ability to undergo small, incremental alterations, however, the game changes. With ecosystems we are dealing with *open* systems (see Chapter 2), so that whenever the action of any catalyst on its downstream member is affected by contingencies (rather than being obligatory), a number of decidedly nonmechanical behaviors can arise (Ulanowicz, 1997). For the sake of brevity, we discuss only a few:

Perhaps most importantly, autocatalysis is capable of exerting *selection* pressure upon its own, ever-changing, malleable constituents. To see this, one considers a small spontaneous change in process B. If that change either makes B more sensitive to A or a more effective catalyst of C, then the transition will receive enhanced stimulus from A. In the *Utricularia* example, diatoms that have a higher P/B ratio and are more palatable to microheterotrophs would be favored as members of the periphyton community. Conversely, if the change in B makes it either less sensitive to the effects of A or a weaker catalyst of C, then that perturbation will likely receive diminished support from A. That is to say, the response of this causal circuit is not entirely symmetric, and out of this asymmetry emerges a direction. This direction is not imparted or cued by any externality; its action resides wholly internal to the system. As one might expect from a causal circuit, the result is to a degree tautologous—autocatalytic systems respond to random events over time in such a way as to increase the degree of autocatalysis. As alluded to above, such asymmetry has been recognized in physics since the mid-1960s, and it transcends the assumption of reversibility. It should be emphasized that this directionality, by virtue of its internal and transient nature cannot be considered teleological. There is no externally determined or preexisting goal toward which the system strives. Direction arises purely out of immediate response by the internal system to a novel, random event impacting one of the autocatalytic members.

To see how another very important directionality can emerge in living systems, one notes, in particular, that any change in B is likely to involve a change in the amounts of material and energy that are required to sustain process B. As a corollary to selection pressure, we immediately recognize the tendency to reward and support any changes that serve to bring ever more resources into B. Because this circumstance pertains to any and all members of the causal circuit, any autocatalytic cycle becomes the epicenter of a *centripetal* flow of resources toward which as many resources as possible will converge (Fig. 6.4). That is, an autocatalytic loop *defines itself* as the focus of centripetal flows. One sees didactic example of such centripetality in coral reef communities, which by their considerable synergistic activities draw a richness of nutrients out of a desert-like and relatively inactive surrounding sea. Centripetality is obviously related to the more commonly recognized attribute of system growth (Chapter 6). A key feature of living systems is how they selectively uptake and accumulate parts of the environment, thus, driving the biogeochemical cycles and affecting the global stores of mineral and energy resources. The autocatalysis moves the systems to a new

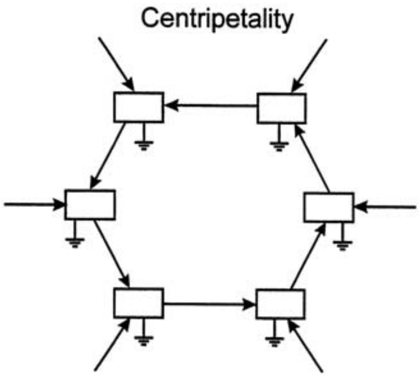

FIGURE 6.4 The centripetality of an autocatalytic system, drawing progressively more resources unto itself.

state that is often novel and more diverse. The system itself gives roles for new entrants into the system (Hordijk and Steele, Cazzolla-Gatti et al., 2018).

6.5 ORIGINS OF EVOLUTIONARY DRIVE

Evolutionary narratives are replete with explicit or implicit references to such actions as "striving" or "struggling," but the origin of such directional behaviors is either not mentioned, or glossed over. Such actions are simply postulated. But with centripetality, we now encounter the roots of such behavior. Suddenly, the system is no longer acting at the full behest of externalities, but it is actively drawing ever more resources unto itself. Russell (1960) called this behavior "chemical imperialism" and identified it as the very crux of evolutionary drive.

Centripetality further guarantees that whenever two or more autocatalytic loops exist in the same system and draw from the same pool of finite resources, *competition* among the foci will necessarily ensue, so that another postulated element of Darwinian action finds its roots in autocatalytic behavior. In particular, whenever two loops share pathway segments in common, the result of this competition is likely to be the exclusion or radical diminution of one of the nonoverlapping sections. For example, should a new element D happen to appear and to connect with A and C in parallel to their connections with B, then if D is more sensitive to A and/or a better catalyst of C, the ensuing dynamics should favor D over B to the extent that B will either fade into the background or disappear altogether (Fig. 6.5). That is, the selection pressure and centripetality generated by complex autocatalysis (a macroscopic ensemble) is capable of influencing the replacement of its own elements. Perhaps the instances that spring most quickly to mind here involve the evolution of obligate mutualistic pollinators, such as yuccas (Yucca) and yucca moths (*Tegeticula, Parategeticula*) (Riley, 1892), which eventually displace other pollinators.

It is well worth mentioning at this point that the random events with which an autocatalytic circuit can interact are by no means restricted to garden-variety perturbations. By the latter are meant simple events that are generic and repeatable. In Chapter 3, it was pointed out how random events can have a complex nature as well and how many such events can be entirely unique for all time. For example, if a reader were to stand on the balcony overlooking Grand Central Station in New York City and photograph a 10 × 10 m space below, she might count some 90 individuals in the picture. The combinatorics involved guarantee that it is beyond the realm of physical reality that repeating the action at a subsequent time would capture the same 90 individuals in the frame—the habits and routines of those concerned notwithstanding (Elsasser, 1969). Nor are such unique events in any way rare. Even the

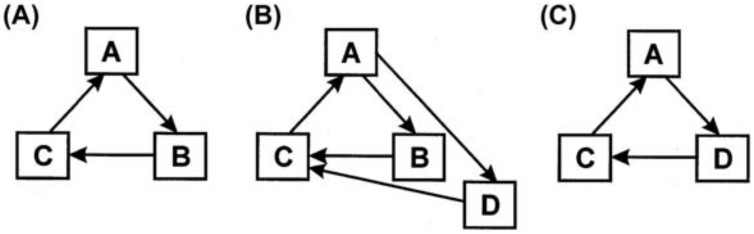

FIGURE 6.5 Autocatalytic action causing the replacement of element B by a more effective one, D. The evolution of the network of three elements A, B, and C towards a new similar network A, B, and D is shown. As D enters the network in completion with compartment B and eventually replaces it as this autocatalytic cycle turns out to be more efficient than the previous one.

simplest of ecosystems contains more than 90 distinguishable individual organisms. Unique events are occurring all the time, everywhere, and at all levels of the scalar hierarchy. Furthermore, the above-cited selection by autocatalytic circuits is not constrained to act only on simple random events. They can select from among complex, entirely novel events as well.

This ability of an autocatalytic circuit to sift from among the welter of complex events that can impinge upon it opens the door fully to emergence. For in a Newtonian system, any chance perturbation would lead to the collapse of the system. With Darwin systems, causality was opened up to chance occurrences, but that notion failed to take hold for a long while after Darwin's time, for his ideas had fallen into the shadows by the end of his century (Depew and Weber, 1995). It was not until Fisher and Wright during the late 1920s had rehabilitated Darwin through what is commonly known as "The Grand Synthesis" that evolution began to eclipse the developmentalism that had prevailed in biology during the previous decades. The Grand Synthesis bore marked resemblance to the reconciliation effected in the physical sciences by Boltzmann and Gibbs in that Fisher applied almost the identical mathematics that had been used by Gibbs in describing an ideal gas to the latter's treatment of noninteracting genetic elements. Furthermore, the cardinal effect of the synthesis was similar to the success of Gibbs—it reestablished a degree of predictability under a very narrow set of circumstances.

With the recognition of complex chance events, however, absolute predictability and determinism had to be abandoned. There is simply no way to quantify the probability of an entirely unique event (Tiezzi In review). Events must recur at least several times before a probability can be estimated. As compensation for the loss of perfect predictability, emergence no longer need take on the guise of an enigma. Complex and radically chance events are continuously impinging upon autocatalytic systems. The overwhelming majority has no effect whatsoever upon the system (which remains *indifferent* to them). A small number impacts the system negatively, and the system must reconfigure itself in countering the effect of the disturbances. An extremely small fraction of the radical events may actually resonate with the autocatalysis and shift it into an entirely new mode of behavior, which can be said to have emerged spontaneously.[3]

Forrester (1987), for example, describes major changes in system dynamics as "shifting loop dominance," by which he means a sudden shift from control by one feedback loop to dominance by another. The new loop could have been present in the background prior to the shift, or it could be the result of new elements entering or arising within the system to complete a new circuit. Often loops can recover from single insults along their circuit, but multiple impacts to several participants, as might occur with complex chance, are more likely to shift control to some other pathway.

One concludes that autocatalytic configurations of flows are not only characteristic of life, they are central to it. As Popper (1990) once rhapsodically proclaimed, "Heraclitus was right: We are not things, but flames. Or a little more prosaically, we are, like all cells, processes of metabolism; nets of chemical pathways." The central agency of networks of processes is illustrated nicely with Tiezzi's (2006) comparison of the live and dead deer (just moments after death). The mass of the deer remains the same, as does its form, chemical constitution, energy, and genomic configuration. What the live deer had that the dead deer does not possess is its configuration of metabolic and neuronal processes.

6.6 QUANTIFYING DIRECTIONALITY IN ECOSYSTEMS

It is one thing to describe the workings of autocatalytic selection verbally, but science demands at least an effort at describing how one might go about quantifying and measuring key concepts. At the outset of such an attempt, we should emphasize again the nature of the directionality with which we are dealing. The directionality associated with autocatalysis does not appear in either physical space or, for that matter, in phase space. It is rather more like the directionality associated with time. There direction, or sense, is indicated by changes in a system-level index—the system's entropy. Increasing entropy identifies the direction of increasing time.

The hypothesis in question is that augmented autocatalytic selection and centripetality are the agencies behind increasing self-organization. Here, we note that as autocatalytic configurations displace more scattered interactions, material and energy become increasingly constrained to follow only those pathways that result in greater

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[3] This emergence differs from Prigogine's "order through fluctuations" scenario in that the system is not constrained to toggle into one of two predetermined states. Rather, complex chance can carry a system into entirely new modes of behavior (Tiezzi, 2006). The only criterion for persistence is that the new state be more effective, autocatalytically speaking, than the original.

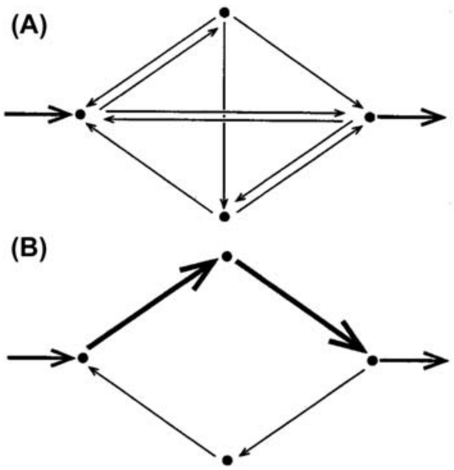

FIGURE 6.6 Cartoon showing the generic effects of autocatalysis. (A) Inchoate system. (B) Same system after autocatalytic loop has developed.

autocatalytic activities. This tendency is depicted in cartoon fashion in Fig. 6.6. At the top is an arbitrary system of four components with an inchoate set of connections between them. In the lower figure, one particular autocatalytic feedback loop has come to dominate the system, resulting in fewer effective flows and greater overall activity (as indicated by the thicker surviving arrows). Thus, we conclude that quantifying the degree of constraint in an ecosystem must reflect these changes in both the magnitude and intensity of autocatalytic activities. Looked at in obverse fashion, ecosystems with high autocatalytic constraints will offer fewer choices of pathways along which resources can flow.

The appearance of the word "choice" in the last sentence suggests that information theory might be of some help in quantifying the results of greater autocatalysis. And, so it is. Box 6.1 details the derivation of a measure called the *System Ascendency*, which quantifies both the total activity of the system as well as the degree of overall constraint extant in the system network. A change in the system pattern as represented in Fig. 6.6 will result in a higher value of the ascendency.

BOX 6.1

ASCENDENCY, A MEASURE OF ORGANIZATION

In order to quantify the degree of constraint, we begin by denoting the transfer of material or energy from prey (or donor) i to predator (or receptor) j as T_{ij}, where i and j range over all members of a system with n elements. The total activity of the system then can be measured simply as the sum of all system processes, $\mathrm{TST} = \sum_{i,j=1}^{n+2} T_{ij}$, or what is called the "total system throughput" (TST). With a greater intensity of autocatalysis, we expect the overall level of system activity to increase, so that T appears to be an appropriate measure. For example, growth in economic communities is reckoned by any increase in gross domestic product, an index closely related to the TST.

In Fig. B6.1 is depicted the energy exchanges (kcal m^{-2} y^{-1}) among the five major compartments of the Cone Spring ecosystem (Tilly, 1968). The TST of Cone Spring is simply the sum of all the arrows appearing in the diagram. Systematically, this is calculated as follows:

$$\begin{aligned}
\mathrm{TST} &= \sum_{i,j} T_{ij} \\
&= T_{01} + T_{02} + T_{12} + T_{16} + T_{17} + T_{23} + T_{24} \\
&\quad + T_{26} + T_{27} + T_{32} + T_{34} + T_{36} + T_{37} + T_{42} \\
&\quad + T_{45} + T_{47} + T_{52} + T_{57} \\
&= 11184 + 635 + 8881 + 300 + 2003 + 5205 \\
&\quad + 2309 + 860 + 3109 + 1600 + 75 + 255 \\
&\quad + 3275 + 200 + 370 + 1814 + 167 \\
&\quad + 203 \\
&= 42{,}445 \text{ kcal m}^{-2}\text{ y}^{-1},
\end{aligned}$$

BOX 6.1 (*cont'd*)

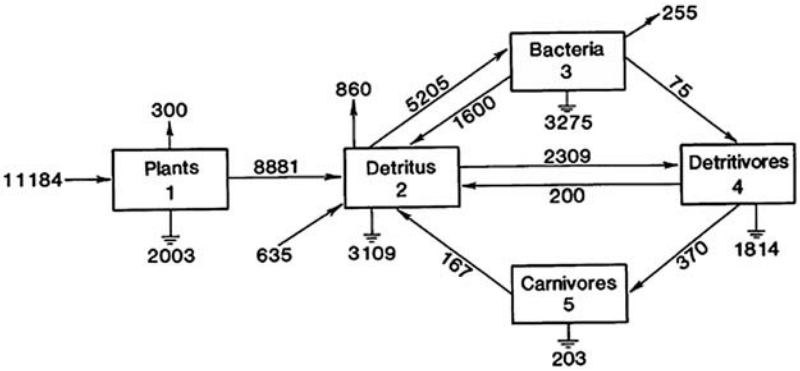

FIGURE B6.1 Schematic of the network of energy exchanges (kcal m^{-2} y^{-1}) in the Cone Spring ecosystem (Tilly, 1968). Arrows not originating from a box represent inputs from outside the system. Arrows not terminating in a compartment represent exports of useable energy out of the system. Ground symbols represent dissipations.

where the subscript 0 represents the external environment as a source, 6 denotes the external environment as a receiver of useful exports, and 7 signifies the external environment as a sink for dissipation.

Again, the increasing constraints that autocatalysis imposes on the system channel flows ever more narrowly along fewer, but more efficient pathways—"efficient" here meaning those pathways that most effectively contribute to the autocatalytic process. Another way of looking such "pruning" is to consider that constraints cause certain flow events to occur more frequently than others. Following the lead offered by information theory (Abramson, 1963; Ulanowicz and Norden, 1990), we estimate the joint probability that a quantum of medium is *constrained* both to leave i and enter j by the quotient T_{ij}/T. We then note that the *unconstrained* probability that a quantum has left i can be acquired from the joint probability merely by summing the joint probability over all possible destinations. The estimator of this unconstrained probability thus becomes $\sum_q T_{iq}/T$. Similarly, the unconstrained probability that a quantum enters j becomes $\sum_k T_{kj}/T$. Finally, we remark how the probability that the quantum could make its way by pure chance from i to j, *without* the action of any *constraint*, would vary jointly as the product of the latter two frequencies, or $\sum_q T_{iq}\sum_k T_{kj}/T^2$. This last probability obviously is not equal to the constrained joint probability, T_{ij}/T.

Information theory uses as its starting point a measure of the rareness of an event, first defined by Boltzmann (1872) as ($-k$ log P), where P is the probability ($0 \le P \le 1$) of the given event happening and k is a scalar constant that imparts dimensions to the measure. One notices that for rare events ($P \approx 0$), this measure is very large and for very common events ($P \approx 1$), it is diminishingly small. For example, if $P = .0137$, the rareness would be 6.19 k-bits, whereas if $P = .9781$, it would be only 0.032 k-bits.

Because constraint usually acts to make things happen more frequently in a particular way (e.g., flow along certain pathways), one expects that, on average, an unconstrained probability would be rarer than a corresponding constrained event. The rarer (unconstrained) circumstance that a quantum leaves i and accidently makes its way to j can be quantified by applying the Boltzmann formula to the joint probability defined above, i.e., $-k \log\left(\sum_k T_{kj}\sum_q T_{iq}/T^2\right)$, and the correspondingly less rare condition that the quantum is constrained both to leave i and enter j becomes $-k$ $\log(T_{ij}/T)$. Subtracting the latter from the former and combining the logarithms yields a measure of the hidden constraints that channel the flow from i to j as $k \log\left(T_{ij}T \middle/ \sum_k T_{kj}\sum_q T_{iq}\right)$.

Finally, to estimate the average constraint at work in the system as a whole, one weights each individual constraint by the joint probability of constrained flow

Continued

BOX 6.1 (*cont'd*)

from i to j and sums over all combinations of i and j. That is,

$$\mathrm{AMC} = k\sum_{i,j}\left(\frac{T_{ij}}{T}\right)\log\left(\frac{T_{ij}T}{\sum_k T_{kj}\sum_q T_{iq}}\right),$$

where AMC is the "average mutual constraint" known in information theory as the average mutual information (Rutledge et al., 1976).

To illustrate how an increase in AMC actually tracks the "pruning" process, the reader is referred to the three hypothetical configurations in Fig. B6.2. In configuration (a) where medium from any one compartment will next flow is maximally indeterminate. AMC is identically zero. The possibilities in network (b) are somewhat more constrained. Flow exiting any compartment can proceed to only two other compartments, and the AMC rises accordingly. Finally, flow in schema (c) is maximally constrained, and the AMC assumes its maximal value for a network of dimension 4.

One notes in the formula for AMC that the scalar constant, k, has been retained. We recall that although autocatalysis is a unitary process, one can discern two separate effects: (1) an extensive effect whereby the activity, T, of the system increases and (2) an intensive aspect whereby constraint is growing. We can readily unify these two aspects into one measure simply by making the scalar constant k represent the level of system activity, T. That is we set $k = T$, and we name the resulting product the system *ascendency*, A, where

$$A = \sum_{i,j} T_{ij}\log\left(\frac{T_{ij}T}{\sum_k T_{kj}\sum_q T_{iq}}\right).$$

Referring again to the Cone Spring ecosystem network in Fig. B6.1, we notice that each flow in the diagram generates exactly one and only one term in the indicated sums. Hence, we see that the ascendency consists of the 18 terms:

$$\begin{aligned}
A = {} & T_{01}\log\left(\frac{T_{01}T}{\sum_k T_{k1}\sum_q T_{0q}}\right) \\
& + T_{02}\log\left(\frac{T_{02}T}{\sum_k T_{k2}\sum_q T_{0q}}\right) + \ldots + T_{57}\log\left(\frac{T_{57}T}{\sum_k T_{k7}\sum_q T_{5q}}\right). \\
& = 20629 - 1481 + 13796 - 94 - 907 + 9817 + 4249 \\
& \quad + 1004 + 446 + 295 - 147 + 142 + 4454 - 338 + 1537 \\
& \quad + 2965 + 123 + 236 \\
& = 56{,}725\ \mathrm{kcal} - \mathrm{bits}\ \mathrm{m}^{-2}\mathrm{y}^{-1}
\end{aligned}$$

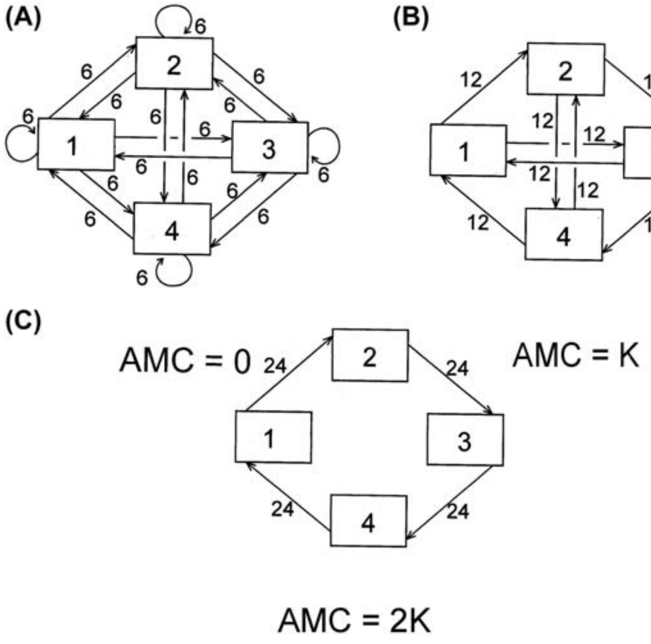

FIGURE B6.2 Three configurations of processes illustrating how autocatalytic "pruning" serves to increase overall system constraint. (A) A maximally indeterminate four-component system with 96 units of flow. (B) The system in (A) after constraints have arisen that channel flow to only two other compartments. (C) The maximally constrained system with each compartment obligated to support only one other component.

BOX 6.1 (*cont'd*)

While ascendency measures the degree to which the system possesses inherent constraints, we wish also to have a measure of the degree of flexibility that remains in the system. To assess the degrees of freedom, we first define a measure of the full diversity of flows in the system. To calculate the full diversity, we apply the Boltzmann formula to the joint probability of flow from i to j, T_{ij}/T, and calculate the average value of that logarithm. The result is the familiar Shannon formula,

$$H = -\sum_{i,j}\left(\frac{T_{ij}}{T}\right)\log\left(\frac{T_{ij}}{T}\right),$$

where H is the diversity of flows. Scaling H in the same way we scaled A, i.e., multiplying H by T, yields the system development capacity, C, as

$$C = -\sum_{i,j} T_{ij}\log\left(\frac{T_{ij}}{T}\right).$$

Now, it can readily be proved that $C \geq A \geq 0$, so that the residual, $(C - A) \geq 0$, as well. Subtracting A from C and algebraically reducing the result yields the residual, Φ, which we call the systems "overhead" as

$$\Phi = C - A = -\sum_{i,j} T_{ij}\log\left(\frac{T_{ij}^2}{\sum_k T_{kj}\sum_q T_{iq}}\right).$$

The overhead gauges the degree of flexibility remaining in the system.

Just as we substituted the values of the Cone Spring flows into the equation for ascendency, we may similarly substitute into this equation for overhead to yield a value of 79,139 kcal-bits $\mathrm{m}^{-2}\,\mathrm{y}^{-1}$. Similarly, substitution into the formula for C yields a value of 135,864 kcal-bits $\mathrm{m}^{-2}\,\mathrm{y}^{-1}$, demonstrating that the ascendency and the overhead sum exactly to yield the capacity.

In his seminal paper, "The strategy of ecosystem development," Odum (1969) identified 24 attributes that characterize more mature ecosystems, i.e., that indicate the direction of ecological succession. These can be grouped into categories labeled species richness, dietary specificity, recycling, and containment. All other things being equal, a rise in any of these four attributes also serves to augment the system ascendency (Ulanowicz, 1986). One proposal at the time was that "in the absence of major perturbations, ecosystems have a propensity to increase in ascendency." While this tendency is true during early stages of growth and development, further research (Ulanowicz, 2009) has shown that ecosystems have a dual nature exemplified by a trade-off between ascendency and redundancy, as described further below.

The ecologist reading this book is likely to have a healthy appreciation for those elements in nature that do not resemble tightly constrained behavior, as one finds with autocatalysis. In fact, Chapter 3 was devoted in large measure to describing the existence and role of aleatoric events and ontic openness. Hence, increasing ascendency is only half of our dynamical story. Ascendency accounts for how efficiently and coherently the system processes medium. Using the same mathematics as employed above, however, it is also shown in Box 6.1 how one can compute as well an index called the system overhead, Φ, that is complementary to the ascendency and captures how much flexibility the system retains (Ulanowicz and Norden, 1990).

The flexibility quantified by overhead is manifested as the inefficiencies, incoherencies, and functional redundancies present in the system. Although these latter properties may encumber overall system performance at processing medium, we saw in Chapter 3 how they become absolutely essential to system survival whenever the system incurs a novel perturbation. At such time, the overhead comes to represent the repertoire of potential tactics from which the system can draw to adapt to the new circumstances. Without sufficient overhead, a system is unable to create an effective response to the exigencies of its environment. The configurations we observe in nature, therefore, appear to be the results of a dynamical tension between two antagonistic tendencies (ascendency vs. overhead, Ulanowicz, 2009). The ecosystem needs this tension in order to persist. Should either direction in the transaction atrophy, the system will become fragile either to external perturbations (low overhead) or internal disorder (low ascendency). System fragility is discussed further in Chapter 8.

One disadvantage of ascendency as an index of directionality is that its calculation requires a large amount of data. Currently, there are few examples of networks accompanying a series of ecological stages. One of the earliest examples for which data are available is a comparison of two tidal marsh communities, one of which was perturbed by a 6°C rise in temperature caused by thermal effluent from a nearby nuclear power plant, and the other of which remained unimpacted (Homer et al., 1976). Under the assumption that perturbation regresses an ecosystem to an earlier stage, one would expect the unimpacted system to be more "mature" and exhibit a higher ascendency than the heated system.

Homer et al. parsed the marsh gut ecosystem into 17 compartments. They estimated the biomass in each taxon in mgC m^{-2} and the flows between taxa in mgC m^{-2} d^{-1}. The total system throughput (T) in the control ecosystem was estimated to be 22,420 mgC m^{-2} d^{-1}, and that in the impacted system as 18,050 mgC m^{-2} d^{-1} (Ulanowicz, 1986). How much of the decrease could be ascribed to diminution of autocatalytic activities could not be assessed, suffice it to say that the change was in the expected direction. The ascendency in the heated system fell to 22,433 mgC-bits m^{-2} d^{-1} from a value of 28,337 mgC-bits m^{-2} d^{-1} for the control. The preponderance of the drop could be ascribed to the fall in *T*, as the corresponding average mutual constraint (AMC) fell by only 0.3%.

6.7 DEMYSTIFYING DARWIN

One possible way around the copious data required to calculate the ascendency might be to search for an indirect measure of the effect of autocatalysis. Along those lines, Jørgensen and Mejer (1977) suggested that the directionality in ecosystem succession might be gauged by the amount of exergy stored among the components of the ecosystem. Exergy being the net amount of total energy that can be converted directly into work. More to come in Chapter 7. The working hypothesis is that ecosystems accumulate more stored exergy as they mature. Exergy can be estimated once one knows the biomass densities of the various species, the chemical potentials of components that make up those species and the genetic complexity of those species (Jørgensen et al., 2005, see also Chapter 6). In Fig. 6.7, one sees that the stored ecological exergy among the biota of Surtsey Island began to increase markedly after about 1985.

It is perhaps worthwhile at this juncture to recapitulate what has been done: First, we have shifted our focus in ecosystem dynamics away from the normal (symmetrical) field equations of physics and concentrated instead upon the origins of asymmetry in any system—the boundary constraints. We then noted how biotic entities often serve as the origins of such constraint upon other biota, so that the kernel of ecodynamics is revealed to be the mutual (self-entailing) constraints that occur within the ecosystem itself. We then identified a palpable and measurable entity (the network of material—energy exchanges) upon which this myriad of mostly hidden constraints writes its signature. Finally, we described a calculus that could be applied to the network to quantify the effects of autocatalytic selection. Hence, by following changes in the ascendency and overhead of an ecosystem, we are focusing squarely upon that which makes ecodynamics fundamentally different from classical dynamics (Ulanowicz, 2004a,b).

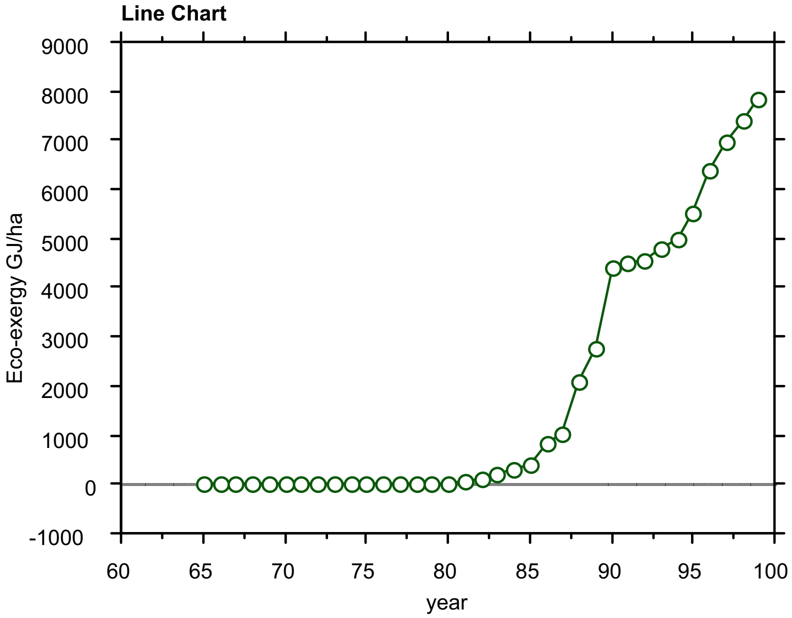

FIGURE 6.7 Estimated stored exergy among the biota inhabiting Surtsey Island.

The dynamical roots of much of Darwinian narrative having been demystified by the directionality inherent in autocatalysis, it is perhaps a bit anticlimatic to note that several other behaviors observed among developing ecosystems also can trace their origins to autocatalysis and its attendant centripetality. Jørgensen and Mejer (1977), as mentioned above, have concluded that ecosystems always develop in the direction of increasing the amount of exergy stored in the system. Maximal exergy storage has proved a useful tool with which to estimate unknown parameters and rates (Jørgensen, 1992; see also growth and development forms in Chapter 7). Schneider and Kay (1994) hypothesize how systems develop so as to degrade available exergy gradients at the fastest rate possible. This is, however, only correct for the first growth form, growth of biomass because more biomass needs more exergy for respiration to maintain the biomass far from thermodynamic equilibrium. For further details, see Chapter 7. Third, the inputs of ecosystems engender manifold system circulations among the full community—a process called network aggradation (Fath and Patten, 2001). All three behaviors can be traced to autocatalysis and its attendant centripetality (Ulanowicz et al., 2006).

It should be noted in passing how autocatalytic selection pressure is exerted in top-down fashion—contingent action by the macroscopic ensemble upon its constituent elements. Furthermore, centripetality is best identified as an agency acting *at* the focal level. Both of these modes of action violate the classical Newtonian stricture called closure, which permits only mechanical actions at smaller levels to elicit changes at higher scales. As noted above, complex behaviors, including directionality, can be more than the ramification of simple events occurring at smaller scales.

Finally, it is worthwhile to note how autocatalytic selection can act to stabilize and regularize behaviors across the hierarchy of scales. Under the Newtonian worldview, all laws are considered to be applicable universally, so that a chance happening anywhere rarely would ramify up and down the hierarchy without attenuation, causing untold destruction. Under the countervailing assumption of ontic openness, however, the effects of noise at one level are usually subject to autocatalytic selection at higher levels and to energetic culling at lower levels. As a result, nature as a whole takes on habits (Hoffmeyer, 1993) and exhibits regularities; but in place of the universal effectiveness of all natural laws, we discern instead a *granularity* inherent in the real world. That is, models of events at any one scale can explain matters at another scale only in inverse proportion to the remoteness between them. For example, one would not expect to find any connection between quantum phenomena and gravitation, given that the two phenomena are separated by some 42 orders of magnitude, although physicists have searched ardently, but in vain, to join the two. Obversely, the domain within which irregularities and perturbations can damage a system is usually circumscribed. Chance need not unravel a system. One sees demonstrations of systems "healing" in the higher organisms, and even in large-scale organic systems such as the global ecosystem (Lovelock, 1979).

6.8 DIRECTIONALITY IN EVOLUTION?

With the cybernetic and thermodynamic narrative of ecosystem development (the new ecology) now before us, it is perhaps useful to revisit the question of whether the process of biotic evolution might exhibit any form of directionality? Perhaps an unequivocal response is premature, suffice it here to compare the differences in the dynamics of ontogeny, ecosystem development, and evolution. With ontogenetic development, there is no denying the directionality evident in the developing organism. Convention holds that such direction is "programmed" in the genomic material, and no one is going to deny the degree of correspondence between genome and phenome. The question remains, however, as to where does the agency behind such direction reside? It is awkward, to say the least, to treat the genome as some sort of homunculus that directs the development process. Genomic material such as DNA is unlikely to have evolved by random assembly, and outside its network of enzymatic and proteomic reactions it can do nothing of interest (Kauffman, 1993). Its role in ontogeny is probably best described as that of material cause, sensu Aristotle—it is materially necessary, but passive with respect to more efficient (again, sensu Aristotle) agencies that actively read and carry out the anabolic processes. As regards those processes, they form a network that indubitably contains autocatalytic pathways, each with its accompanying directions.

The entire scenario of ontogeny is rather constrained, and noise plays a distinct secondary role. In contrast, the role of genomes is not as prominent in the development of ecosystems (Stent, 1981). While some hysteresis is required of the participating species, the central agencies that provide directions (as argued above) are the autocatalytic loops among the species. The constraints among the species are nowhere near as tight as at the ontogenetic level, and noise plays a much larger role in the direction that a system takes over time.

Evolutionary patterns are not as stereotypical as those in ecological succession. What happens before some cataclysm can be very different from what transpires after the disaster. So evolutionary theorists are probably correct in pointing to random events as playing the larger role over the long run. It appears premature, however, to rule out directional processes altogether. Many species and their genomes survive catastrophes, as do entire autocatalytic ensembles of species at the level of the ecosystem. They provide a degree of history that helps to direct the course of evolution until the next upheaval.

This dynamic is already familiar to us from the workings of Polya's Urn, which we considered earlier. In fact, a reasonable simile would be to consider what might happen if Polya's Urn were upset after some 1000 draws and only a random subset of say 15 balls could be recovered and put back into the Urn to continue the process. Although the subsequent evolution of the ratio of red to blue balls might not converge very closely to what it was before the spill, some remnants of the history would likely keep the ratio from making an extreme jump. Suppose, for example, that before the spill the ratio had converged rather tightly to 0.739852, and that after the accident 10 red balls and 5 blue balls were recovered. It is exceedingly unlikely that the continuing process would converge to, say 0.25835.

And, so it may be on the evolutionary theater. Not all directions established by ecosystems during one era are necessarily destroyed by a catastrophe that initiates the next. Surviving directions are key to the evolutionary play during the next interval. Thermodynamic and other physical directions notwithstanding, anyone who argues that evolution involves only chance and no directionality is making an ideological statement and not a reasoned conjecture because ecosystem have directionality.

6.9 SUMMARY

Ecology, from its very inception, has been concerned with temporal direction. Ecological communities are perforce open systems and thus are subject to the imperatives of the second law, but there is yet another, internal drive within ecosystems, efforts by evolutionary theorists to deny directionality notwithstanding. Ecosystem dynamics are rooted in configurations of autocatalytic processes, which respond to random inputs in a nonrandom manner. Autocatalytic processes build upon themselves, and in the process give rise to a centripetal pull of energy and resources into the community. Such centripetality is central to the very notion of life and is more basic than even competition, upon which conventional evolutionary theory is built. Configurations of processes can select from among complex chance events, any of which can exhibit its own, accidental directionality. Ensuing directionality can be quantified as an increase in an information theoretic measure called *ascendency*. This directionality opposes the tendency of the second law to disorder systems, but healthy ecosystems need a modicum of *both* trends—efficiency and redundancy—in order to persist. The resulting dynamic resembles that of a natural dialectic. Finally, although evolution over the longer span might appear adirectional, selection in the nearer ecological time span always provides the ecosystem with an inherent direction that is an obligate element in a complete description of any particular evolutionary scenario.

CHAPTER

7

Ecosystems Have Complex Dynamics—Growth and Development

Newton's Laws explain how an apple falls to the ground,
Ecological principles explain how an apple got above the ground in the first place.

PREAMBLE

The story of Sir Isaac Newton sitting under an apple tree is a well-known story in science. He intuited that the apple that fell on his head was propelled by the force of gravity, which acting on all objects at all times can also explain the motion of planetary bodies falling, but never landing, through space and time. This is a story of irreversible energy degradation, the utilization of a thermodynamic gradient (height above ground) to do work on the surface through impact. The usefulness of that insight played out over centuries of scientific advancement. However, the flipside of the scenario, of how the apple found itself in a position with gravitational potential, was not so thoroughly investigated or understood. This story is one of gradient formation and how ecological systems are able to use energy flows to create structure and organization. In this case, the tree, through its own biochemical processes, worked against the gravitational forces to raise a trunk, and branches, and leaves, and the accompanying flowers and fruits, several meters above the ground (the local equilibrium), which furthermore was pollinated by flying insects also using ecological principles to work against gradients. This is one example of why we refer to ecological systems as operating at "far from equilibrium." This chapter explores some of those natural and lawful processes that move the system toward organized complexity and greater dissipative gradients.

7.1 VARIABILITY IN LIFE CONDITIONS

All known life on earth resides in the thin layer enveloping the globe known as the ecosphere. This region extends from sea level to about 10 kilometers into the ocean depths and approximately the same distance up into the atmosphere. It is so thin that if an apple were enlarged to the size of the earth, then the ecosphere would be thinner than the peel. Yet a vast and complex biodiversity has arisen in this region. Furthermore, the ecosphere acts as integrator of abiotic factors on the planet, accumulating in disproportionate quantities particular elements favored by the biosphere (Table 7.1). In particular, note that carbon is not readily abundant in the abiotic spheres yet is highly concentrated in the biosphere, where nitrogen, silicon, and aluminum, while largely available, are mostly unincorporated.

However, even in this limited domain the conditions for living organisms may vary enormously in time and space.

The climatic conditions are as follows:

1) The temperature can vary from about −70 to about 55 centigrade.
2) The wind speed can vary from 0 km/h to several hundred km/h
3) The humidity may vary from almost 0% to 100%
4) The precipitation from a few mm in average per year to several m/y which may or may not be seasonally aligned
5) Annual variation in day length according to longitude
6) Unpredictable extreme events such as tornadoes, hurricanes, earthquakes, tsunamis, and volcanoes

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TABLE 7.1 Percent Composition Spheres for the First Five Elements.

Lithosphere		Atmosphere		Hydrosphere		Biosphere	
Oxygen	62.5	Nitrogen	78.3	Hydrogen	65.4	Hydrogen	49.8
Silicon	21.22	Oxygen	21.0	Oxygen	33.0	Oxygen	24.9
Aluminum	6.47	Argon	0.93	Chloride	0.33	Carbon	24.9
Hydrogen	2.92	Carbon	0.03	Sodium	0.28	Nitrogen	0.27
Sodium	2.64	Neon	0.002	Magnesium	0.03	Calcium	0.073

The physical—chemical environmental conditions are as follows:

1) Nutrient concentrations (C, P, N, S, Si, etc.)
2) Salt concentrations (it is important both for terrestrial and aquatic ecosystems)
3) Presence or absence of toxic compounds, whether they are natural or anthropogenic in origin
4) Rate of currents in aquatic ecosystems and hydraulic conductivity for soil
5) Space requirements
6) The solar constant, on average 1388 Watt per square meter

The biological conditions are as follows:

1) The concentrations of food for herbivorous, carnivorous, and omnivorous organisms
2) The density of predators
3) The density of competitors for the resources (food, space, etc.)
4) The concentrations of pollinators, symbionts, and mutualists
5) The density of decomposers

The human impact on natural ecosystems today. The remarkable interplay between biotic features and the environmental context adds to this complexity.

The list of factors determining the life conditions is much longer—we have only mentioned the most important factors. Yet, in spite of this great variety, life has evolved and adapted to occupy almost all reaches of the planet.

In addition to these contextual conditions, the ecosystems have history or path dependency, meaning that the initial conditions determine the possibilities of development. If we modestly assume that 100 factors are defining the life conditions and each of these 100 factors may be on 100 different levels, then 10^{200} different life conditions are possible, which can be compared with the number of elementary particle in the Universe 10^{81} (see also Chapter 3). The confluence of path dependency and an astronomical number of combinations affirms that the ecosphere could not experience the entire range of possible states, otherwise known as nonergodicity. Furthermore, its irreversibility ensures that it cannot track back to other possible configurations. Time's arrow is unidirectional. In addition to these combinations, the formation of ecological networks means that the number of indirect effects are magnitudes higher than the direct ones and they are not negligible; on the contrary, they are often more significant than the direct ones, as discussed in Chapter 4.

What is the result of this enormous variability in the natural life conditions? We have found about 0.5×10^7 species on earth and it is presumed that the number of species is double or 10^7. They have developed all types of mechanisms to live under the most varied life conditions including ones at the margin of their physiological limits. They have developed defense mechanisms. For example, some plants are toxic to avoid grazing, others have thorns, etc. Animals have developed horns, camouflage patterns, well-developed auditory senses, fast escaping rates, etc. They have furthermore developed integration mechanisms, fitting into their local web of life, often complementing and creating their environmental niche. The multiplicity of life forms is inconceivable.

The number of species may be 10^7, but living organisms are all different. An ecosystem has normally from 10^{15} to 10^{20} individual organisms that are all different, which, although is a lot, makes ecosystems middle number systems. This means that the number of organisms is magnitudes less than the number of atoms in a room, but all the organisms, opposite the atoms in the rooms, have individual characteristics. Whereas large number systems such as the number of atoms in a room are amenable to statistical mechanics and small number problems such as planetary systems to classical mechanics or individual-based modeling, middle number problems contain their own set of challenges. For one thing, this variation, within and among species, provides diversity through coadaptation and coevolution, which is central both to Darwinian selection and network aggradation.

The competitive exclusion principle (Gause, 1934) claims that when two or more species are competing for the same limited resource, only one will survive. The contrast between this principle and the number of species has for long time been a paradox. The explanation is rooted in the enormous variability in time and space of the conditions and in the variability of a wide spectrum of species' properties. A competition model, where three or more resources are limiting, gives a result very different from the case where one or two resources are limiting. Due to significant fluctuations in the different resources, one species is prevented from becoming dominant and a model can demonstrate that many species occurring around the same resources can coexist. It is therefore not surprising that there exists many species in an environment characterized by an enormous variation of abiotic and biotic factors. The diversity itself contributes to greater diversity; development begets codevelopment. This is a positive feedback loop pushing the ecosystem toward greater and greater diversity and complexity.

To summarize, the number of different life forms is enormous because there are a great number of both challenges and opportunities. The complexity of ecosystem dynamics is rooted in these two incomprehensible types of variability.

7.2 ECOSYSTEM DEVELOPMENT

Ecosystem development in general is a question of the energy, matter, and information flows to and from the ecosystems. No transfer of energy is possible without matter and information and no matter can be transferred without energy and information. The higher the levels of information, the higher the utilization of matter and energy for further development of ecosystems away from the thermodynamic equilibrium; see also Chapters 2 and 6. These three factors are intimately intertwined in the fundamental nature of complex adaptive systems such as ecosystems in contrast to physical systems that most often can be described completely by material and energy relations. Life is therefore both a material and a nonmaterial (informational) phenomenon. The self-organization of life essentially proceeds by exchange of information.

E.P. Odum has described ecosystem development from the initial stage to the mature stage as a result of continuous use of the self-design ability (Odum, 1969, 1971); see the significant differences between the two types of systems listed in Table 7.2 and notice that the major differences are on the level of information. Table 7.2 show what we often call E.P. Odum's successional attributes, but also a few other concepts such as, for instance, exergy and ecological networks have been introduced in the table.

The information content increases in the course of ecological development because an ecosystem integrates all the modifications that are imposed by the environment. Thus, it is against the background of genetic information that systems develop which allow interaction of information with the environment. Herein lies the importance in the feedback organism−environment that means that an organism can only evolve in an evolving environment, which in itself is modifying.

The conservation laws of energy and matter set limits to the further development of "pure" energy and matter, while information may be amplified (almost) without limit. Limitation by matter is known from the concept of the limiting factor: growth continues until the element that is the least abundant relatively to the needs of the organisms is used up. Very often in developed ecosystems (for instance an old forest) the limiting elements are found entirely in organic compounds in the living organisms, while there is no or very little inorganic forms left in the abiotic part of the ecosystem. The energy input to ecosystems is determined by the solar radiation and, as we shall see later in this chapter, many ecosystems capture about 75%−80% of the solar radiation, which is their upper physical limit. Unlike energy capture which has an upper limit, the information content may continue to increase in terms of both structural information (i.e., the network) and also genetic information (see Fig. 7.1).

Information has some properties that are very different from mass and energy.

1) *Information, unlike matter and energy, is not conserved—it can disappear without a trace.* When a frog dies, the enormous information content of the living frog may still be there microseconds after the death in form of the right amino acid sequences but the information is useless and after a few days the organic polymer molecules have decomposed. In contrast, the living organism is able to multiply information by copying already achieved successful information. The information is able to provide a pattern of biochemical processes that ensure survival of the organisms as they interact with the physical−chemical environment and the other organisms present in the ecosystem. Organisms copy the information embodied in the genomes as they grow and reproduce. Growth and reproduction require input of energy in terms of environmental food resources. The food has energy content, but it also has information content, which like the dead frog, no longer has the capacity to act upon. Another way to

TABLE 7.2 Differences Between Initial Stage and Mature Stage are Indicated.

Properties	Early Stages	Late or Mature Stage
(A) ENERGETIC		
Production/respiration	>>1	Close to 1
Production/biomass	High	Low
Respiration/biomass	High	Low
Yield (relative)	High	Low
Specific entropy	High	Low
Entropy production/time	Low	High
Eco-exergy	Low	High
Information	Low	High
(B) STRUCTURE		
Total biomass	Small	Large
Inorganic nutrients	Extrabiotic	Intrabiotic
Diversity, ecological	Low	High
Diversity, biological	Low	High
Patterns	Poorly organized	Well organized
Niche specialization	Broad	Narrow
Organism size	Small	Large
Life cycles	Simple	Complex
Mineral cycles	Open	Closed
Nutrient exchange rate	Rapid	Slow
Life span	Short	Long
Ecological network	Simple	Complex
(C) SELECTION AND HOMEOSTASIS		
Internal symbiosis	Undeveloped	Developed
Stability (resistance to external perturbations)	Poor	Good
Ecological buffer capacity	Low	High
Feedback control	Poor	Good
Growth form	Rapid growth	Feedback controlled growth
Types	r-strategists	K-strategists

look at this is using the concept of emergy instead of energy. Emergy is defined later in this chapter (Box 7.2). The emergy of the food would be calculated as the amount of solar energy it takes to provide the food, which would require multiplication by a weighting factor >> 1.

2) *The disappearance and copying of information, that are characteristic processes for living systems, are irreversible processes.* A made copy cannot be taken back and death is an irreversible process. Although information can be expressed as eco-exergy in energy units, it is not possible to recover chemical energy from information on the molecular level as known from the genomes. It would require a Maxwell's Demon that could sort out the molecules and it would therefore violate the second law of thermodynamics. There are, however, challenges to the second law (e.g., Capek and Sheehan, 2005), and this process of copying information could be considered one of them. Note that since the big bang, enormous amounts of matter have been converted to energy ($E = mc^2$) in a form that makes it

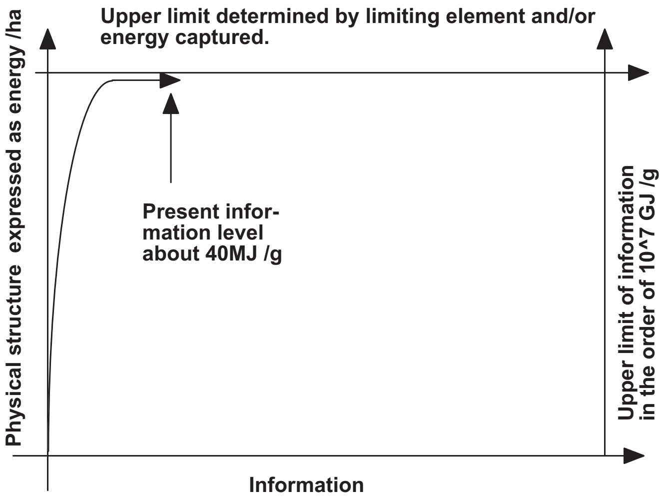

FIGURE 7.1 Life conditions are currently changed and have a high variability in time and space. This creates new challenges (problems) to survival. Organisms adapt or a shift to other species takes place. This requires an information system that is able to transfer the information about good solutions to the coming generations of organisms. Consequently, an information system is very beneficial, but it has to be considered as a new source of constraints that however can open up for new possibilities.

impossible *directly* to convert the energy again to mass. Similarly, the conversion of energy to information that is characteristic for many biological processes cannot be reversed directly in most cases. The transformation matter → energy → molecular information, which can be copied at low cost is possible on earth, but these transformation processes are irreversible.

3) *Information exchange is communication, which brings about the self-organization of life.* Life is an immense communication process that happens over several hierarchical levels (Chapter 5). Information exchange is possible with a very tiny consumption of energy, while information storage requires that it is linked to material substances. For instance, genetic information is stored in the genomes and it is transferred to the amino acid sequence.

A major design principle observed in natural systems is the feedback of energy from storages to stimulate the inflow pathways as a reward from receiver storage to the inflow source (Odum, 1971a). See also the "centripetality" in Chapter 6. By this feature, the flow values developed reinforce the processes that are doing useful work. Feedback allows the circuit to learn. A wider use of the self-organization ability of ecosystems in environmental or rather ecological management has been proposed by Odum (1983, 1988).

Researchers have modified and further developed E.P. Odum's idea of using attributes to describe the development and the conditions of an ecosystem during the ensuing years. Here, we assess ecosystem development using ecological orientors to indicate that the development is not necessarily following all E.P. Odum's details because ecosystems are ontically open (Chapter 3). In addition, it is also rare that we can obtain data to demonstrate the validity of the attributes in complete detail. This recent development is presented in the next section.

The concept of ecological indicators was introduced around 30 years ago. These metrics indicate the ecosystem condition or the ecosystem health and are widely used to understand ecosystem dynamics in an environmental management context. E.P. Odum's attributes could be used as ecological indicators. Another approach is to use specific indicator species that show with their presence or absence that the ecosystem is either healthy or not. Specific contaminants that indicate a specific disease are used as indicators. Finally, it should be mentioned that indicators such as biodiversity or thermodynamic variables are used to indicate a holistic image of the ecosystems' condition; for further details see Chapter 10. The relationship between biodiversity and stability was previously widely discussed (e.g., May, 1973, which showed that there is not a simple relationship between biodiversity and stability of ecosystems). Tilman and coworkers (Tilman and Downing, 1994) have shown that temperate grassland plots with more species have a greater resistance or buffer capacity to the effect of drought (a smaller change in biomass between a drought year and a normal year). However, there is a limit—each additional plant contributed less; see Fig. 7.2. Many experiments (Tilman and Downing, 1994) have also shown that higher biodiversity increases the biomass.

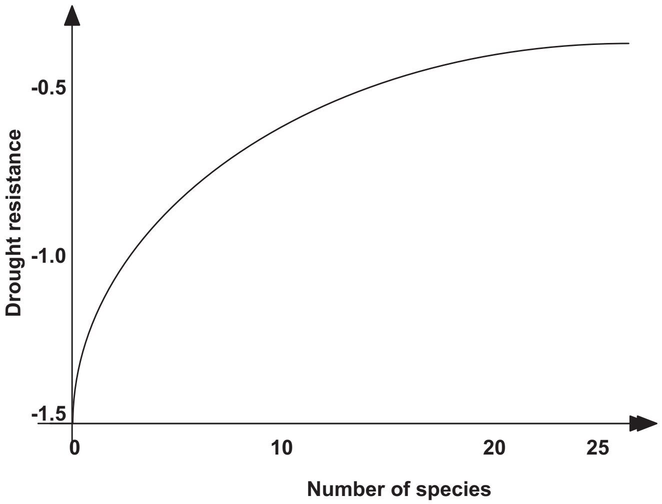

FIGURE 7.2 The resistance of a temperate grassland towards drought increases with number of species in an asymptotic manner so that the relative importance of adding new species decreases.

BOX 7.1

DEFINITIONS OF ORIENTORS, INDICATORS, AND GOAL FUNCTIONS

Ecological Orientors: Ecosystem variables that describe the range of directions in which ecosystems have a propensity to develop. The word *orientors* is used to indicate that we cannot give complete details about the development, only the direction.

Ecological Indicators: These indicate the present ecosystem condition or health. Many different indicators have been used such as specific species, specific contaminants, indices giving the composition of groups of organisms (for instance, an algae index), E.P. Odum's attributes and holistic indicators included biodiversity and thermodynamic variables such as entropy or exergy.

Ecological Goal Functions: Ecosystems do not have defined goals, but their propensity to move in a specific direction indicated by ecological orientors can be described in ecological models by goal functions. Clearly, in a model, the description of the development of the state variables of the model has to be rigorously indicated, which implies that goals are made explicit. The concept should only be used in ecological modeling context.

Box 7.1 gives the definitions for ecological orientors and ecological indicators. In ecological modeling, goal functions are used to develop structurally dynamic models. Also, the definition of this third concept is included in the box.

It is theoretically possible to divide most of E.P. Odum's attributes into groups, defining four different growth and development forms for ecosystems (Jørgensen et al., 2000; Fath et al., 2004):

I. Boundary Growth refers to the capture of energy input by the ecosystem and bringing it in across its system boundaries. This is the basic prerequisite for all further activities in the ecosystem and maintaining them as open far-from-equilibrium systems.

II. Biomass Growth refers to the increase of protoplasm—the biomass substance of the ecosystem. This explains why P/B and R/B decreases with the development and the nutrients go from extrabiotic to intrabiotic pools.

III. Network Growth and Development refers directly to increased complexity of the ecological network, more complex life and mineral cycles, a slower nutrient exchange rate, and a more narrow niche specialization. It also implies a longer retention time in the system for energy and matter. This is not only an increase in the network connectivity but also the placement or articulation of those links.

IV. Information Growth and Development refers to the evolutionary advances that explain the higher diversity, larger animals, longer life span, more symbiosis and feedback control, and a shift from r-strategists to K-strategists.

7.3 ORIENTORS AND SUCCESSION THEORIES

The orientor approach that was briefly introduced above describes ideal-typical trajectories of ecological properties on an integrated ecosystem level. Therefore, it follows the traditions of various concepts in ecological theory, which are related to environmental dynamics. A significant example is succession theory, describing "directional processes of colonization and extinction of species in a given site" (Dierssen, 2000). Although there are big intersections, these conceptual relationships have not become sufficiently obvious in the past, due to several reasons, which are mainly based on methodological problems and critical opinions that have been discussed eagerly after the release of Odum's paper on the strategy of ecosystem development (1969). Which were the reasons for these controversies?

Traditional succession theory is basically oriented toward vegetation dynamics. The pioneers of succession research, Clements (1916) and Gleason (1917), were focusing mainly on vegetation. Consequently, also the succession definitions of Whittacker (1953), Egler (1954), Grime (1979), or Picket et al. (1987) are related to plant communities, while heterotrophic organisms often are neglected (e.g., Connell and Slayter, 1977, Horn, 1974). Therefore, also the conclusions of the respective investigations often have to be reduced to the development of vegetation components of ecosystems, while the orientor approach refers to the *whole ensemble* of organismic and abiotic subsystems and their interrelations. These conceptual distinctions for sure are preferable sources for misunderstandings.

A sufficient number of long-term data sets are not available. Therefore, as some authors state throughout the discussions of Odum's "strategy" paper (1969), the theoretical predictions of succession theory seem to be "based on untested assumptions or analogies" (e.g., Connell and Slayter, 1977; Drury and Nisbet, 1973, Horn, 1974), while there is only small empirical evidence. This situation becomes even more problematic if ecosystem data are necessary to test the theoretical hypotheses. Consequently, we will also in the future have to cope with this lack of data, but we can use more and more empirical investigations, referring to the orientor principle, which have been reported in the literature (e.g., Marques et al., 2003, Müller et al. i.p.). We can hope for additional results from ecosystem analyses and Long-Term Ecological Research Programs. Meanwhile validated models can be used as productive tools for the analysis of ecosystem dynamics.

The conceptual starting points differ enormously. Referring to the general objections against the maturity concept, Connell and Slayter (1977) funnel their heavy criticism about Odum's 24 ecosystem features into the questions of whether mature communities really are "internally controlled" and if "steady states really are maintained by internal feedback mechanisms." Having doubts in these facts, they state that therefore no characteristics can be deduced from this idea. Today, there is no doubt about the existence of self-organizing processes in all ecosystems (e.g., Jørgensen, 2002). Of course, there are external constraints, but within the specific degrees of freedom, in fact the internal regulation processes are responsible for the development of ecosystems. Hence, the basic argument against the maturity concept has lost weight throughout the years.

Comparing successional dynamics, often different spatial and temporal scales are mixed. This point is related to the typical time scales of ecological investigations. They are most often carried out in a time span of 2–4 years. Of course, it is very difficult to draw conclusions over centuries from these short-term data sets. Also using paleoecological methods give rise to broad uncertainties, and when spatial differences are used to represent the steps of temporal developments, the questions of the site comparability introduces problems which might reduce the evidence of the findings enormously. Furthermore, there is the general problem of scale. If we transfer short-term results to long-term processes, then we cannot be sure to use the right algorithms and to take into account the correct, scale conform constraints and processes (O'Neill et al., 1986). And, looking at the spatial scale, the shifting mosaic hypothesis (Remmert, 1991) has shown that there will be huge differences if different spatial extents are taken into account, and that local instabilities can be leading to regional steady-state situations. What we can see is that there are many empirical traps we can fall into. Maybe the connection of empirical research and ecological modeling can be helpful as a "mechanism of self-control" in this context.

Due to the "ontic openness" *of ecosystems, predictability in general is rather small but in many cases, exceptions can be found*. The resulting dilemma of a system's inherent uncertainty can be regarded as a consequence of the internal complexity of ecosystems, the nonlinear character of the internal interactions, and the often unforeseeable dynamics of environmental constraints. Early on, succession researchers found the fundamentals of this argument, which are broadly accepted today. The nondeterministic potential of ecological developments has already been introduced in Tansley's polyclimax theory (1935), which is based on the multiple environmental influences that function as constraints for the development of an ecosystem. Simberloff (1982) formulates that "the deterministic path of succession, in the strictest Clementsian mono-climax formulation, is as much an abstraction as the Newtonian particle trajectory" and Whittaker (1972) states, "the vegetation on the earth's surface is in incessant flux." Stochastic elements, complex interactions, and spatial heterogeneities take such important influences that the idea of Odum (1983) that "community changes … are predictable," must be considered in relative terms today, if detailed prognoses (e.g., on the species level) are desired. However, this does not mean that general developmental tendencies can be avoided, i.e., this fact does not contradict the general sequence of growth and development forms as formulated in this volume. Quite the opposite: This concept realizes the fact that not all ecosystem features are optimized throughout the whole sequence, a fact that has been pointed out by Drury and Nisbet (1973) and others.

Disturbances are causes for separating theoretical prognoses from practical observations. One example for these nondeterministic events is disturbance, which plays a major role in ecosystem development (e.g., Drury and Nisbet, 1973; Sousa, 1984). Odum (1983) has postulated that succession "culminates in the establishment of as stable an ecosystem as its biologically possible on the site in question" and he notes that mature communities are able to buffer the physical environment to a greater extent than the young community. In his view, stability and homoeostasis can be seen as the result (he even speaks about a purpose) of ecological succession from the evolutionary standpoint. However, the guiding paradigm has changed: Today Holling's adaptive cycle model (1986) has become a prominent concept, and destruction is acknowledged as an important component of the continuous adaptation of ecosystems to changing environmental constraints. This idea also includes the feature of brittleness in mature states, which can support the role of disturbance as a setting of new starting points for an oriented development.

Terminology has inhibited the acceptance of acceptable ideas. The utilization of terms like "strategy," "purpose," or "goal" has led to the feeling that holistic attitudes toward ecological successions in general are loaded with a broad teleological bias. Critical colleagues argued that some of these theories are imputing ecosystems to be "intentionally" following a certain target or target state. This is not correct: The series of states is a consequence of internal feedback processes that are influenced by exterior constraints and impulses. The finally achieved attractor state thus is a result, not a cause. These indicators track that development but do not cause the observed changes.

Summarizing, many of the objections against the initial theoretical concepts of ecosystem development and especially against the stability paradigm have proven to be correct, and they have been modified in between. Analogies are not used anymore, and the number of empirical tests is increasing. On the other hand, the theory of self-organization has clarified many critical objections. Thus, a consensus can be reached if cooperation between theory and empiricism is enhanced in the future.

7.4 THE MAXIMUM POWER PRINCIPLE

Lotka (1925, 1956) formulated the maximum power principle. He suggested that systems that succeed are those that develop designs to maximize the flow of *useful* (for maintenance and growth) energy, and Odum used this principle to explain much about the structure and processes of ecosystems (Odum and Pinkerton, 1955). Boltzmann (1905) said that the struggle for existence is a struggle for free energy available for work, which is a definition very close to the maximum exergy principle introduced in the next section. Similarly, Schrödinger (1944) pointed out that organization is maintained by extracting order from the environment. These two last principles may be interpreted as the systems that are able to gain the most free energy under the given conditions, i.e., to move most away from the thermodynamic equilibrium will succeed. Such systems will gain most biogeochemical energy available for doing work and therefore have most energy stored to use for maintenance and buffer against perturbations.

Odum (1983) defines the maximum power principle as a maximization of *useful* power. It is applied on the ecosystem level by summing up all the contributions to the *total* power that are useful. This means that nonuseful power is not included in the summation. Usually the maximum power is found as the sum of all flows expressed in energy terms, for instance kJ/24h.

Brown et al. (1993) and Brown (1995) has restated the maximum power principle in more biological terms. According to the restatement it is the transformation of energy into work (consistent with the term useful power) that determines success and fitness. Many ecologists have incorrectly assumed that natural selection tends to increase efficiency. If this were true, then endothermy could never have evolved. Endothermic birds and mammals are extremely inefficient compared with reptiles and amphibians. They expend energy at high rates in order to maintain a high, constant body temperature, which, however, gives high levels of activities independent of environmental temperature (Turner, 1970). Brown (1995) defines fitness as reproductive power, dW/dt, the rate at which energy can be transformed into work to produce offspring. This interpretation of the maximum power principle is even more consistent with the maximum exergy principle that is introduced in the next section, than with Lotka's and Odum's original idea.

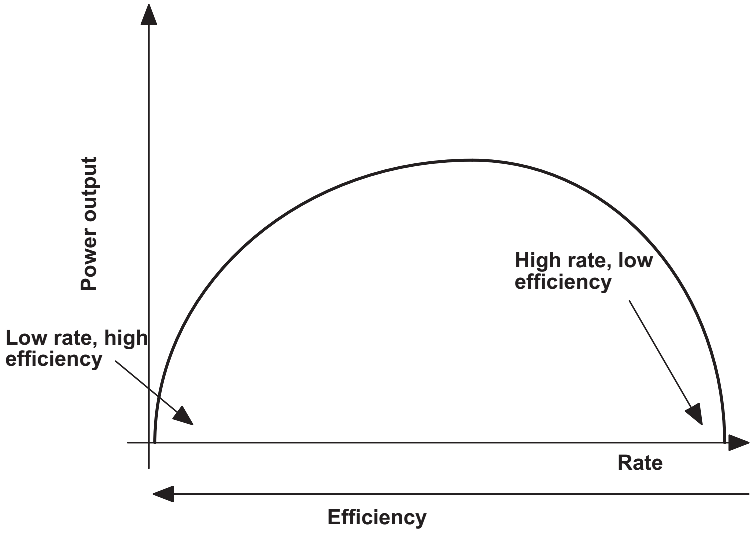

FIGURE 7.3 The power output shows a parabolic relationship as a function of the rate having low outputs if rates are very low or very high. The efficiency being the highest at lowest rates.

In the book *Maximum Power: The Ideas and Applications of H.T. Odum*, Hall (1995) has presented a clear interpretation of the maximum power principle, as it has been applied in ecology by H.T. Odum. The principle claims that power or output of useful work is maximized, not the efficiency and not the rate, but the trade-off between a high rate and high efficiency yielding most useful energy or useful work (see Fig. 7.3).

Hall is using an interesting seminatural experiment to illustrate the application of the principle in ecology. Streams were stocked with different levels of predatory cutthroat trout. When predator density was low, there was considerable invertebrate food per predator, and the fish used relatively little maintenance energy searching for food per unit of food obtained. With a higher fish-stocking rate, food became less available per fish, and each fish had to use more energy searching for it. Maximum production occurred at intermediate fish-stocking rates, which means intermediate rates at which the fish utilized their food.

Hall (1995) mentions another example. Deciduous forests in moist and wet climates tend to have a leaf area index (LAI) of about 6 m^2/m^2. Such an index is predicted from the maximum power hypothesis applied to the net energy derived from photosynthesis. Higher LAI values produce more photosynthate, but do so less efficiently because of the metabolic demand of the additional leaf. Lower leaf area indices are more efficient per leaf, but draw less power than the observed intermediate values of roughly 6.

The same concept applies for regular fossil fuel power generation. The upper limit of efficiency for any thermal machine such as a turbine is determined by the Carnot efficiency. A steam turbine could run at 80% efficiency, but it would need to operate at a nearly infinitely slow rate. Obviously, we are not interested in a machine that generates electricity or revenues infinitely slowly, no matter how efficiently. Actual operating efficiencies for modern steam powered generator are therefore closer to 40%, roughly half the Carnot efficiency.

These examples show that the maximum power principle is embedded in the irreversibility of the world. The highest process efficiency can be obtained by endoreversible conditions, meaning that all irreversibilities are located in the coupling of the system to its surroundings, there are no internal irreversibilities. Such systems will, however, operate too slowly. Power is zero for any endoreversible system. If we want to increase the process rate, then we also increase the irreversibility and thereby decrease the efficiency. The maximum power is the compromise between endoreversible processes and very fast completely irreversible processes.

The concept of emergy (embodied energy) was introduced by Odum (1983) and attempts to account for the energy required in the formation of organisms in different trophic levels. The idea is to correct energy flows for their energy quality. Energies of different types are converted into equivalents of the same type by multiplying by the energy transformation ratio. For example, fish, zooplankton, and phytoplankton can be compared by multiplying their actual energy content by their solar energy transformation ratios. The more transformation steps there are between two kinds of energy, the greater the quality and the greater the solar energy required to produce a unit of energy (J) of that type. When one calculates the energy of one type that generates a flow of another, this is sometimes referred to as

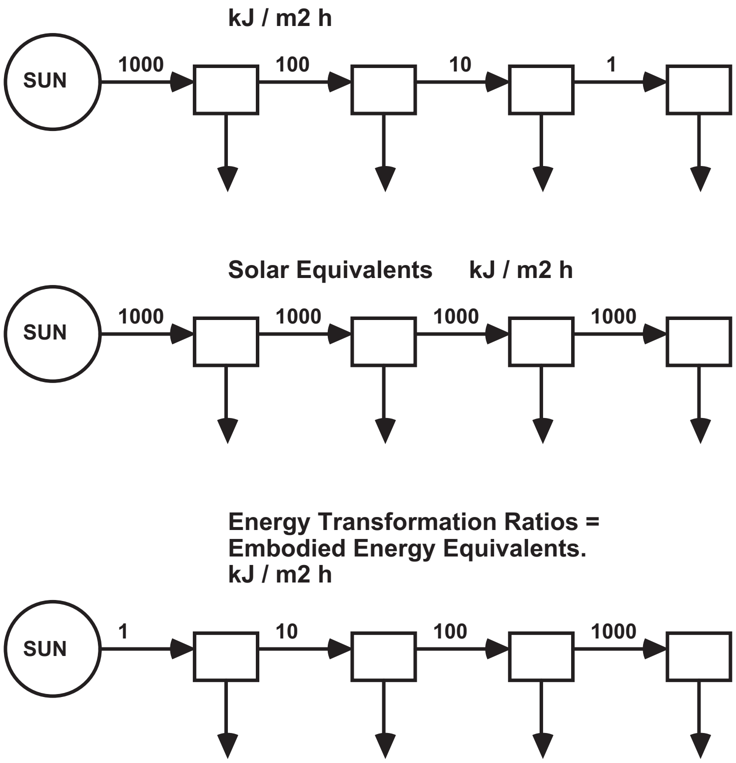

FIGURE 7.4 Energy flow, solar equivalents, and energy transformation ratios = embodied energy equivalents in a food chain (Jørgensen, 2002).

the embodied energy of that type. Fig. 7.4 presents the concept of embodied energy in a hierarchical chain of energy transformation. One of the properties of high-quality energies is their flexibility (which requires information). Whereas low-quality products tend to be special, requiring special uses, the higher quality part of a web is of a form that can be fed back as an amplifier to many different web components.

A good down-to-earth example of what emergy is might be the following: in 1 year one human can survive on 500 fish each of the size of 500 g, that may have consumed 80,000 frogs with the size of 20 g. The frogs may have eaten 18×10^6 insects of the size of 1 g. The insects have got their food from 200,000 kg dry matter of plants. As the photosynthetic net production has an efficiency of 1%, the plants have required an input of about 3.7×10^9 J, presuming an energy content of plant dry matter of 18.7 kJ g^{-1}. To keep one human alive costs therefore 3.7×10^9 J, although the energy stock value of a human being is only in the order 3.7×10^5 J or 10,000 times less. The transformity is therefore 10,000. The flipside of this is that if the humans eat the plant matter directly it could instead feed 1000 people by foregoing the three additional trophic transfers.

H.T. Odum has revised the maximum power principle by replacing power with emergy–power (empower), meaning that all the contributions to power are multiplied by a solar equivalent factor that is named transformity to obtain solar equivalent joules (sej) (see Box 7.2). The difference between embodied energy flows and power, see Eq. (7.1), simply seems to be a conversion to solar energy equivalents of the free energy.

Embodied energy is, as seen from these definitions, determined by the biogeochemical energy *flow* into an ecosystem component, measured in solar energy equivalents. The stored emergy, *Em*, per unit of area or volume to be distinguished from the emergy flows can be found from:

$$Em = \sum_{i=1}^{n} \Omega_i c_i \tag{7.1}$$

where Ω_i is the quality factor which is the conversion to solar equivalents, as illustrated in Fig. 7.4, and c_i is the concentration expressed per unit of area or volume.

The calculations reduce the difference between stored emergy (= embodied energy) and stored exergy (see next section), to the energy quality factor. The quality factor for exergy accounts for the information embodied in the various components in the system (detailed information is given in the next section), while the quality factor for

BOX 7.2

EMERGY

"*Emergy* is the available energy of one kind previously used up directly and indirectly to make a service or product. Its unit is the emjoule [(ej)]" and its physical dimensions are those of energy (Odum, 1996). In general, since solar energy is the basis for all the energy flows in the biosphere, we use *Solar emergy* (measured in *sej*, solar emjoules), the solar energy equivalents required (directly or indirectly) to make a product.

The total emergy flowing through a system over some unit time, referenced to its boundary source, is its empower, with units [sej/(time)] (Odum, 1988). If a system, and in particular an ecosystem, can be considered in a relatively steady state, the empower (or emergy flow) can be seen as nature's "labor" required for maintaining that state.

The emergy approach starts from Lotka's maximum power principle (1922, 1956) and corrects the function, which is maximized, since not all the energy types have the same ability of doing actual work. Thus power (flow of energy) is substituted by empower (flow of emergy), that is "in the competition among self-organizing processes, network designs that maximize empower will prevail" (Odum, 1996).

Transformity is the ratio of emergy necessary for a process to occur to the exergy output of the process. It is an intensive function and it is dimensionless, even though sej/J is used as unit.

Emergy can be written as a function of transformity and exergy as follows (i identifies the inputs):

$$Em = \sum_i \tau_i EX_i$$

While transformity can be written as

$$\tau_k = Em_k / EX_k$$

even though it is often calculated as

$$\tau_k = \frac{Em_k/\text{time}}{EX_k/\text{time}}$$

By definition the transformity of sunlight is equal to 1 and this assumption avoids the circularity of these expressions. All the transformities (except that of solar energy) are therefore greater than 1.

Transformities are always measured relative to a planetary solar emergy baseline and care should be taken to ensure that the transformities used in any particular analysis are all expressed relative to the same baseline (Brown et al., 2016). However, all the past baselines can be easily related through multiplication by an appropriate factor and the results of an emergy analysis do not change by shifting the baseline (Odum et al., 2000).

Emergy and transformity are not state functions, i.e., they strongly depend on the process that is used to obtain a certain item. There are transformities that are calculated from global biosphere data (i.e., rain, wind, geothermal heat) and others that, being the result of more complex and variable processes have high variability: for example, electricity can be generated by many processes (using wood, water, coal, gas, tide, solar radiation, etc.) each with a different transformity (Odum, 1996).

In general, transformity can be seen as a measure of "quality": while emergy, following "memorization" laws, can in general remain constant or grow along transformation chains, since as energy decreases, transformities increase. On the other hand, when comparing homologous products, the lower the transformity, the higher the efficiency in transforming solar emergy into a final product.

Emergy is a donor-referenced concept and a measure of convergence of energies, space, and time, both from global environmental work and human services into a product. It is sometimes referred to as "energy memory" (Scienceman, 1987) and its logic (of "memorization" rather than "conservation") is different from other energy-based analyses as shown by the emergy "algebra." The rules of emergy analysis are as follows:

- All source emergy to a process is assigned to the processes' output;
- By-products from a process have the total emergy assigned to each pathway;
- When a pathway splits, the emergy is assigned to each "leg" of the split based on its percentage of the total energy flow on the pathway;
- Emergy cannot be counted twice within a system: (a) emergy in feedbacks cannot be double counted; (b) by-products, when reunited, cannot be added to equal a sum greater than the source emergy from which they were derived.

For in-depth discussion of this issue and the differences between energy and emergy analysis see Brown and Herendeen (1996) and Brown et al. (2016).

emergy accounts for the solar energy cost to form the various components. Emergy calculates thereby how much solar energy (which is our ultimate energy resource) it has cost to obtain 1 unit of biomass of various organisms. Both concepts attempt to account for the quality of the energy. Emergy by looking into the energy flows in the ecological network to express the energy costs in solar equivalents. Exergy by considering the amount of biomass and information that has accumulated in that organism. One is measure of the path that was taken to get to a certain configuration, the other a measure of the organisms in that configuration.

7.5 EXERGY, ASCENDENCY, GRADIENTS, AND ECOSYSTEM DEVELOPMENT

The second law of thermodynamics dissipation acts to tear down structure and eliminate gradients, but ecosystems have the ability to move away from thermodynamic equilibrium in spite of the second law dissipation due to an inflow of energy from solar radiation—see the story in the preamble to this chapter. Physical systems can also create structured gradients such as a hurricane, tornado, or the red spot on Jupiter. A Bernard cell is an example of a simple physical system using an inflow of energy to move away from thermodynamic equilibrium. A Bernard cell consists of two plates that are horizontally placed in water a few cm from each other. The lower plate has higher temperature than the upper plate. Consequently, energy is flowing from the lower to the upper plate. When the temperature difference is low, the motion of the molecules is random. When the temperature exceeds a critical value, the water molecules are organized in a convection pattern, series of rolls or hexagons. The energy flow increases due to the convection. The greater the flow of energy the steeper the temperature gradient (remember that work capacity - = entropy times temperature gradient) and the more complex the resulting structure. Therefore, greater exergy flow moves the system further away from thermodynamic equilibrium—higher temperature gradient and more ordered structure containing information corresponding to the order. The origin of ordered structures is therefore openness and a flow of energy (see Chapter 2). Openness and a flow of energy are both necessary conditions (because it will always cost energy to maintain an ordered structure) and sufficient (as illustrated with the Bernard cell). Morowitz (1968, 1992) has shown that an inflow of energy always will create one cycle of matter, which is an ordered structure. Openness and a flow of energy is, however, not a sufficient condition for ecosystems (see Chapter 2), as additional conditions are required to ensure that the ordered structure is an ecosystem.

Biological systems, especially, have many possibilities for moving away from thermodynamic equilibrium, and it is important to know along which pathways among the possible ones a system will develop. This leads to the following hypothesis (Jørgensen and Mejer, 1977, 1979; Jørgensen, 1982, 2001, 2002; Jørgensen et al., 2000): If a system receives an input of useable energy (exergy), then it will utilize this energy to perform work in a hierarchy of steps. First, work performed is used to maintain the system (far) away from thermodynamic equilibrium; exergy is lost during the transformation into heat at the temperature of the environment. Second, if more exergy is available, then the system moves further away from thermodynamic equilibrium, reflected in growth of gradients. Third, if there is more than one pathway to depart from equilibrium, then the one yielding the highest exergy storage (denoted Ex) will tend to be selected (in ecological examples, eco-exergy is used rather than engineering exergy—see Box 7.3). Another way to express this last point is: A**mong the many ways for ecosystems to move away from thermodynamic equilibrium, the one maximizing dEx/dt under the prevailing conditions will have a propensity to be selected**.

de Wit (2005) has expressed preference for a formulation where the flow of exergy is replaced by a flow of free energy, which of course is fully acceptable and makes the formulation closer to classic thermodynamics. However, eco-exergy storage can hardly be replaced by free energy because it is a free energy *difference* between the system and the same system at thermodynamic equilibrium. The reference state is therefore different from ecosystem to ecosystems, which is considered in the definition of eco-exergy. In addition, free energy is not a state function far from thermodynamic equilibrium—just consider the immediate loss of eco-exergy when an organism dies. Before death, the organism has high eco-exergy because it can utilize the enormous information that is embodied in the organism, but at death the organism loses immediately the ability to use this information that becomes therefore worthless. Moreover, the information part of the eco-exergy cannot be utilized directly as work; see the properties of information presented in Section 7.2.

Just as it is not possible to prove the three laws of thermodynamics by deductive methods, so can the above hypothesis only be "proved" inductively. A number of concrete cases which contribute generally to the support of the hypothesis will be presented below and in Chapters 9—11. Models are often used in this context to test the hypothesis. The exergy can be approximated using the calculation methods in Box 7.3. Strictly speaking, exergy is a measure of the useful work that can be performed by the system. Conceptually, this obviously includes the energetic content

BOX 7.3

CALCULATION OF ECO-EXERGY

It is possible to distinguish between the exergy of information and of biomass (Svirezhev, 1998). p_i defined as c_i/B, where

$$B = \sum_{i=1}^{n} c_i$$

is the total amount of matter in the system, is introduced as new variable in Eq. (2.8):

$$Ex = B\,RT \sum_{i=1}^{n} p_i \ln \frac{p_i}{p_{i,o}} + B \ln \frac{B}{B_o}$$

As the biomass is the same for the system and the reference system, $B \approx B_o$ exergy becomes a product of the total biomass B (multiplied by RT) and Kullback measure:

$$K = \sum_{i=1}^{n} p_i \ln \frac{p_i}{p_{i,o}}$$

where p_i and $p_{i,o}$ are probability distributions, a posteriori and a priori to an observation of the molecular detail of the system. It means that K expresses the amount of information that is gained as a result of the observations. If we observe a system that consists of two connected chambers, then we expect the molecules to be equally distributed in the two chambers, i.e., $p_1 = p_2$ is equal to $1/2$. If we, on the other hand, observe that all the molecules are in one chamber, then we get $p_1 = 1$ and $p_2 = 0$.

Specific exergy is exergy relatively to the biomass and for the ith component: Sp. ex.$_i = Ex_i/c_i$. It implies that the total specific exergy per unit of area or per unit of volume of the ecosystem is equal to RTK.

For the components of the ecosystem, 1 (covers detritus), 2, 3, 4 … N, the probability, $p_{i,o}$, is the probability of producing the organic matter (detritus), i.e., $p_{1,o}$, and the probability, $p_{i,a}$, to find the correct composition of the enzymes determining the biochemical processes in the organisms. Living organisms use 20 different amino acids and each gene determines on average a sequence of about 700 amino acids (Li and Grauer, 1991). $p_{i,a}$, can be found from the number of permutations among which the characteristic amino acid sequence for the considered organism has been selected.

By summing up the contributions originating from all components, we find the total eco-exergy. The contribution by inorganic matter can be neglected as the contributions by detritus and even to a higher extent from the biological components are much higher due to an extremely low probability of these components in the reference system. Roughly, the more complex (developed) the organism is the more enzymes with the right amino acid sequence are needed to control the life processes, and therefore the lower is the probability $p_{i,a}$, The probability. $p_{i,a}$, for various organisms has been found on basis of our knowledge about the genes that determine the amino acid sequence. As the concentrations are multiplied by RT and ln $(p_i/p_{i,o})$, denoted β_i a table with the β-values for different organisms have been prepared; see Table 7.2. The contribution by detritus, dead organic matter, is in average 18.7 kJ/g times the concentration (in g/unit of volume). The eco-exergy can now be calculated by the following equation:

$$\text{Eco} - \text{Exergy total} = \sum_{i=1}^{n} \beta_i c_i (\text{as detritus equivalent})$$

The β-values are found from Table 7.3 and the concentration from modeling or observations. Multiplying by 18.7 converts the eco-exergy into kJ.

TABLE 7.3 β-Values = Exergy Content Relatively to the Exergy of Detritus (Jørgensen et al., 2005).

Early Organisms	Plants	Animals	β-Values
Detritus			1.00
Virus			1.01
Minimal cell			5.8
Bacteria			8.5
Archaea			13.8
Yeast			17.8
Protists	Algae		20

Continued

BOX 7.3 (*cont'd*)

TABLE 7.3 β-Values = Exergy Content Relatively to the Exergy of Detritus (Jørgensen et al., 2005).—cont'd

Early Organisms	**Plants**	**Animals**	**β-Values**
		Mesozoa, Placozoa	33
		Protozoa, amoeba	39
		Phasmida (stick insects)	43
Fungi, molds			61
		Nemertini	76
		Cnidaria (corals, sea anemones, jelly fish)	91
	Rhodophyta		92
		Gastroticha	97
Prolifera, sponges			98
		Brachiopoda	109
		Platyhelminthes (flatworms)	120
		Nematoda (round worms)	133
		Annelida (leeches)	133
		Gnathostomulida	143
	Mustard weed		143
		Kinorhyncha	165
	Seedless vascular plants		158
		Rotifera (wheel animals)	163
		Entoprocta	164
	Moss		174
		Insecta (beetles, flies, bees, wasps, bugs, ants)	167
		Coleodiea (sea squirt)	191
		Lipidoptera (buffer flies)	221
		Crustaceans	232
		Chordata	246
	Rice		275
	Gymnosperms (inl. *Pinus*)		314
		Mollusca, bivalvia, gastropoda	310
		Mosquito	322
	Flowering plants		393
		Fish	499
		Amphibia	688
		Reptilia	833
		Aves (birds)	980
		Mammalia	2127
		Monkeys	2138
		Anthropoid apes	2145
		Homo sapiens	2173

BOX 7.3 *(cont'd)*

Notice that

$$Ex_{\text{bio}} = \sum_{i=1}^{n} c_i \text{ (as detritus equivalent)}$$

while

$$Ex_{\text{info}} = \sum_{i=1}^{n} (\beta_i - 1) c_i \text{ (as detritus equivalent)}$$

of the material, i.e., biomass, but also the state of organization of the material. One way to measure the organization is the information content of the material, which could be the complexity at the genetic, organismal, or ecosystem levels. Currently, we express the organizational aspect of exergy as Kullbach's measure of information based on the genetic complexity of the organism:

$$Ex = B\,RT\,K \tag{7.2}$$

where B is the biomass, R the gas constant, T the Kelvin temperature, and K Kullbach's measure of information (further details see Box 7.3). In this manner, the information that the organism carries is the basis for the organism's eco-exergy:

$$Ex_i = \beta_i c_i \tag{7.3}$$

where Ex_i is the exergy of the ith species, β_i is a weighting factor that consider the information the ith species is carrying in c_i (Table 7.2). Jørgensen et al. (2005) show the β-values for different organisms. A high uncertainty is, however, associated with the assessment of the β-values, which implies that the exergy calculations have a corresponding high uncertainty. In addition, the eco-exergy is calculated based upon models that are simplifications of the real ecosystems. Therefore, the eco-exergy calculations should only be used relatively and considered an index and not a real absolute exergy value.

Consistency of the eco-exergy storage hypothesis, as we may call it, with other theories (goal functions, orientors; see Sections 7.2 and 7.3) describing ecosystem development will be demonstrated as a pattern in a later section of this chapter. It should, however, in this context be mentioned that eco-exergy storage in the abovementioned main hypothesis can be replaced by maximum power. Eco-exergy focuses on the storage of biomass (energy) and information, while power considers the energy flows resulting from the storages.

Ascendency (Box 6.1) is a measure of the information and flows embodied in the ecological network. At the crux of ascendency lies the action of autocatalysis (Chapter 6). One of the chief attributes of autocatalysis is what Ulanowicz (1997) calls "centripetality" or the tendency to draw increasing amounts of matter and energy into the orbit of the participating members. This tendency inflates ascendency both in the quantitative sense of increasing total system activity and qualitatively by accentuating the connections in the loop, above and beyond, pathways connecting nonparticipating members. At the same time, increasing storage of exergy is a particular manifestation of the centripetal tendency, and the dissipation of external exergy gradients to feed system autocatalysis describes centripetality in almost tautological fashion.

In retrospect, the elucidation of the connections among ascendency, eco-exergy, and aggradation (Ulanowicz et al., 2006) has been affected by stages that are typical of theory-driven research. First, it was noted in phenomenological fashion how quantitative observations of the properties were strongly correlated; the correlation coefficient, r_2, was found for a number of models to be 0.99 (Jørgensen, 1995). Thereafter, formal definitions were used to forge theoretical ties among the separate measures. Finally, the perspective offered by these new theoretical connections facilitated a verbal description of the common unitary agency that gave rise to the independent trends that had been formalized as separate principles. Eco-exergy and ascendency represent two sides of the same coin or two different angles in the description of ecosystem growth and development. A simple physical phenomenon as light requires both a description as waves and as particle to be fully understood. It is therefore understandable that ecosystem growth and development, which is much more complicated than light, requires multiple descriptions. Eco-exergy covers the storage, maximum power the flows, and ascendency the ecological network and all three concepts contribute to the overall aggradation, moving away from thermodynamic equilibrium. All three concepts have well-structured roots in the theoretical soil. Their shortcomings are, however, that calculations of eco-exergy, maximum power, and ascendency always will be incomplete due to the enormous complexity of ecosystems (see Section 7.1).

Ecosystems can also be understood as a high number of interacting and interdependent gradients, which are formed by self-organizing processes (Mueller and Leupelt, 1998). Gradient formation and maintenance costs exergy that is transformed by decomposition processes to heat at the temperature of the environment, i.e., the exergy is lost. The gradients can be classified in various ways. Here, we distinguish three types of gradients corresponding to the four growth and development forms (see Section 7.2): (1) gradients due to organisms in the ecosystems (trees are good illustrations); (2) gradients due to formation of a more complex network (for instance, the spatial distribution of more or fewer niches); and (3) gradients due to information (the level of information could be used directly as illustration). The first mentioned class of gradients requires the most exergy for maintenance, while information gradients require very little or no exergy for maintenance. Gradients summation is captured in the exergy measure since work capacity is an extensive variable times a gradient (see Chapter 2).

Eco-exergy storage is the simplest of the three concepts to calculate; but clearly, the assessment of the β-values has some shortcomings. The latest list is more differentiated than the previous ones (Jørgensen et al., 1995; Fonseca et al., 2000) and is based on the results of the entire genome analyses for 11 species plus a series of complexity measures for a number of species, families, orders or classes. The list will likely be improved as experiments reveal more information about the genomes and proteomes of more species. The total information of an ecosystem should furthermore include the information of the network. All ecological models that are used as basis for the eco-exergy calculations are much simpler than the real network and the information contained in the network of the model become negligible compared to the eco-exergy in the compartments. A calculation method to assess the information of the real ecological network is needed to account for the contribution to the total ecosystem eco-exergy.

Measuring power is more difficult because it is related to the amount of flow. Most ecological observations are based on concentrations and not on flows, making it harder to validate the flow values resulting from ecological models. In addition, the number of flows in the real ecological network is magnitudes higher than the few flows that can be included in our primitive calculations. Calculations of ascendency have the same shortcomings as calculations of power.

The three concepts may all have a solid theoretical basis but their applications in practice still have definite weaknesses that are rooted in the complexity of real ecosystems. Integrating the three concepts, we are able to expand on the earlier hypothesis based on eco-exergy alone and let it comprise ascendency and power in addition.

7.6 SUPPORT FOR THE PRESENTED HYPOTHESES

Below we present a few case studies from Jørgensen (2002) and Jørgensen et al. (2000) supporting the eco-exergy storage hypothesis, noting that maximum power or ascendency could also have been applied as discussed in Section 7.5. Additional examples can be found in these references and in Chapter 9.

Genome Size

In general, biological evolution has been toward organisms with an increasing number of genes and diversity of cell types (Futuyma, 1986). If a direct correspondence between free energy and genome size is assumed, then this can reasonably be taken to reflect increasing eco-exergy storage accompanying the increased information content and processing of "higher" organisms.

Le Chatelier's Principle

The eco-exergy storage hypothesis might be taken as a generalized version of "Le Chatelier's Principle." Expressing biomass synthesis as a chemical reaction, we get:

$$\text{energy} + \text{nutrients} = \text{molecules with more free energy (exergy) and organization} + \text{dissipated energy}. \tag{7.4}$$

According to Le Chatelier's Principle, as we add energy into a reaction system at equilibrium, then the system will shift its equilibrium composition in a way to counteract the change. This means that more molecules with more free energy and organization will be formed. If more pathways are offered, then those giving the most relief from the disturbance (displacement from equilibrium) by using the most energy, and forming the most molecules with the most free energy, will be the ones followed in restoring equilibrium.

The Sequence of Organic Matter Oxidation

The sequence of biological organic matter oxidation (e.g., Schlesinger, 1997) takes place in the following order: by oxygen, by nitrate, by manganese dioxide, by iron (III), by sulfate, and by carbon dioxide. This means that oxygen, if present, will always out compete nitrate, which will out compete manganese dioxide, and so on. The amount of eco-exergy stored as a result of an oxidation process is measured by the available kJ/mol of electrons which determines the number of adenosine triphosphate molecules (ATPs) formed. ATP represents an exergy storage of 42 kJ/mol. Usable energy as exergy in ATPs decreases in the same sequence as indicated above. This is as expected if the eco-exergy storage hypothesis were valid (Table 7.4). If more oxidizing agents are offered to a system, then the one giving the highest storage of free energy will be selected.

In Table 7.3, the first (aerobic) reaction will always out compete the others because it gives the highest yield of stored exergy. The last (anaerobic) reaction produces methane; this is a less complete oxidation than the first because methane has a greater exergy content than water.

Formation of Organic Matter in the Primeval Atmosphere

Numerous experiments have been performed to imitate the formation of organic matter in the primeval atmosphere on earth four billion years ago (Morowitz, 1968). Energy from various sources were sent through a gas mixture of carbon dioxide, ammonia, and methane. There are obviously many pathways to utilize the energy sent through simple gas mixtures, but mainly those forming compounds with rather large free energies (amino acids and RNA-like molecules with high exergy storage, decomposed when the compounds are oxidized again to carbon dioxide, ammonia and methane) will form an appreciable part of the mixture (according to Morowitz, 1968).

Photosynthesis

There are three biochemical pathways for photosynthesis: (1) the C3 or Calvin—Benson cycle, (2) the C4 pathway, and (3) the crassulacean acid metabolism (CAM) pathway. The latter is least efficient in terms of the amount of plant biomass formed per unit of energy received. Plants using the CAM pathway are, however, able to survive in harsh, arid environments that would be inhospitable to C3 and C4 plants. CAM photosynthesis will generally switch to C3 as soon as sufficient water becomes available (Shugart, 1998). The CAM pathways yield the highest biomass production, reflecting eco-exergy storage, under arid conditions, while the other two give highest net production (eco-exergy storage) under other conditions. While it is true that a gram of plant biomass produced by the three pathways has different free energies in each case, in a general way, improved biomass production by any of the pathways is consistent, under the conditions, with the eco-exergy storage hypothesis.

TABLE 7.4 Yields of kJ and ATP's/mol of Electrons, Corresponding to 0.25 mol of CH_2O Oxidized (Carbohydrates).

Reaction	kJ/mol e^-	ATP's/mol e^-
$CH_2O + O_2 = CO_2 + H_2O$	125	2.98
$CH_2O + 0.8\ NO_3^- + 0.8\ H^+ = CO_2 + 0.4\ N_2 + 1.4\ H_2$	119	2.83
$CH_2O + 2\ MnO_2 + H^+ = CO_2 + 2\ Mn_2^+ + 3\ H_2O$	85	2.02
$CH_2O + 4\ FeOOH + 8\ H^+ = CO_2 + 7\ H_2O + Fe^{2+}$	27	0.64
$CH_2O + 0.5\ SO_4^{2-} + 0.5\ H^+ = CO_2 + 0.5\ HS^- + H_2O$	26	0.62
$CH_2O + 0.5\ CO_2 = CO_2 + 0.5\ CH_4$	23	0.55

The released energy is available to build ATP for various oxidation processes of organic matter at pH = 7.0 and 25°C.

Leaf Size

Givnish and Vermelj (1976) observed that leaves optimize their size (thus mass) for the specific conditions. This may be interpreted to mean that they maximize their free energy content. Larger leaves have higher respiration and evapotranspiration, but also can capture more solar radiation. Deciduous forests in moist climates have a LAI of about 6 m^2/m^2 (see also Section 2.4). Such an index can be predicted from the hypothesis of highest possible leaf size, resulting from the trade-off between the benefits (sunlight capture) and costs (maintenance) (Givnish and Vermelj, 1976), which is even noticeable on leaves from different parts of the on the same plant such as sun and shade conditions. Leaf size in a given environment depends on the solar radiation and humidity regime, and in a general way, leaf size and LAI relationships are consistent with the hypothesis of maximum eco-exergy storage.

Biomass Packing

The general relationship between animal body weight, W, and population density, D, is $D = A/W$, where A is a constant (Peters, 1983). Highest packing of biomass depends only on the aggregate mass, not the size of individual organisms. This means that it is biomass rather than population size that is maximized in an ecosystem, as density (number per unit area) is inversely proportional to the weight of the organisms. Of course, the relationship is complex. A given mass of mice would not contain the same eco-exergy or number of individuals as an equivalent weight of elephants. Also, genome differences (Example 1) and other factors would figure in. Later we will discuss exergy dissipation as an alternative objective function proposed for thermodynamic systems. If this were maximized rather than storage, then biomass packing would follow the relationship $D = A/W^{0.65-0.75}$ (Peters, 1983). As this is not the case, biomass packing and the free energy associated with this lend general support for the eco-exergy storage hypothesis.

Cycling

If a resource (for instance, a limiting nutrient for plant growth) is abundant, then it will typically cycle faster. This is a little strange because cycling is not needed when a resource is nonlimiting. A modeling study (Jørgensen, 2002) indicated that free energy storage increases when an abundant resource cycles faster. Fig. 7.5 shows such results for a lake eutrophication model. The ratio of nitrogen (N) to phosphorus (P) cycling that gives the highest exergy is

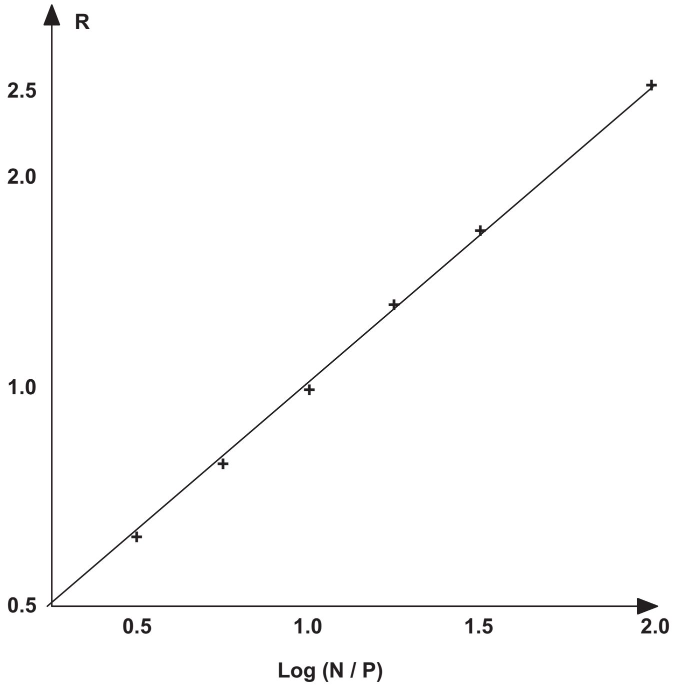

FIGURE 7.5 Log−log plot of the ratio of nitrogen to phosphorus turnover rates, R, at maximum exergy versus the logarithm of the nitrogen/phosphorus ratio, log N/P. The plot is consistent with Vollenweider (1975).

plotted in a logarithmic scale versus log(N/P) (Fig. 5.5). This plot is also consistent with empirical results (Vollenweider, 1975). Of course, one cannot "inductively test" anything with a model, but the indications and correspondence with data do tend to support in a general way the eco-exergy storage hypothesis. The cycling ratio giving the highest ascendency is also correlated similarly to the N/P ratio (Ulanowicz pers. comm.). In the light of the close relationship between eco-exergy and ascendency this result is not surprising (see above, Jørgensen, 1995; Ulanowicz et al., 2006).

Structurally Dynamic Modeling

Dynamic models whose structure changes over time are based on nonstationary or time-varying differential or difference equations. We will refer to these as *structurally dynamic models.* A number of such models, mainly of aquatic systems (Jørgensen, 1986, 1988, 1990; Nielsen, 1992a,b; Jørgensen and Padisak, 1996; Coffaro et al., 1997; Jørgensen and de Bernardi, 1997, 1998), but also as population dynamic models (Jørgensen, 2002) and terrestrial systems (Jørgensen and Fath, 2004a) have been investigated to see how structural changes are reflected in eco-exergy changes. Changes in parameters, and thus system structure, not only reflect changes in external boundary conditions but also mean that such changes are necessary for the ongoing maximization of exergy. For all models investigated along these lines, the changes obtained were in accordance with actual observations (see references). These studies therefore affirm, in a general way, that systems adapt their parameter values to maximize their content of eco-exergy. The shortcomings of assessing the eco-exergy content of an ecosystem were discussed above. At least in models, the applicability of eco-exergy calculations have shown their more practical use, which can be explained by robust model calculations.

It is noteworthy that Coffaro et al. (1997), in his structural-dynamic model of the Lagoon of Venice, did not calibrate the model describing the spatial pattern of various macrophyte species such as *Ulva* and *Zostera*, but used eco-exergy-index optimization to estimate parameters determining the spatial distribution of these species. He found good accordance between observations and model, which was able to explain more than 90% of the observed spatial distribution of various species of *Zostera* and *Ulva* (Box 7.4).

Seasonal Changes

In natural history, it is often observed, particularly at latitudes where there are winters, that taxonomically more primitive forms tend to pass through their nondormant phenological states earlier in growing seasons and more advanced forms later. It is as though ecosystems must be rebuilt after the "creative destruction" of winter, and until they are reconstituted, the active life-history stages of more complex forms of life cannot be supported. Does the maximum eco-exergy storage principle comply with the annual activity cycles of species and communities? Phenological fluctuations of biota, in fact the growth of individual organisms themselves are generally parallel to the four stages of succession, and also the four ecosystem growth and development forms (Jørgensen et al., 2000). This is true for the progression of individual species and their assemblages and is best seen at mid to high latitudes. Toward the tropics, a great variety of the life history stages of the rich assortment of species is expressed at any given time. At higher latitudes, phenological cycles are more obviously entrained to seasonal fluctuations. Focusing at midlatitudes, and letting "time" be relative to the unit in question (i.e., biological time, whether for a species or whole ecosystem), "winter" represents the initial condition (Stage 0). During "spring"," the growth and development forms unfold in quick succession. Form I dominates early (Stage I), Form II later (Stage II), and Form III in "summer"," which advances toward seasonal maturity (Stage III). Ephemeral species pass quickly through their own Stage III to seed set, dispersal, senescence (Stage IV), and often, disappearance. Permanent species remain more or less in Stage III until near the end of the growing season when they or their parts pass into quasi-senescent states (Stage IV), as in leaf fall and hibernation.

Eco-exergy storage and utilization patterns may be intuited from the principles laid down for succession (Figs. 7.7 and 7.8 related text) to follow these seasonal trends also, in mass, throughflow, and informational characteristics. In winter, biomass and information content are at seasonal lows. The observations of the seasonal changes may be considered an indirect support for the hypothesis. In spring, the flush of new growth (dominantly Form I) produces rather quickly a significant biomass component of exergy (Fig. 7.8), but the information component remains low due to the fact that most active flora, fauna, and microbiota of this nascent period tend to be lower phylogenetic forms.

These lower forms rapidly develop biomass but make relatively low informational contributions to the stored eco-exergy. As the growing season advances, in summer, Growth and Development Forms II and III become successively

BOX 7.4

ILLUSTRATION OF STRUCTURALLY DYNAMIC MODELING

Jørgensen and Fath (2004b) developed a structurally dynamic model of Darwin's finches reflecting the comprehensive available knowledge. The main feature of the model was the validation of the changes in the beak size as a result of climatic changes, which led to variation in the amount, availability, and quality of the seeds that compromise the finches' food. The medium ground finches, *Geospiza fortis*, on the island Daphne Major were selected due to very detailed information found in Grant (1986). The model has three state variables: seed, Darwin's Finches adult, and Darwin's finches juvenile. The juvenile finches are promoted to adult finches 120 days after birth. The mortality of the adult finches is expressed as a normal mortality rate (Grant, 1986) + an additional mortality rate due to food shortage and an additional mortality rate caused by a disagreement between bill depth and the size and hardness of seeds.

The beak depth can vary between 3.5 and 10.3 cm (Grant, 1986), the beak size $= \sqrt{DH}$, where D is the seed size and H the seed hardness which are both dependent on the precipitation, particularly during January−April(Grant, 1986). Grant (1986) determines a handling time for the finches for a given $\sqrt{DH}$ as function of the bill depth, which explains that the accordance between $\sqrt{DH}$ and the beak depth becomes an important survival factor. The relationship is used in the model to find a function called "diet" which is compared with $\sqrt{DH}$ to find how well the bill depth fits to the $\sqrt{DH}$ of the seed. This fitness function is based on information given by Grant (1986) about the handling time. It influences, as mentioned above, the mortality of adult finches, but has also impacts the number of eggs laid and the mortality of the juvenile finches. The growth rate and mortality of seeds are dependent on the precipitation which is a forcing function know

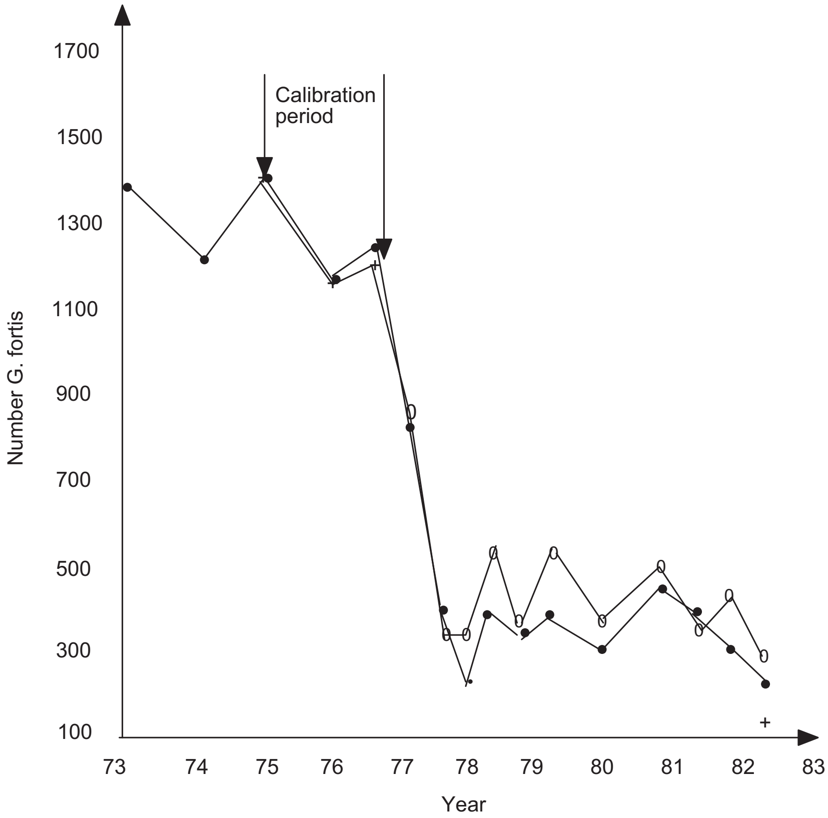

FIGURE 7.6 The observed number of finches (•) from 1973 to 1983, compared with the simulated result (0). 75 and 76 were used for calibration and 77/78 for the validation referred to in Box 6.5.

BOX 7.4 (*cont'd*)

as function of time (Grant, 1986). A function called food shortage is calculated from the known food requirements (Grant, 1986), and from the food available (the seed state variable). Food shortage influences the mortality of juvenile finches and adult finches; and, the seed biomass and number of *G. fortis* as function of time from 1975 to 1982 are known (Grant, 1986). The values from 1975 to 1976 were used to calibrate the following parameters:

i) the influence of the fitness function on (1) adult finches mortality, (2) juvenile finches mortality, and (3) the number of eggs laid;
ii) the influence of food shortage on the mortality of adult and juvenile finches is known (Grant, 1986). The influence is therefore calibrated within a narrow range of values;
iii) the influence of precipitation on the seed biomass (growth and mortality).

All other parameters are known from the literature.

The eco-exergy density is calculated (estimated) as 275 × the concentration of seed + 980 × the concentration of Darwin's finches (see Table 7.2). The model algorithm searches every 15 days if a feasible change in the beak size, given the generation time and the variations in the beak size into consideration, will give a higher eco-exergy. If it is the case, then the beak size is changed accordingly. The modeled changes in the beak size were confirmed by the observations. The model results of the number of Darwin's finches are compared with the observations (Grant, 1986) in Fig. 7.6. The standard deviation between modeled and observed values was 11.6% and the correlation coefficient, r^2, for modeled versus observed values is 0.977. The results of a nonstructural dynamic model would not be able to predict the changes in the beak size and would therefore give too low values for the number of Darwin's finches because their beak would not adapt to the lower precipitation yielding harder and bigger seeds.

dominant. Following the expansion of system organization that this represents, involving proliferation of food webs and interactive networks of all kinds, and all that this implies, waves of progressively more advanced taxonomic forms can now be supported to pass through their life cycles. Albedo and reflection are reduced, dissipation increases to seasonal maxima following developing biomass, and as seasonal maxima are reached, further increments

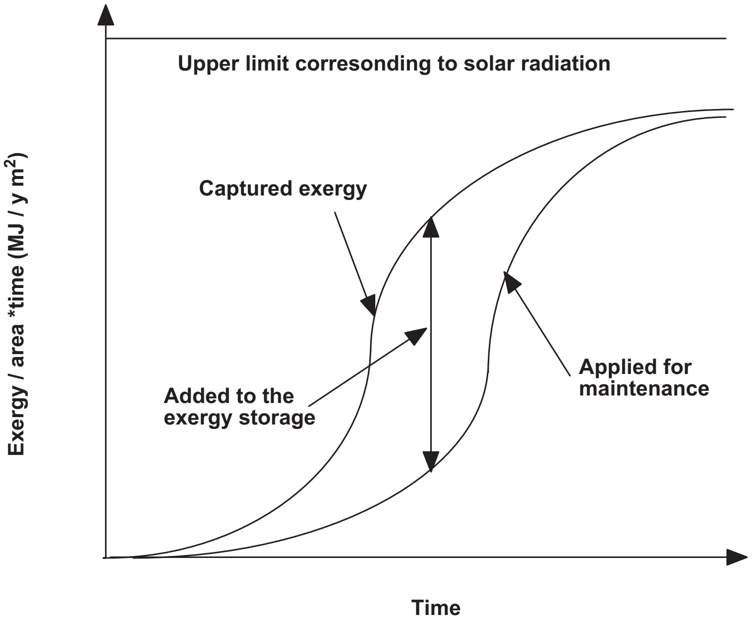

FIGURE 7.7 Exergy utilization of an ecosystem under development is shown versus time. Notice that the consequence of the growth in exergy is increased utilization of exergy for maintenance.

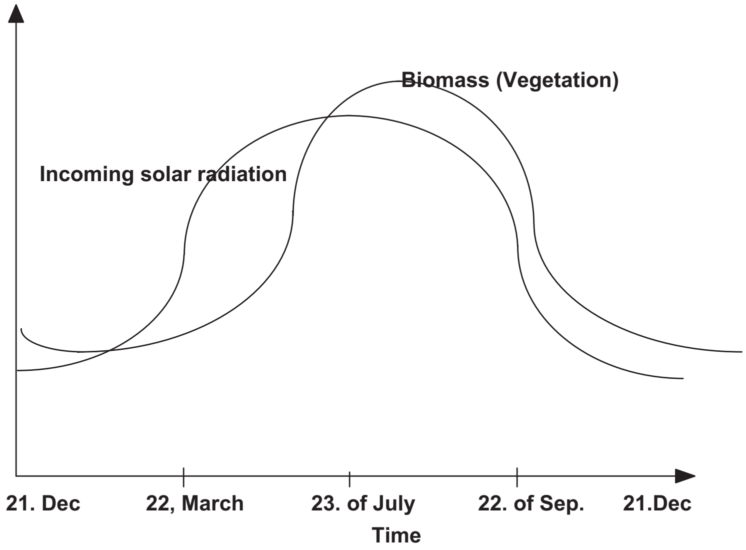

FIGURE 7.8 The seasonal changes in incoming solar radiation and biomass (vegetation) are shown for a typical temperate ecosystem. The slope of the curve for biomass indicates the increase in exergy due to Growth Form I. The Growth Form I can continue as long as the captured solar radiation is larger than the exergy applied for maintenance. Therefore the biomass has its maximum at about August 1. The biomass is at minimum about the February 1 because at that time is the captured exergy and the exergy applied for maintenance in balance.

taper to negligible amounts (Fig. 7.8). The biotic production of advancing summer reflects more and more advanced systemic organization, manifested as increasing accumulations of both biomass and information to the exergy stores. In autumn, the whole system begins to unravel and shut down in pre-adaptation to winter, the phenological equivalent of senescence. Networks shrink, and with this all attributes of eco-exergy storage, throughflow, and information transfer decline as the system slowly degrades to its winter condition. Biological activity of the ecosystem returns to more "primitive" states of eco-exergy organization required for adaptation to winter. The suggestion from phenology is that the exergetic principles of organization apply also to the seasonal dynamics of ecosystems.

7.7 TOWARD A CONSISTENT ECOSYSTEM THEORY

Ecosystem properties can only be revealed by a plurality of views. It is therefore not surprising that there are many different ecosystem theories published in the scientific literature. It is also important to try to understand the theories in relation to each other and examine if they are contradictory or form a pattern that can give a better understanding of the nature of ecosystems and to solve the global environmental problems. The goal is to give a common framework of reference for *further* development of a more profound and comprehensive ecosystem theory than the one we are able to present today. The next stage will be more holistic, comprehensive, and empirical, but in the meantime the framework proposed here is a good working platform. This pattern should serve as a "conceptual diagram"," which can be used as a basis for further discussion of ecosystems. We are still in an early stage of an ecosystem-theoretical development. Modeling has taught us that it is better to consolidate one's thoughts in a conceptual diagram at an early stage and then be ready to make changes than to let all modeling efforts wait until all details are known, as this will never be the case due to the immense complexity of nature (Jørgensen, 2002). Moreover, recent development in ecosystem theory has made it possible to conclude that the theories presented here are indeed consistent and complimentary (Fath et al., 2001). The special issue in Ecological Modeling 158.3 (2002) has demonstrated that the theory can be applied to explain ecological observations, although the ecosystem theory presented here does not contain laws in the classical physical sense that we can make exact predictions. The theory is rather closer to quantum mechanics (we have to accept an uncertainty), chaos theory (sometimes predictions of complex systems are impossible), and the Prigogine thermodynamics (all processes are irreversible). Given the limitations in our theory, that ecosystems are enormously complex and we can therefore not know all details and that ecosystems have an ontic openness (see Chapter 3), it is still possible to apply the theory in ecology and environmental management.

The core pattern concerns the systemness of life, and how these interactions lead to complex organization and dynamics. Understanding, measuring, and tracking these patterns is of paramount importance and the various holistic indicators have been developed to do so. Taken together, we can use this systems-oriented thermodynamic approach to formulate a limited number of propositions or hypotheses to explain a very large number of ecological observations. These recent developments in systems ecology represent a profound paradigm shift. The paradigm that is now receding has dominated our culture for several hundred years. It views the universe as a mechanical system composed of elementary building blocks. The new paradigm is based on a holistic worldview. The world is seen as an integrated whole and recognizes the fundamental interdependence of all phenomena.

In the paper by Jørgensen et al. (2000), Fig. 7.9 illustrated the concomitant development of ecosystems, exergy captured (most of that being degraded), and eco-exergy stored (biomass, structure, information). Data points correspond to different ecosystems (see Table 7.5, which shows the values). Debaljak (2001) showed the same shape of the curve when determining exergy captured and eco-exergy stored in managed forest and virgin forest on different stages of development (Fig. 7.10). The exergy captured was determined as in Table 7.5 by measuring the temperature of the infrared radiation, while the coexergy storage was determined by a randomized measurement of the size of all trees and plants. The stages are indicated on the figure, where also pasture is included for comparison. Catastrophic events as storm or fire may cause destructive regeneration, which is described below.

Holling (1986), see Fig. 7.11 has suggested how ecosystems progress through the sequential phases of renewal (mainly Growth and Development Form I), exploitation (mainly Growth and Development Form II), conservation (dominant Growth and Development Form III), and creative destruction. The latter phase fits also into the four growth and development forms, but will require a further explanation. The creative destruction phase is either a result of external or internal factors. In the first case (for instance, hurricanes and volcanic activity), further explanation is not needed as an ecosystem has to use the growth and development forms under the prevailing conditions, which are determined by the external factors. If the destructive phase is a result of internal factors, then the question is "why would a system be self-destructive?"

A possible explanation is that the onset of some senescence that weakens the robustness and buffer capacity of the ecosystem as it ages. For example, once in the conservation phase, almost all nutrients will be contained in organisms, leaving little or no nutrients available to test new and possibly better solutions to move further away from

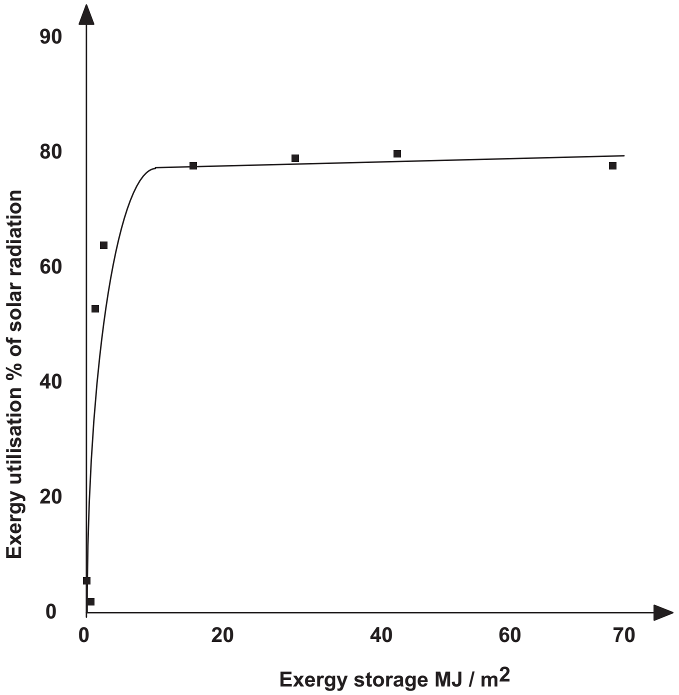

FIGURE 7.9 The exergy captured (Kay and Schneider, 1992, % of solar radiation) is plotted versus the exergy stored (unit J/m^2 or J/m^3), calculated from characteristic compositions of the focal eight ecosystems. The numbers from Table 6.5 are applied to construct this plot. Notice that exergy utilization is parallel (proportional) to energy absorbed.

TABLE 7.5 Exergy Utilization and Storage in a Comparative Set of Ecosystems.

Ecosystem	Exergy Utilization, %	Eco-exergy Storage, MJ/m^2
Quarry	6	0
Desert	2	0.073
Clear-cut forest	49	0.594
Grassland	59	0.940
Fir plantation	70	12.70
Natural forest	71	26.00
Old-growth deciduous forest	72	38.00
Tropical rain forest	70	64.00

thermodynamic equilibrium. Therefore, the next stage, collapse, can open up new opportunities and new beginnings (Fath et al., 2015). Holling also recognizes this by calling the release phase as "creative destruction."

In the long run, it is beneficial for the ecosystem to decompose the organic nutrients into inorganic components that can be utilized to test the new solutions. The creative destruction phase can be considered a method to utilize the three other phases and the four growth and development forms more effectively (Fath et al., 2004). This is indicated on the figure as "trend of each further cycle" and it is shown that the ecosystem is moving toward a higher specific exergy (and biomass if possible, as growth of biomass is dependent on the available amount of the limiting element), if the inorganic components are available to form more biomass for each cycle (Fig. 7.12).

Five of the presented hypotheses to describe ecosystem growth and development are examined with respect to four growth and development forms, excluding the boundary growth:

A. Entropy production tends to be minimum (proposed by Prigogine (1947, 1955, 1980) for linear systems at steady nonequilibrium state, not for far from equilibrium systems). Mauersberger (1981, 1983, 1995) applied this to

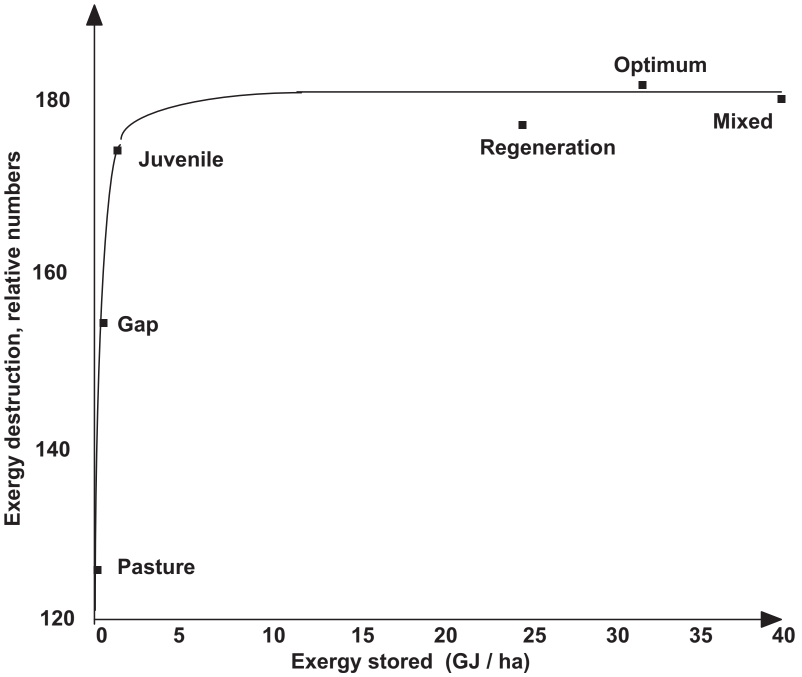

FIGURE 7.10 The plot shows the result by Debeljak (2002). He examined managed a virgin forest in different stages. Gap has no trees, while the virgin forest changes from optimum to mix to regeneration and back to optimum, although the virgin forest can be destroyed by catastrophic events as fire or storms. The juvenile stage is a development between the gap and the optimum. Pasture is included for comparison.

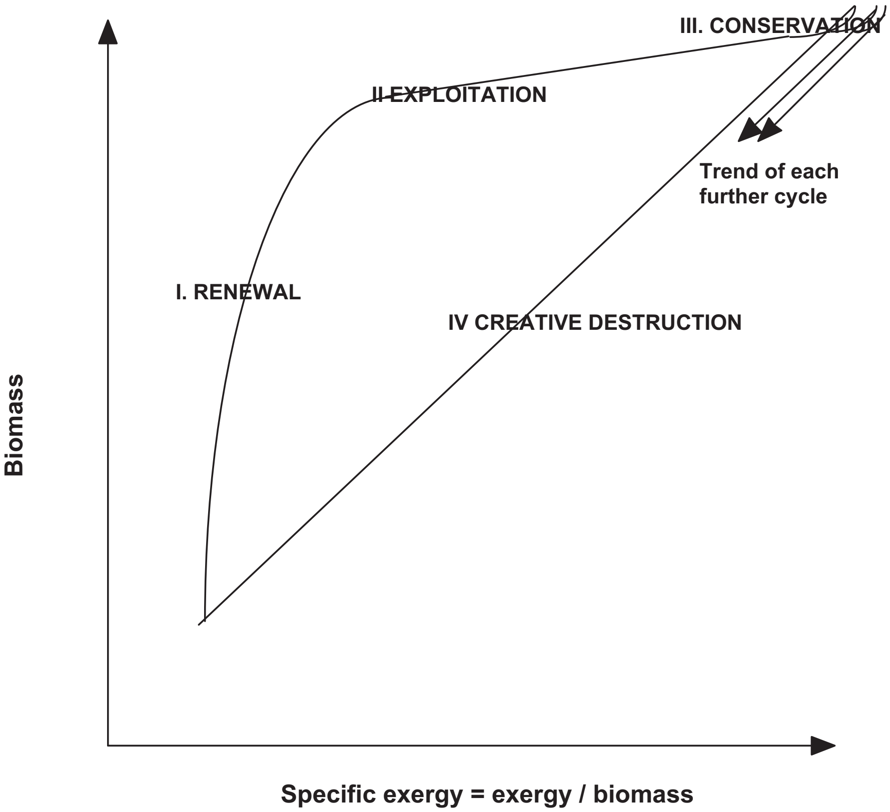

FIGURE 7.11 Holling's four phases of ecosystems, described terms of biomass versus specific exergy. The presentation is inspired by Ulanowicz (1997).

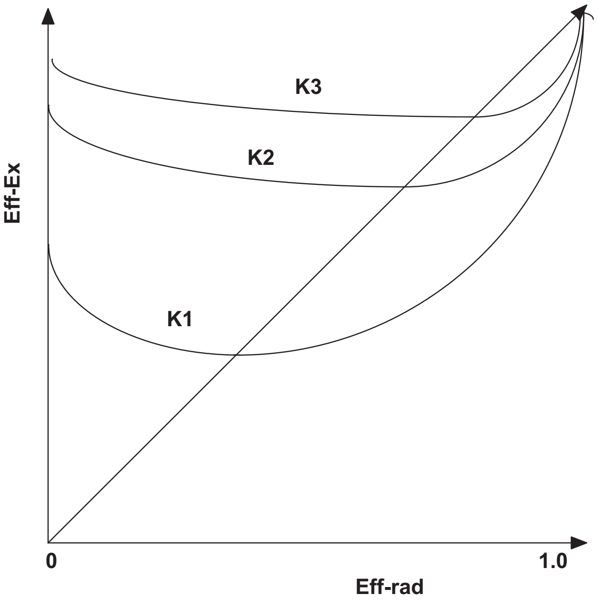

FIGURE 7.12 η_{Ex} is plotted versus η_{rad} for three information level $K_3 > K_2 > K_1$. Increasing Kullback's measure of information implies that the ecosystem will generate more information up to a higher η_{rad}.

derive expressions for bioprocesses at a stable stationary state (see also Chapter 2). Reduction of the entropy production means that the energy utilization is increased, which is obtained by an increased cycling of the energy and reduced loss of energy to the environment, or expressed differently: the retention time of a given portion of energy in the system is increased.

B. Natural selection tends to maximize the energy flux through the system, so far as compatible with the constraints to which the system is subject (Odum, 1983). This is the maximum power principle; see Section 7.4.

C. Ecosystems organize to maximize exergy degradation (Kay, 1984). Living systems transform more exergy to heat at the temperature of the environment, or said differently, produce more entropy, than their nonliving complements. Living systems therefore increases the destruction of exergy but at the same time living systems increase the order and organization.

D. A system that receives a throughflow of exergy will move away from thermodynamic equilibrium, and the system has the propensity to select the organization that gives the system as much stored eco-exergy as possible, see Section 7.5, Jørgensen and Mejer (1977, 1979), Jørgensen (1982, 2002), Mejer and Jørgensen (1979).

E. Ecosystem have a propensity to develop toward an optimization of robustness, which is a measure of the trade-off between the articulation (ascendency) and redundancy (Ulanowicz, 2018); see Section 7.5.

The usual description of ecosystem development illustrated, for instance, by the recovery of Yellowstone Park after fire, an island formed after a volcanic eruption, reclaimed land, etc. is well covered by Odum (1969): at first the biomass increases rapidly which implies that the percentage of captured incoming solar radiation increases but also the energy needed for the maintenance. Growth and development Form I is dominant in this first phase, where eco-exergy stored increases (more biomass, more physical structure to capture more solar radiation), but also the throughflow (of useful energy), exergy dissipation, and the entropy production increases due to increased need of energy for maintenance. Living systems are effectively capturing (lower the albedo) and utilizing energy (exergy) (both the exergy decomposed due to respiration and the exergy stored in the living matter are increased) from the ambient physical systems.

Growth and Development Forms II and III become, in most cases, dominant later, although an overlap of the three forms takes place. A smaller ecosystem will have a high relative openness (see Chapter 2), which allows Forms II and III to operate more quickly as refuge species recolonize the space. Patrício et al. (2006) examined the recovery of small intertidal rocky communities finding that biodiversity and specific eco-exergy (= eco-exergy/biomass) recover much faster than biomass and eco-exergy, i.e., that the Forms II and III are dominant in the initial phase of recovery.

When the percentage of solar radiation captured reaches about 80%, it is not possible to increase the amount of captured solar radiation further (due in principle to the second law of thermodynamics). Further growth of the physical structure (biomass) does therefore not improve the exergy balance of the ecosystem. In addition, all or almost all the essential elements are in the form of dead or living organic matter and not as inorganic compounds ready to be used for growth. Therefore, Form I will and cannot proceed, but Growth and Development Forms II and III can still operate. The ecosystem can still improve the ecological network and can still evolve novel, more complex organisms and environments. One tendency is to increase the occurrence of larger, longer-lived organisms (Cope's law: the later descendant may be increasingly larger than their ancestors; for instance, the horse today is much bigger than the horse fossils from 20 to 30 million years ago). Growth and Development Forms II and III are efficient energetically, and do not require more exergy for maintenance. Exergy degradation is therefore not increasing but is maintained at a constant level (see Figs. 7.9 and 7.10). The accordance with the five descriptors + specific entropy production and the four growth and development forms based on this description of ecosystem development is shown in Table 7.6 (see also Fath et al., 2001).

I. Biomass Growth is the increase in physical structure of the ecosystem, which occurs primarily by the capture and conversion of incoming solar radiation into organic compounds. This first stage implies that more exergy is degraded due to an increased demand constructing and maintaining biomass. The most dynamic indicator of this form is the exergy degradation, although the eco-exergy storage, throughflow, and ascendency also will increase. While there is an upper limit to the amount of solar radiation available, and to the amount that can be harvested by ecosystems, system development continues through Forms II and III.

II. Network Growth and Development entails a richer, more complex interaction structure, which through increased cycling offers better utilization of the available energy. In turn, both throughflow and exergy storage increase without an increase in exergy degradation. It means that specific exergy degradation and specific entropy production are decreasing during this stage. Throughflow, eco-exergy, specific, and eco-exergy can all be used as dynamic indicators for this growth form.

TABLE 7.6 Growth and Development (G&D) Forms and the Proposed Descriptors. Note, in addition to the three mentioned in the text this includes Form 0 which is boundary growth when the ecosystem receives a greater amount of energy across its boundary.

	G&D	G&D	G&D	
Hypothesis	**Form 0**	**Form I**	**Form II**	**Form III**
Eco-exergy storage	Up	Up	Up	Up
Power/throughflow	Up	Up	Up	Up
Exergy dissipation	Up	Up	Equal	Equal
Retention time	Equal	Equal	Up	Up
Entropy production	Up	Up	Equal	Equal
Exergy/Biomass = specific exergy	Equal	Equal	Up	Up
Entropy/biomass = spec. entropy prod.	Equal	Equal	Down	Down
Ratio indirect/Direct effects	Equal	Equal	Up	Up
Retention time	Equal	Equal	Up	Up

III. Information Growth and Development represents an increase in the genetic and organizational diversity in the ecosystem. One way this occurs is through an increase in the number of species with longer and more complex life histories, larger body size, and complex physiologies. This implies that, similar to Form II, throughflow and eco-exergy storage increase while specific exergy degradation and entropy production decrease. Eco-exergy and specific eco-exergy can all be used as indicators for this growth and development form, with specific eco-exergy capturing the genetic information.

7.8 SUMMARY AND CONCLUSIONS

Ecosystems have a very complex dynamics. It is rooted in the enormous number of different life forms that is the result of the enormous variability in the interplay of life and environment. Ecosystem development can be described by a wide spectrum of ecological indicators and orientors from single species and concentrations of specific chemical pollutants to holistic indicators such as biodiversity and thermodynamic functions. Physical—chemical systems can usually be described by matter and energy relations, while biological systems require a description that encompasses matter, energy, and information.

Due to the high complexity of ecosystems, it is, however, not possible to apply these different descriptors of ecosystem dynamics for the entire ecosystems with all its detailed information, but only for models of ecosystems. Dependent on the knowledge about the ecosystem, it can be advantageous to apply eco-exergy (when the concentrations or biomasses of the focal species are known), ascendency (when a good model of the ecological network is known) or power (when the flows are known). Eco-exergy can be found as the sum of the concentrations and weighting factors considering the information that the various organisms are carrying. Eco-exergy indicates the distance from thermodynamic equilibrium according to the definition, while emergy indicates the cost in terms of solar radiation. The ratio between the two thermodynamic concepts, exergy/emergy, indicates the efficiency of the system—more efficiency if more exergy is obtained relatively to the solar radiation. In Chapter 10, it is shown how this ratio can be applied as a powerful indicator for an ecosystem.

Ecosystems have four growth and development forms or methods to move away from thermodynamic equilibrium: boundary, biomass, network, or information. When an ecosystem has attained a certain level of energy capture, it will be able to continue to generate organismal and structural information such that eco-exergy, throughflow, and ascendency increase throughout development without necessarily an increase in the physical biomass. The abovementioned three descriptors, eco-exergy, power, and ascendancy, will all increase with the four growth and development forms, while exergy destruction and entropy production only increases with the first growth form and specific entropy only decreases with the second and third growth form.

CHAPTER

8

Ecosystems Have Complex Dynamics—Disturbance and Decay

Du siehst, wohin du siehst nur Eitelkeit auf Erden.
Was dieser heute baut, reißt jener morgen ein:
Wo itzund Städte stehn, wird eine Wiese sein
Auf der ein Schäferskind wird spielen mit den Herden:

Was itzund prächtig blüht, soll bald zertreten werden.
Was itzt so pocht und trotzt ist morgen Asch und Bein
Nichts ist, das ewig sei, kein Erz, kein Marmorstein.
Itzt lacht das Glück uns an, bald donnern die Beschwerden.

Der hohen Taten Ruhm muß wie ein Traum vergehn.
Soll denn das Spiel der Zeit, der leichte Mensch bestehn?
Ach! was ist alles dies, was wir für köstlich achten,

Als schlechte Nichtigkeit, als Schatten, Staub und Wind;
Als eine Wiesenblum, die man nicht wiederfind't.
Noch will, was ewig ist, kein einig Mensch betrachten! ***Andreas Gryphius, 1616–64: Es ist alles eitel***

8.1 THE NORMALITY OF DISTURBANCE

Up to this point, the focus of this book has been on growth and development processes in ecosystems. In fact, these are most important features of ecosystem dynamics and they provide the origins of various emergent ecosystem properties. But the picture remains incomplete if disturbance and decay are not taken into account. On the following pages, we will try to include those "destructive" processes into the "new" ecosystem theory as elaborated in this book. As a starting point for these discussions, we can refer to common knowledge and emotion, as it is described in the poem of Andreas Gryphius *(see above)* who outlines the transience of human and environmental structures: Nothing lasts forever, towns will turn into meadows, flourishing nature easily can be destroyed, our luck can turn into misfortune, and in the end, what remains is emptiness, shadow, dust, and wind. Although the poet seems to be comprehensible concerning the significance of decay, we cannot agree with his pessimistic ultimate: In the end, the inevitable death of organisms and disturbance of ecosystems can be useful elements of the growth, development, and survival of the whole structure, i.e., if they expire within suitable thresholds and if we observe their outcomes over multiple scales.

On a small scale, we can notice that the individual living components of ecosystems have limited life spans that range from minutes to millennia (see Table 8.1). For any species, environmental conditions play a role in the life expectancy. Average human life expectancy is around 70 years but ranges from 52 years in Afghanistan to 89 years in Monaco. As life expectancy increases and death rates drop, birth rates need to fall even more to maintain stable populations, a goal for any species working within the constraints of a carrying capacity (meaning all species, including humans). Death and decay of *organisms* and their subsystems are integral elements of natural dynamics. From a functional viewpoint, these processes are advantageous, to replace highly loaded or exhausted components (e.g., short life expectancies of some animal cells), or to adjust physiologies to changing environmental conditions (e.g., leaf litter fall in autumn). As a consequence of these processes, energy and nutrients are provided for the saprophagous branches of food webs, which in many cases show higher turnover rates than the phytophagous branches of the energy and nutrient flow networks. In those situations of death, self-organized units give up their

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TABLE 8.1 Some Data About Life Expectancies of Cells and Organisms.

Example	Average Life Span
Generation time of *Escherichia coli*	20 min
Life spans of some human cells	
- Small intestine	1–2 days
- White blood cells	1–3 days
- Stomach	2–9 days
- Liver	10–20 days
Life span of some animals	
- Water flea	0.2 years
- Mouse	3–4 years
- Nightingale	4 years
- Dog	12–20 years
- Horse	20–40 years
- Human	67 years
- Giant tortoise	177 years
Life span of some plants	
- Sunflower	1 year
- *Corylus avellana*	4–10 years
- *Fagus sylvatica*	200–300 years
- *Pinus aristata*	4900 years

autonomy and their ability to capture and actively transform exergy, their structures are subject to dissipation, reactivity, self-regulation, and the ability for replication and repair are desist, releasing the internal order and constituents which thus potentially become ingredients of the higher system-level self-organization (see Chapter 3).

Also, *populations* have limited durations at certain places on earth. Operating in a hierarchy of constraints, populations break down, e.g., if the exterior conditions are modified, if imperative resources are depleted, if the living conditions are modified by human actions, or if competition processes result in a change of the community assemblage. Following the thermodynamic argumentation of this book (see Chapters 2 and 7), in these situations a modified collection of organisms will take over, being able to increase the internal flows and to reduce the energetic, material, and structural losses into the environment in a greater quantity than the predecessors. During such processes, of course, only the very immediate conditions can be influential: The developmental direction is defined due to a short-term reaction, which increases orientor values at the moment the decision is made, on the basis of the disposable elements and the prevailing conditions. Thereafter, the structural fate of the system is defined by new constraints, an irreversible reaction has taken place, and the sustainability of this pathway will be an object of the following successional processes.

Of course, such community dynamics have consequences for the environmental processes and structures. There is an interplay between the life processes and the perceived abiotic processes. In fact, we (Fath and Müller, 2019) have proposed a new term, *conbiota*—with biota, to capture the deep dependency that environmental features (such as temperature, humidity, soil chemistry, etc.) have on ecological processes. Therefore, also *ecosystems* themselves exist for a limited period of time only. Their typical structural and organizational features are modified, if the external conditions change significantly, but also if due to internal competition processes certain elements attain dominance displacing other species. These processes can be observed on many different scales with distinct temporal characteristics: Slow processes can occur as results of climatic changes (e.g., postglacial successions throughout the Holocene), shifts of biomes (e.g., Pleistocene dynamics of rain forests), or continuous invasions of new species. On the contrary, abrupt processes often modify ecosystems very efficiently within rather short periods of time.

The most commonly known extreme event has taken place at the end of the Cretaceous age, 65 million years ago, when—purportedly due to an asteroid impact—enormous changes of the global community structures took place: on land no organism bigger than 25 kg survived, planktonic foraminifera went extinct by 83%, the extinctions of ammonites reached 100%, marine reptiles were affected by 93%, and the nonavian dinosaurs were driven totally extinct. No doubt, this was a big loss of biodiversity, and many potential evolutionary pathways disappeared; but, as we know 65 million years later, this event was also a starting shot for new evolutionary traits and for the occupation of the niches by new species, e.g., for the rapid development of mammals or organisms which are able to read and write books (see Box 8.1).

BOX 8.1

CREATIVITY NEEDS DISTURBANCE (SEJ)

Necessity is the Mother of Invention

Constraints mean problems, but problems require solutions, and (new) solutions require creativity. Let us exemplify this by two evolutionary processes, the genetic code and language. The constraints in the chemical beginning of the evolution were that whenever a primitive but relatively well-functioning assemblage of organic molecules was formed, the composition that made the entity successful was forgotten with its breakdown. The next entity would have to start from scratch again. If at least the major part of the well-functioning composition could be remembered, then the entities would be able to improve their composition and processes generation by generation.

For organisms the problem is to survive. When new living conditions are emerging, the accompanying problems for the phenotypes are solved by new properties of the genotypes or their interactions in the ecological networks. Survival based on the two growth and development forms “biomass growth” and “network growth” occurs by adaptation to the currently changed prevailing conditions for life. But information growth is needed, too, because survival under new emergent conditions requires a system to transfer information to make sure that solutions are not lost. The problem on the need for information transfer has been solved by the development of a genetic system that again puts new constraints on survival. Fitting into the environmental structures to survive is possible due to an adopted genetic system. Furthermore, genes have created new possibilities because mutations and, later in the evolution, sexual recombinations create new possible solutions. Therefore, as shown in Fig. 8.1, what starts with constraints and new and better properties of the organisms or their ecological networks ends up as new possibilities through a coding system that also may be considered initially as a constraint.

An organism’s biochemistry is determined by the composition of a series of enzymes that again are determined by the genes. Successful organisms will be able to produce more offspring than less successful organisms and as the gene composition is inherited, the successful properties will be more and more represented generation after generation. This explains that evolution has directed more and more complex organisms that have new and emerging properties.

The genetic code is a language or an alphabet. It is a constraint on the living organisms that have to follow the biochemical code embodied in the genes. The sequence of three amino bases with four possibilities determines the sequence of amino acids in the proteins. There are $4 \times 4 \times 4 = 64$ different codings of the three amino bases; but as there are only 20 amino acids to select from, the amino base coding contains redundant combinations in the sense that for some amino acids two or more combinations of amino bases are valid. As an alphabet is a constraint for a language (certain combinations are acceptable and convey meaning and others do not), the genetic code is a constraint for a living organism. But as the alphabet gives a writer almost unlimited opportunities to express thoughts and feelings, so the genetic code has

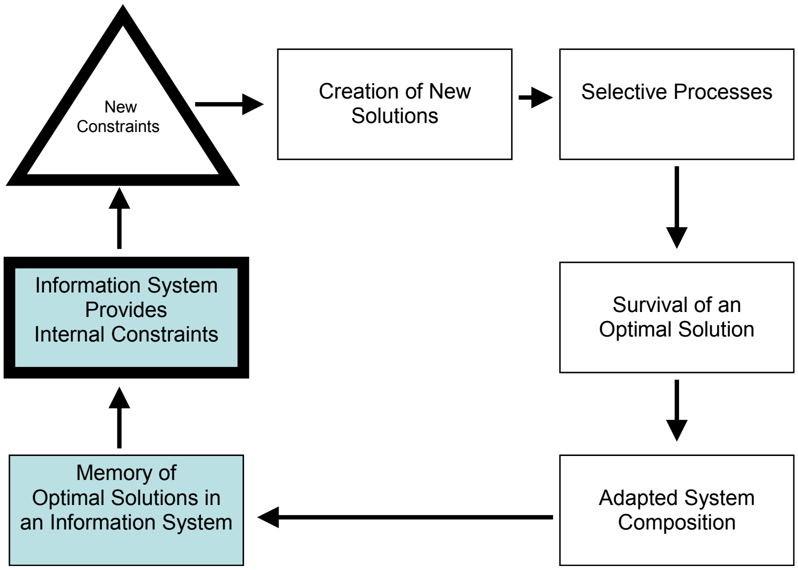

FIGURE 8.1 Life conditions are currently changed and have a high variability in time and space. This creates new challenges (problems) to survival. Organisms adapt or a shift to other species takes place. This requires an information system that is able to transfer the information about good solutions to the coming generations of organisms. Consequently, an information system is very beneficial, but it has to be considered as a new source of constraints that however can open up for new possibilities.

Continued

BOX 8.1 *(cont'd)*

given living organisms opportunity to evolve, becoming more and more complex, more and more creative, having more and more connectivity among the components and becoming more and more adaptive to the constraints that are steadily varying in time and space. The genetic code, however, has not only solved the problem associated with these constraints, but it has also been able to give the living organisms new emergent properties and has enhanced the evolution.

When the human language was created a couple of million years ago, it first provided new constraints for humans. They had to learn the language and use it, but once they mastered the language it also gave new opportunities because it made it possible to discuss cooperation such as a better hunting strategy, which would increase the possibility for survival. Written language was developed to solve the problem of making the message transfer more independent of time and space. To learn to write and read were new constraints to humans that, however, also opened many new possibilities of expressing new ideas and thoughts and thereby moving further away from thermodynamic equilibrium. Animals also communicate through sounds for warnings or chemicals, for instance, by marking of hunting territories with urine. The use of these signals has most likely been a factor that has reduced the mortality and increased the chance of survival.

We will use a numeric example to illustrate the enormous evolutionary power of genes to transfer information from generation to generation. If a chimpanzee would try to write this book by randomly using a computer keyboard, the chimpanzee would not have been able to write the book even if he started at the big bang 15 billion years ago, but if we could save the signs that were correct for the second round and so on, then 1/40 of the volume would be correct in the first round (assuming 40 different symbols on the keyboard), $(39 \times 39)/(40 \times 40)$ would still be incorrect after the second round, $(39 \times 39 \times 39)/(40 \times 40 \times 40)$ after the third round, and so on. After 500 rounds, which may take a few years, there would only be 5 "printed" errors left, if we presume that this book contains 500 000 signs. To write one round of the volume would probably require 500,000 s or about a week. To make 500 rounds would therefore take about 500 weeks or about 9 years.

The variation in time and space of the conditions for living organisms has been an enormous challenge to life (see Chapter 7) because it has required the development of a wide range of organisms. Living nature has met the challenge by creating enormous differentiation. There are 8.7 million known species on earth with new ones discovered daily. It is estimated that the earth has about 10^7 species. We see the same pattern as we have seen for the genetic constraints: the constraints are a challenge for nature, but the solution gives new emergent possibilities with an unexpected creative power.

Table 8.2 shows that there have been several extinction events during the history of the Earth. An interesting hypothesis concerning global extinction rates was published by Raup and Sepkoski (1986): The authors have observed the development of families of marine animals during the last 250 million years. Their result, which is still discussed very critically in paleontology, was that mass extinction events seem to have occurred at rather regular temporal intervals of approximately 26 million years. Explanations were discussed as astronomic forces that might operate with rather precise schedules, as well as terrestrial events (e.g., volcanism, glaciation, sea level change). We will have to wait for further investigations to see whether this hypothesis has been too daring.

Today, we can use these ideas to rank the *risk of perturbations* in relation to their temporal characteristics: While mass extinctions seem to be rather rare (Table 8.2), smaller perturbations can appear more frequently (Fig. 8.2). In hydrology, floods are distinguished due the temporal probability of their occurrence: 10-, 100-, and 1000-year events are characterized not only by their typical probabilities (translated into typical frequencies) but also by their extents. The rarer the event is, the higher is the risk of the provoked damages. A 100-year flood will result in bigger disturbances than a 10-year event. Also, the effects of other disturbance types can be ordered due to their "typical frequencies" (Table 8.3). An often discussed example is fire. The longer the period between two events, the higher is the probability that the amount of fuel (accumulated burnable organic material) has also increased, and therefore the consequences will be higher if the fire interval has been longer. Similar interrelations can be found concerning

TABLE 8.2 Five Significant Mass Extinctions.

Geological Period	Million years bp	Families Lost	Potential Reason
Ordovician	440	25%	Sudden global cooling
Devonian	370	19%	Global climate change
Permian	245	54%	Global climate change induced by a bolide
Triassic	210	23%	Under debate, but leading theory is climate change and sea level rise
Cretaceous	65	17%	Asteroid strike

After Eldredge, N., 1998. Life in the Balance: Humanity and the Biodiversity Crisis. Princeton University Press, Princeton, NJ, 224 pp.

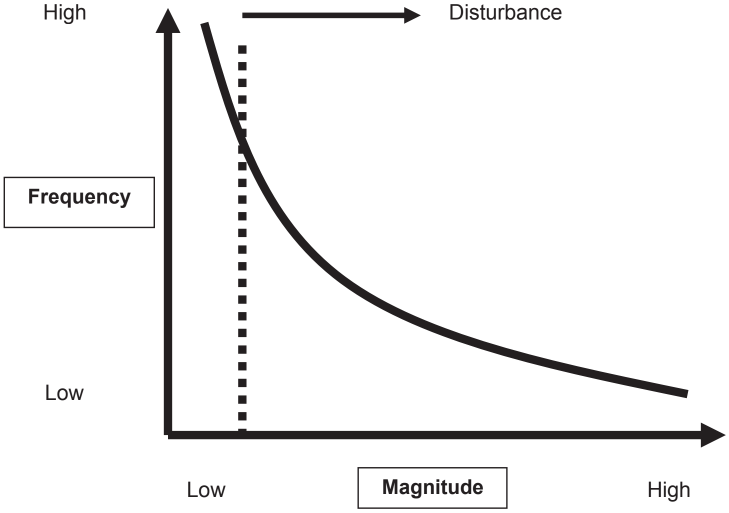

FIGURE 8.2 Interrelationship between frequencies and magnitudes of perturbations and disturbances. *After White, P.S., Jentsch, A., 2001. The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62, 2—3. Checkliste ffir die Anwendung. In: Frfinzle, O., Miiller, F., Schröder, W. (Eds.), Handbuch der Umweltwissenschaften, Chapter III. Ecomed-Verlag, Landsberg, pp. 2—3.*

TABLE 8.3 Temporal Characteristics of Some Disturbances.

Example	Typical Temporal Scale (Orders of Magnitude)
Plate tectonics	~ 10^5 years
Climatic cycles	~ 10^4 years
Killing frost	~ 10^2 years
Drought cycles	~ 10^1 years
El Nino	~ 10^1 years
Seasonal change	1 year

After Di Castri F, Hadley M., 1988. Enhancing the credibility in ecology: interacting along and across hierarchical scales. Geo. J. 17, 5—35, Müller, E., 1992. Hierarchical approaches to ecosystem theory. Ecol. Model. 63, 215—242, and Gundersson, L.H., Holling, C.S. (Eds.), 2002a. Panarchy. Washington, DC.

the other significant sources of "natural" disturbances, such as volcanoes, droughts, soil erosion events, avalanches, landslides, windstorms, pests, or pathogen outbreaks. The consequences of such rare events can be enormous, and they can be compounded due to human interventions and management regimes. Further information about the hierarchical distinction of rare events included the required time for recovery (Box 8.2).

BOX 8.2

HIERARCHICAL DISTINCTION OF RARE EVENTS

In Chapter 5, hierarchy theory has been introduced. A key message of this concept is that under steady-state conditions the slow processes with broad spatial extents provide constraints for the small-scale processes, which operate with high frequencies, thus demonstrating an interplay between top-down and bottom-up effects. When disturbances occur, these hierarchies can be broken and as a consequence (as demonstrated in Section 8.5) small-scale processes can determine the developmental directions of the whole ensemble. An extended theory to describe this process, called panarchy, which combines the Greek root, *pan* meaning all, with *archy* meaning rules. So the system behavior is determined by (i.e., ruled by) all scales.

In Fig. 8.3, disturbance events are arranged hierarchically, based on quantifications and literature reviews from Vitousek (1994) and Di Castri and Hadley (1988). Here we can also find direct interrelations between spatial and temporal characteristics, i.e., concerning the processes of natural disasters: The broader the spatial scale of a disturbance, the longer time is necessary for the recovery of the system. Furthermore, as shown in Section 8.1, we can assume that events that provoke long recovery times occur with smaller frequencies than disturbances with smaller effects.

Gigon and Grimm (1997) argue that the effect chain of disturbances can also be comprehended from a hierarchical viewpoint. The disturbing event occurs with typical spatiotemporal characteristics, and initially it mainly hits those ecosystem structures that operate on the same scales. Thereafter, an indirect effect chain starts because the internal constraints have changed abruptly. Thus, in a next step potentially those components should be affected that operate on a lower scale than the initially changed component. The realization that a component is both part and whole has been given the

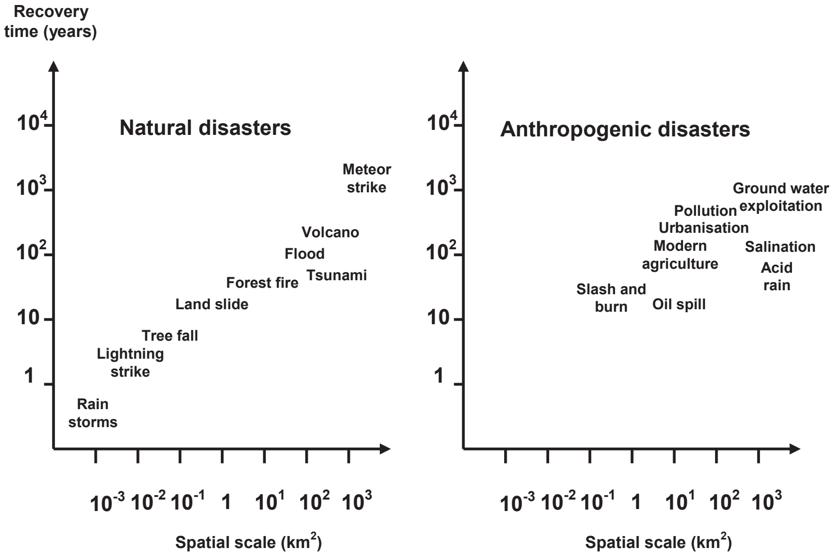

FIGURE 8.3 Spatial and temporal characteristics of some natural and anthropogenic disasters. The temporal dimension is being depicted by the specific recovery times after the disturbances have taken place. *After Vitousek, P.M., 1994. Beyond global warming: ecology and global change. Ecology 75, 1861–1876 and Di Castri, F., Hadley, M., 1988. Enhancing the credibility in ecology: interacting along and across hierarchical scales. Geo. J. 17, 5–35.*

BOX 8.2 (*cont'd*)

name holon (a combination of “holistic” and “particle”). Consequently, the biological potential is modified, and then also higher levels of the hierarchy can be affected in an ongoing and cascading manner.

Another important feature of disturbance is that certain disturbances are necessary for the long-term development and stability of the affected system. For instance, forest fires are events that necessarily belong into the developmental history of forests. Therefore, the concepts of stratified stability or incorporated disturbances have been set up (e.g., Urban et al., 1987; van der Maarel, 1993). They can today be used as illustrative examples for the natural functioning of the adaptive cycle concept. Looking at Fig. 8.3 there are numerous natural disasters that occur in the absence of anthropogenic disturbances, which over the long term of ecological and evolutionary development have driven planetary changes. The anthropogenic disturbances have increased considerably in the past two centuries and moreover are chronic pressures on the fundamental drivers such as biogeochemical cycles and land conversion. These influences seem to be so manifold and complex that only a minor scale dependency can be found. Furthermore, the recovery potential may be based on internal processes and is therefore not dependent on the quantification of openness.

The figure can also be used to illustrate the quantification of openness as introduced in Section 2.6 (Table 2.3). The recovery time is approximately proportional to the periphery of the affected area and can be represented by the square root of the area. As seen on the figure for natural disasters, a meteor strike is affecting an area approximately six orders of magnitude higher than rainstorms. The recovery time after the strike should therefore require three orders of magnitude longer time than after the rainstorm. This is approximate due to the relationships of the peripheries, which express the exposure of an area to the environment.

8.2 THE RISK OF ORIENTOR OPTIMIZATION

Translating these general points into our ecosystem theory, it is obvious that *two general processes* are governing the dynamics of ecosystems: besides growth and development processes, living systems are also susceptible to influences that move them back toward thermodynamic equilibrium: On the one hand, there are long phases of *complexification*. Starting with a pioneer stage, orientor dynamics bring about slow mutual adaptation processes with long durations, if there is a dominance of biological processes (see Müller and Fath, 1998; Ulanowicz, 1986).

A system of interacting structural gradients is created, which provokes very intensive internal flows and regulated exchanges with the environment (Müller, 1998). The processes are linked hierarchically, and the domain of the governing attractor (Fig. 8.4) remains rather constant, whereupon optimization reactions provoke a long-term increase of orientors, efficiencies, and information dynamics.

The highest state of internal mutual adaptation is attained at the *mature* stage of the ecosystem growth and development (Odum, 1969). But, the further the system has been moved away from thermodynamic equilibrium, the higher is the risk of getting moved back (Schneider and Kay, 1994) because the forces are proportional to the gradients. Since there is a temporal scale of disturbance events, the more time that has been used for complexification, the higher is the risk of being seriously hit by disturbance (Table 8.3). Similarly, the longer the elements of the system have increased their mutual connectedness, the stronger is the mutual interdependency (Chapter 4) and the total system's brittleness (Holling, 1986). Table 8.4 combines some features of mature ecosystems and lists some risk-related consequences of the orientor dynamics. In general, it can be concluded that the adaptability after changes of the constraints may be decreased when a high degree of maturity is attained.

8.3 THE CHARACTERISTICS OF DISTURBANCE

In such mature states, if certain thresholds are exceeded, fast dynamics can easily become *destructive*. If there is a change of the exterior conditions, or if strong physical processes become predominant, then the inherent brittleness (Holling, 1986) enhances the risk of gradient degradation, thus the flow schemes are interrupted, and energy,

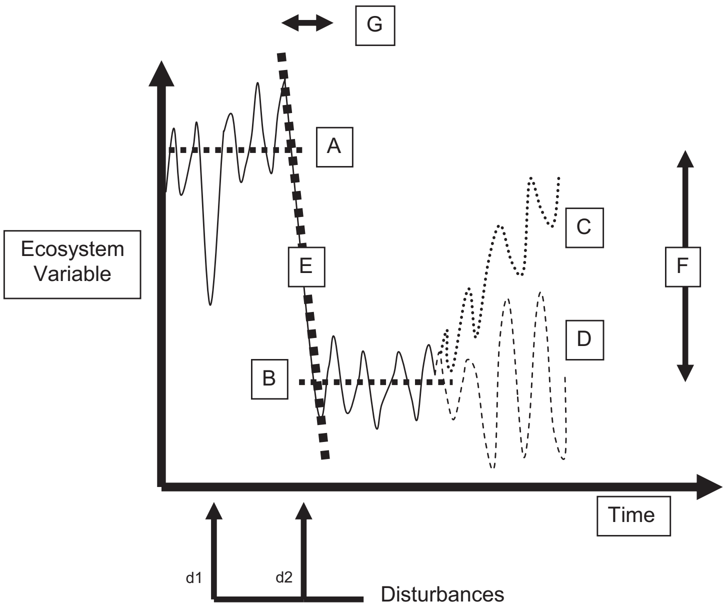

FIGURE 8.4 Some characteristics of disturbances. The state of the ecosystem is indicated by one ecosystem variable. Due to the disturbance d2 the system is shifted from state A to B, the indicator value thus decreases significantly. The effective disturbance d2 has a higher abruptness (E), a longer duration (G), and a higher magnitude (F) than d1 which does not affect the system. Throughout the following development a high impact affects the trajectory D, which provides a long-term decrease of the ecosystem variable, while a more resilient ecosystem turns back to orientor dynamics (C). *After White, P.S., Jentsch, A., 2001. The search for generality in studies of disturbance and ecosystem dynamics. Progress in Botany 62, 2–3. Checkliste für die Anwendung. In: Fränzle, O., Müller, F., Schröder, W. (Eds.), Handbuch der Umweltwissenschaften, Chapter III. Ecomed-Verlag, Landsberg, pp. 2–3.*

information, and nutrients are lost. Hierarchies break down, the attractors are modified, and the system experiences a reset to a new starting point.

Ecologists have studied these events with emphasis on the processes of disturbances. Picket and White (1985) have used a structural approach to define these events: "*any relatively discrete event in space and time that disrupts ecosystem, community, or population structure and changes resources, substrates, or the physical environment is called disturbance*." Certainly, also functional features are exposed to respective changes, ecosystem processes and interactions are also disrupted. Chronic stress or background environmental variabilities are not included within this definition, although these relations can also cause significant ecosystem changes. If a disturbance exceeds certain threshold values, then flips and *bifurcations* can occur, which provoke irreversible changes of the system's trajectory. Therefore, understanding ecosystems requires an understanding of their disturbance history.

A focal problem of any disturbance definition is the question how to indicate the "normal state" of an ecosystem (White and Jentsch, 2001) because most biological communities "are always recovering from the last disturbance" (Reice, 1994). For our orientor-based viewpoint it might be appropriate to distinguish the temporal phases during which orientor dynamics are executed from phases of decreasing complexifications caused by exceeding threshold values.

Some basic terms from disturbance ecology are introduced in Fig. 8.4. Disturbances exhibit certain *magnitudes* (sizes, forces, and intensities of the events, as variables of the source components*), specificities* (spectrum of disturbed elements), and *severities* (the impacts of the events on system properties). They can be characterized by various *temporal indicators*, such as their spatiotemporal scales, their duration, abruptness, recurrence interval, frequency, or return times. In the literature, exogeneous disturbances resulting from processes outside the system are distinguished from endogeneous disturbances. The latter result from internal ecosystem processes, e.g., as a product of successional development.

Disturbance can have various effects on structural *biodiversity*. It is clear that high magnitudes can easily reduce diversity enormously, while minor inputs might have no effects at all. Connell and Slayter (1977) have found that the highest species numbers are produced by *intermediate disturbances* because such situations provide suitable living conditions for the highest number of species with relation to their tolerance versus the prevailing disturbances (Sousa, 1984). Furthermore, disturbance is a primary cause of *spatial heterogeneity* in ecosystems, thus it also determines the potential for biodiversity (Jentsch et al., 2002). This concept has been widely discussed within the pattern

TABLE 8.4 Some Characteristics of Mature Ecosystems and Their Potential Consequences for the System's Adaptability[1].

Orientor Function	Risk-Related Consequences
High exergy capture	The system operates on the basis of high energetic inputs → high vulnerability if the input pathways are reduced
High exergy flow density	Many elements of the flow webs have lost parts of their autonomy as they are dependent on inputs which can be provided only if the functionality of the whole system is guaranteed → high risk of losing mutually adapted components
High exergy storage and residence times	Exergy has been converted into biomass and information → high amount of potential fuel and risk of internal eutrophication
High entropy production	Most of the captured exergy is used for the maintenance of the mature system → minor energetic reserves for structural adaptations
High information	High biotic and abiotic diversity → risk of accelerated structural breakdown if the elements are correlated
High degree of indirect effects	Many interactions between the components → increase of mutual dependency and risk of cascading chain effects
High complexity	Many components are interacting hierarchically → reduced flexibility
High ascendancy and trophic efficiency	Intensive flows and high flow diversities have resulted in a loss reduction referring to all single energetic transfers → changing one focal element can bring about high losses
High degree of symbiosis	Symbiosis is linked with dependencies, i.e., if it is inevitable for one or both partners → risk of cascading chain effects
High intraorganismic storages	Energy and nutrients are processed and stored in the organismic phase → no short-term availability for flexible reactions
Long life spans	Focal organisms have long life expectancies → no flexible reactivity
High niche specialization and K selection	Organisms are specialized to occupy very specific niche systems and often have a reduced fecundity → reduced flexibility

[1] *Maturity is attained due to a long-term mutual adaptation process. In the late stages of development, the interrelations between components are extremely strong, sometimes rigid. Reactivity is reduced. If the constraints change, then this high efficient state runs the risk of being seriously disturbed.*

process hypotheses of patch dynamics (Remmert, 1991). Other ideas concerning the crucial role of disturbance have been formulated, for example, by Drury and Nisbet (1973) and Sousa (1984). Natural disturbances are an inherent part of the internal dynamics of ecosystems (O'Neill et al., 1986) and can set the timing of successional cycles. Natural disturbances thus seem to be crucial for the long-term ecosystem resilience and integrity.

Taking into account these high dynamic disturbance features, correlating them with the orientor principles (which also are based on changes), focusing on long-term dynamics and adopting Heraclitus' knowledge from 500 BC ("nothing is permanent but change"!), it becomes rather difficult to find good arguments for an introduction of the *stability principle*. This conception has been the dominant target of environmental management in the last decades (Svirezhev, 2000), and it was strongly interrelated with the idea of a "balance of nature" or a "natural equilibrium" (Barkmann et al., 2001).

Stability has been described by several measures and concepts, such as resistance (the system is not affected by a disturbance), resilience (the systems is able to return to a referential state) or buffer capacity, which measures the overall sensitivities of system variables related to a certain environmental input. Indicators for the stability of ecosystems are, for instance, the structural effects of the input (recoverability: to what extent—e.g., represented by the percentage of quantified structural elements—do the state variables of a system recover after an input?), the return times of certain variables (how long does it take until the referential state is reached again?), or the variance of their time series values after a disturbance (how big are the amplitudes of the indicator variable and how does that size develop?). All of these measures have to be understood in a multivariate manner; due to indirect effects, disturbances always affect many different state variables.

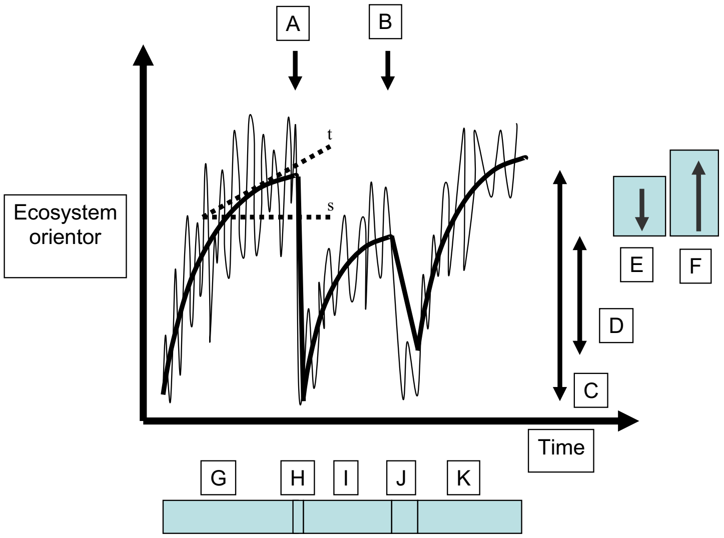

FIGURE 8.5 Sketch of the dynamics of ecosystem variables on two scales, both variables are influenced by the disturbances (A and B) with different magnitudes (C and D) and durations (H and J), and both variables are due to orientor dynamics during the phases G, I, and K. The development of the fast variable shows a high variance, which can be averaged to the slow dynamics. The long-term effects of the disturbances A and B can be distinguished on the base of the orientor differences E (reduced resilience and recovery potential) and F (enhanced potential for resilience and recovery).

Our foregoing theoretical conceptions show both, that (a) the basic feature of natural systems is a thermodynamic *disequilibrium* and that (b) ecosystems are following *dynamic orientor trajectories* for most time of their existence. Steady state thus is only a short-term interval where the developmental dynamics are artificially frozen into a small-scale average value. Therefore, more progressive indicators of ecosystem dynamics should not be reduced to small temporal resolutions that exclude the long-term development of the system. They should be much more oriented toward the long-term orientor dynamics of ecosystem variables and try to represent the respective potential to continue to change instead of evaluating a system due to its potential to return to one defined (nondevelopmental and perhaps extremely brittle) state. A good potential seems to lie in the concept of *resilience*, if we define it as the capacity of a disturbed system to return to its former complexifying *trajectory* (not to a certain referential state). Therefore, the reference situation (or the aspired dynamics of ecosystem management) would not be the static lines in Fig. 8.5, but the orientor trajectory t. Similar ideas and a distinction of stability features with reference to the systems' stability are discussed in Box 8.3.

BOX 8.3

STABILITY IS RELATED TO UNCORRELATED COMPLEXITY

Summary: The complexity of the pattern of ecosystem transfers can be gauged by the Shannon—Weaver diversity measure applied to the various flows. This index, in turn, can be decomposed into a component that refers to how the flows are constrained by (correlated with) each other and another that represents the remaining degrees of freedom which the system can reconfigure into responses to novel perturbations. It is the latter (uncorrelated) complexity that supports system stability.

Development: In order to see how system stability is related only to part of the overall system complexity, it helps to resolve the complexity of a flow network into two components, one of which represents coherent complexity and the other, its incoherent counterpart (Rutledge et al., 1976.)

Prior to Rutledge et al., complexity in ecosystems had been reckoned in terms of a single distribution, call it $p(a_i)$. The most common measure used was the Shannon (1948) "entropy,"

$$H = -\sum_i p(a_i)\log[p(a_i)].$$

BOX 8.3 *(cont'd)*

Rutledge et al. showed how information theory allows for the comparison of two different distributions. Suppose one wishes to choose a "reference" distribution with which to compare $p(a_i)$. Call the reference distribution $p(b_j)$. Now Bayesian probability theory allows one to define the joint probability, $p(a_i,b_j)$, of a_i occurring jointly with b_j. Ulanowicz and Norden (1990) suggested applying the Shannon formula to the joint probability to measure the full "complexity" of a flow network as,

$$H = -\sum_{i,j} p(a_i, b_j)\log[p(a_i, b_j)].$$

Then, using Rutledge's formulation, this "capacity" could be decomposed into two complementary terms as,

$$H = \sum_{i,j} p(a_i, b_j)\log\left[\frac{p(a_i, b_j)}{p(a_i)p(b_j)}\right] - \sum_{i,j} p(a_i, b_j)\log\left[\frac{p(a_i, b_j)^2}{p(a_i)p(b_j)}\right],$$

where the first summation represents the coherence between the a_i and the b_j, and the second on the remaining dissonance between the distributions.

The genius of Rutledge et al. was to identify $p(a_i)$ and $p(b_j)$ with the compartmental distributions of inputs and outputs, respectively. That is, if T_{ij} represents the quantity of flow from compartment *i* to *j*, and $T_{..}$ represents the sum of all the flows (a dot in place of a subscript means summation over that index), then

$$p(a_i, b_j) \sim \frac{T_{ij}}{T_{..}},\ p(a_i) \sim \sum_j \frac{T_{ij}}{T_{..}},\ \text{and}\ \ p(b_j) \sim \sum_i \frac{T_{ij}}{T_{..}}.$$

Substituting these estimates into the decomposition equation yields,

$$H = \sum_{i,j} \frac{T_{ij}}{T_{..}} \log\left[\frac{T_{ij}}{T_{..}}\right] = \sum_{i,j} \frac{T_{ij}}{T_{..}} \log\left[\frac{T_{ij}T_{..}}{T_{i.}T_{.j}}\right] - \sum_{i,j} \frac{T_{ij}}{T_{..}} \log\left[\frac{T_{ij}^2}{T_{i.}T_{.j}}\right],$$

$$\text{or} \quad H = I + D,$$

where I is known as the "average mutual information" inherent in the flow structure and D is the residual disorder. In other words, the complexity has been decomposed into a term that measures how well the flows are constrained (coordinated) and how much they remain independent (free.)

Rutledge at al. suggested that the ability of the ecosystem network to respond in new ways to novel disturbance is related to D, while Ulanowicz (1980) argued that I quantifies the organization inherent in the flow network. It is important to notice that I and D are complementary, which is to say that, other things being equal, any change in I will be accompanied by a complementary change in D. The system cannot "have its cake and eat it, too." Coherent performance, I, comes at the expense of reliability, D, and vice versa.

In other words, one should expect system stability to be more related to the value of the disordered complexity, D, and less correlated to the overall complexity, H, as the latter also encompasses the complexity encumbered by system constraints.

The degree of order can be given as the ratio of order to the total system capacity, $a = I/H$ and the complementary degree of freedom (uncorrelation) by $w = D/H$, so that $a + w = 1$. The accumulation of data on many diverse, quantified trophic networks revealed a cluster of most systems around $a = 0.40$, reflecting the large investment ($w = 0.60$) natural systems must make to persevere in a world of radical contingency (Ulanowicz, 2009).

8.4 ADAPTABILITY AS A KEY FUNCTION OF ECOSYSTEM DYNAMICS

Having introduced general aspects of disturbance ecology, we can now start to integrate the complexification and the disturbance-induced dynamics of ecosystems. The respective approach is based upon the concepts of the "Resilience Alliance" (see e.g., Holling, 1986; Gundersson and Holling, 2002; Elmquist et al., 2003; Holling, 2004; Walker et al., 2004; Walker and Meyers, 2004), but they have been restricted to ecosystem dynamics and combined with the sequence of growth and development forms after Jørgensen et al. (2000, see also Fath et al., 2004; Ulanowicz, 1986, 1997). Under these prerequisites, we can distinguish the following principle steps of ecosystem development:

- *Start* of the succession—(pioneer stage, boundary growth after Jørgensen et al., exploitation function after Holling): In this initial state, an input of low-entropy material into the system starts the sere. The developmental potential depends on the genetic information that is available in the seed bank or by lateral inputs. Due to a minor connectivity between the elements, self-regulation is low, leaky-ness is high, and the sum of potential developmental opportunities (developmental uncertainty) is high. The system provides a very high adaptability and flexibility.

- *Fast growth*—(pioneer stage, structural growth after Jørgensen et al., (2007) exploitation function after Holling): Pioneer stages can also be characterized by a high and rapid increase of biomass, correlated with an increase of the numbers and sizes of the ecosystem components. To provide the growing number of participants, the energy throughflow increases as well as exergy degradation which is necessary for the maintenance of the components. Connectivity is low, and therefore external inputs can modify the system easily: the adaptability is high.
- *Fast development*—(middle succession, network growth after Jørgensen et al., transition from exploitation to conservation function after Holling): After a first structure has been established, the successful actors start funneling energy and matter into their own physiology. Due to the mutual adaptation of the winning community, the connectivity of the system increases by additional structural, energetic, and material interrelations and cycling mechanisms. The single species become more and more dependent on each other, uncertainty decreases, and the role of self-regulating processes grows, reinforcing the prevailing structure. Adaptability is reduced.
- *Maturity* (information growth after Jørgensen et al., conservation function after Holling): In this stage, a qualitative development in system behavior takes place, changing from exploitative patterns to more conservative patterns with high efficiencies of energy and matter processing. Species that easily adapt to external variability (r-selected species) have been replaced by the variability controlling K-strategists, the niche structure is enhanced widely, and loss is reduced. The information content of the system increases continuously. A majority of the captured exergy is used for the maintenance of the system; thus, there is only a small energetic surplus which can be used for adaptation processes. Sensitivities versus external perturbations have become high, while the system's buffer capacities are much smaller compared with the former stages of the development. These items result in a rise of the system's vulnerability and a decrease of resilience (see Table 8.4). Adaptability has reached minimum values.
- *Breakdown* (release function after Holling, creative destruction after Schumpeter, 1942): Due to the "brittleness" of the mature stages (Holling, 1986), their structure may break down very rapidly due to minor changes of the exterior conditions. Accumulated resources are released, internal control and organization mechanisms are broken, and positive feedbacks provoke the decay of the mature system. Uncertainty rises enormously, hierarchies are broken, and chaotic behavior can occur (Fig. 8.3). There are only extremely weak interactions between the system components, nutrients are lost, and cycling webs are disconnected. Adaptability and resilience have been exceeded.
- *Reorganization:* During this short period the structural and functional resources can be arranged to favor new directions, new species can occur and become successful, and—in spite of the inherited memory (e.g., seed bank of the old system and neighboring influences)—unpredictable developmental traits are possible. There are weak controls, and innovation, novelty, and change can lead to an optimized adaptation on a higher level.
- *Reset*: A new ecosystem succession starts.

The described sequence has been illustrated in Fig. 8.6 as a function of the system's internal connectedness and the stored exergy. Starting with the exploitation function, there is a slow development. The trajectory demonstrates a

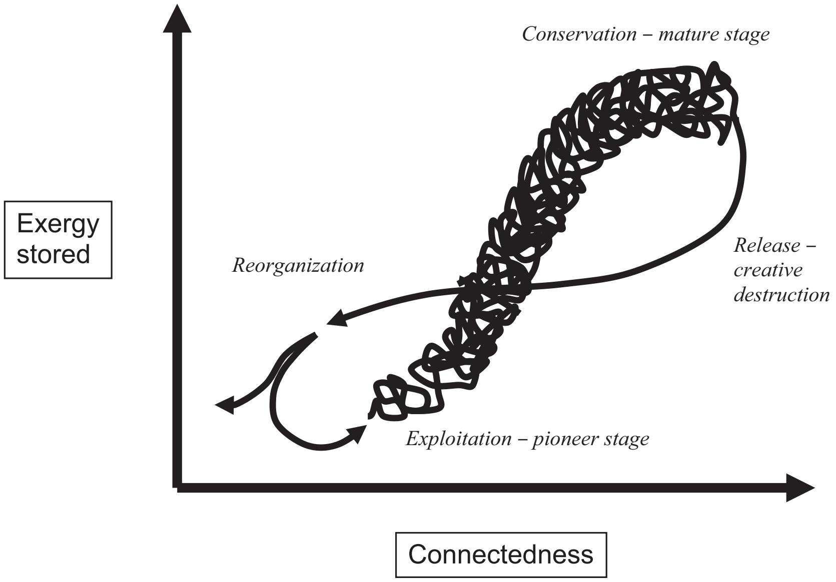

FIGURE 8.6 Ecosystem succession as a function of structural and functional items.

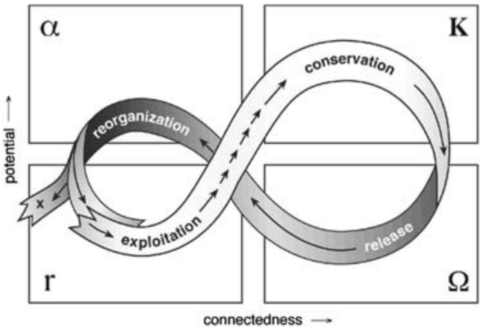

FIGURE 8.7 Adaptive cycle after Holling. *From Gundersson, L.H., Holling, C.S. (Eds.), 2002a. Panarchy. Washington, DC. Schoon, M., and van der Leeuw, S., 2015. The shift toward social-ecological systems perspectives: Insights into the human-nature relationship. In: Natures Sciences Sociétés, 23, 166–174 (2015) © NSS-Dialogues, EDP Sciences 2015 https://doi.org/10.1051/nss/2015034.*

steady increase in mutual interactions as well as an increase in the stored exergy. As has been described above, this energetic fraction can be distinguished into a material fraction (e.g., biomass, symbolizing the growth conception of Ulanowicz, 1986) and the specific exergy which refers to a complexification of the system's structure (development after Ulanowicz). In spite of variability (e.g., annual cycles), the long-term development shows a steady increase up to the mature state. Here, the maximum connectivity can be found, which on the one hand is a product of the system's orientation, but which also is correlated with the risk of missing adaptability, which has been nominated as overconnectedness by some authors. After the fast releasing event, the short-term conditions determine the further trajectory of the system. It might turn into a similar trajectory or find a very different pathway.

Fig. 8.6 looks very similar to the well-known four-box model of the Resilience Alliance, which has been depicted in Fig. 8.7. The difference between these approaches lies in the behavior of the cycle along the y-axis. While for interdisciplinary approaches and analyses of human–environmental system the special definition of "potential" in the adaptive cycle metaphor seems to be advantageous, from our thermodynamic viewpoint, the key variable is an orientor, such as total stored exergy, that gives the overall energetics of the system. In either case, potential or energetics, it is more logically consistent for the collapse to be monotonic, never rising until after creative destruction. The nutrients as well as the energetic resources do not grow after the release, but get eroded or leached, and the change of their availability is due to the activities of the organisms which appear right after the reset of the pioneer stage. Furthermore, the upward trajectory of the exploitation stage explicitly shows the nonsmooth path of progress, including small-scale setbacks along the way to the conservation stage.

To illustrate the risk discussion from above, Fig. 8.8 shows a correlated trajectory of the developmental potential of ecosystems during the adaptive dynamics. This point shows another difference with the concept of the Resilience Alliance, due to another understanding of "potential." Originating from ecosystem theory, we can use the totality of potential trajectories (possibilities, developmental directions) of the system during the whole cycle. As has been described above, there are a high number of developmental possibilities in the beginning during the pioneer

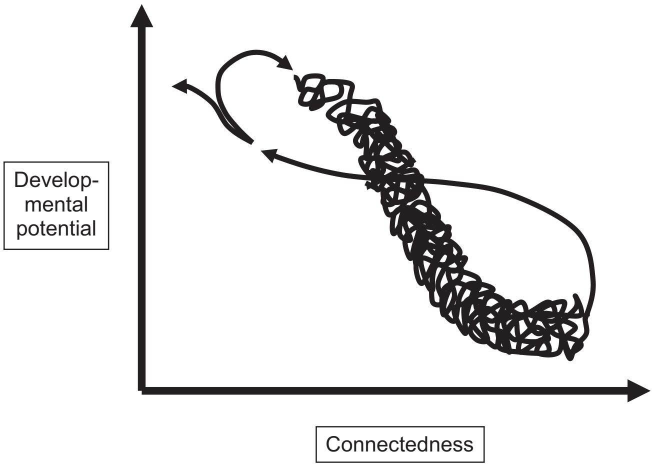

FIGURE 8.8 Developmental opportunities during the successional cycle from Fig. 8.6.

phase while thereafter the prevailing interactions are limiting the degrees of freedom and the adaptability of the system continuously. Self-organizing processes have created internal hierarchical constraints, which reduce the flexibility of the entity. Integrating Figs. 8.6 and 8.8 demonstrates the dilemma of the orientor philosophy: The more complex and efficient an ecological system performs, the better (and more successful) its "old" adaptation to the environmental conditions has been, the lower is its adaptability against unknown environmental changes, and the higher is the system's vulnerability. Thus, a further adaptation to changing conditions is only possible on the base of destruction of the old structures.

8.5 ADAPTIVE CYCLES ON MULTIPLE SCALES

With the following argumentation we want to link these concepts with another approach to ecosystem theories: Ecosystems are organized *hierarchically* (see Chapter 5). Hereafter, we will assume that throughout complexification periods the focal processes always are influenced by the lower levels' dynamics and the higher levels' development, forming a system of constraints and dynamics of biological potentials. Thus, there are four general hierarchical determinants for ecosystem dynamics:

(i) The *constraints* from higher levels are completely effective for the fate of the focal variable. The constraints operate in certain temporal features, with specific regularities and intervals. Some examples for these temporal characteristics are as follows:

- Day—night dynamics (e.g., determining ecosystem temperature, light, or humidity)
- Tides (e.g., determining organism locations in the Wadden Sea)
- Moon phases (e.g., determining sexual behavior)
- Annual dynamics (e.g., determining production phases of plants)
- Longer climatic rhythms (e.g., sun spots influencing production)
- Dynamics of human-induced environmental stress factors
  - Typical periodic land use activities (e.g., crop rotation)
  - Land use change (structural and functional)
  - Emission dynamics and environmental policy (e.g., sulfur emission in Germany and their effects on forests)
  - Global change and greenhouse gas emissions (e.g., temperature rise)
  - Continuous climate change
- Biome transitions

These constraints are interacting and constantly changing; therefore, the maximum degree of mutual adaptation is a dynamic variable as well. This is a focal reason why the orientor approach is nominated as a "very theoretical outline" only: As ecosystems "always are recovering from the last disturbance," the orientor dynamics often are practically superseded by the interacting constraints dynamics.

(ii) The *dynamics of the focal variables* themselves exhibit certain natural frequencies. As in the patch dynamics concepts, there can be internal change dynamics on the observed level itself. For example, we can observe the undisturbed succession on the base of biological processes—from a lake to a fen: The system changes enormously due to its internal dynamics. Throughout this process often a limited number of species become dominant, e.g., stinging nettles in secondary successions on abandoned agricultural systems. This leads to an interruption of orientor dynamics because the dominant organisms do not allow competitors to rise.

(iii) The *biological potential* of the lower levels results from mostly filtered, smoothened, and buffered variables with high frequencies. They can only become effective if the system exceeds certain threshold values. This can happen if disturbances unfold their indirect effects, as has been described above.

(iv) *Disturbances* primarily meet elements that operate on similar spatial and temporal scales. Only after these components have been affected, indirect effects start influencing the interrelated scales and thus can provoke far-reaching changes.

Summarizing these points, we can state that ecosystems under steady-state conditions are regulated by a hierarchy of interacting processes on different scales. The slow processes with large extents build up a system of constraints for the processes with high dynamics. Thereby limiting their degrees of freedom, steady states can be characterized by relatively low variability of low-level processes (O'Neill et al., 1986). Furthermore, under steady-state conditions, these high dynamic processes cannot influence the system of constraints, resulting in a rather high resilience. Thus, the question arises, what will happen during disturbances?

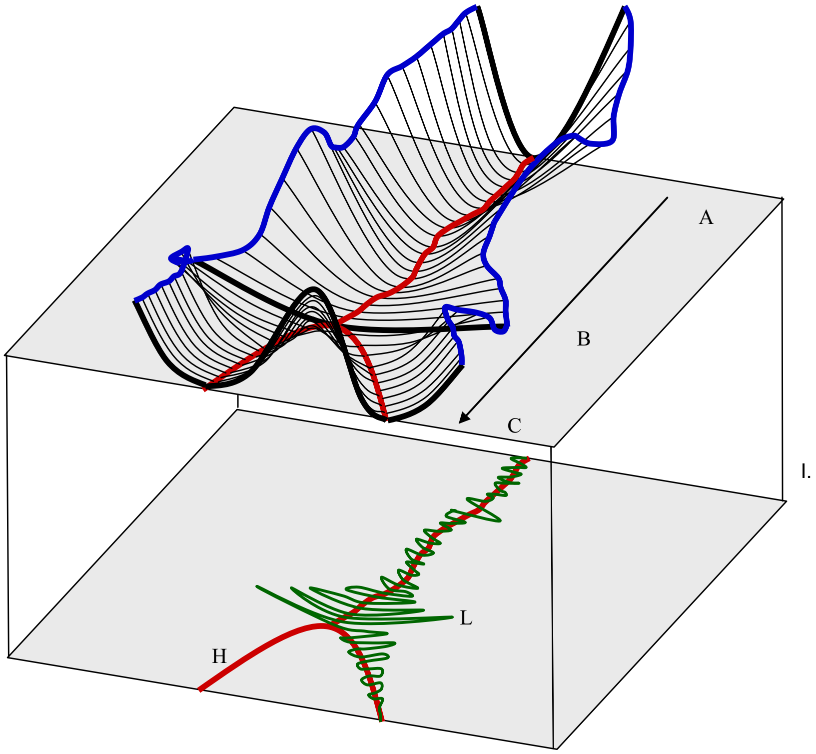

FIGURE 8.9 Hypothetical potential function of a hierarchical system.

This can be depicted by the concept of stability landscapes (see Walker et al., 2004) or hypothetical potential functions. In Fig. 8.9, the system state is plotted on the x-axis, the z-axis represents the parameter values (may also be taken as a temporal development with changing parameter loadings), and the potential function is plotted on the y-axis. This function can be regarded as the slope of a hill, where the bottom of the valley represents steady-state conditions. If we throw a marble into this system, then it will find its position of rest after a certain period of time at the deepest point of the curve. If the parameter values change continuously (A → B → C), then a set of local attractors appears, symbolized by the longitudinal profile of the valley, or the broad-scale bifurcation line (H) at level I. This manifold sketches a sequence of steady states referring to different parameter values. In Fig. 8.9, the straight line below on level I may be interpreted as the sequence of a parameter of a high hierarchical level while the oscillating parameter value line L indicates the states of a lower level holon. The return times of this holon to its different steady states will be different if the states A, B, and C are compared: The steeper the slope, the more rapidly a local steady state will be reached, and smaller amplitudes will be measured. When the parameter value is changed continuously within long-term dynamics we will find small variations near state A. As our parameter shifts from A via B toward C, the potential curve's slopes decrease, finding a minimum at B. In this indifferent state the amplitudes of the low-level holon will be very high (see level I). If there is a further change of the parameter value, then a first-order phase transition takes place. The state can be changed radically passing the bifurcation point B before a more stable state is achieved again, finally reaching C. Passing B there are two potential states the system can take, and the direction our holon takes is determined by all levels of the broken hierarchy, including the high frequent (small scale) dynamics. This process is accompanied by temporal decouplings, by a predominance of positive feedbacks, and by autocatalytic cycles. We would be remiss not to mention that the action of the ball rolling across the landscape, itself, leaves deformation of the landscape in which the ball is rolling. This level of tight coupling, interconnectivity, and feedback is what makes predicting ecosystem (or any other self-organizing, complex adaptive system) behavior.

This property that balances development and structure makes it possible for ecosystems to operate at the edge of chaos (Kaufmann, 1993), but frequently avoid chaos and utilize all the available resources at the same time; see also Box 8.4.

After having elucidated disturbance from the hierarchical viewpoint, one last aspect should be taken into consideration. As we have mentioned above, the adaptive cycle is a metaphor which can be assigned to a multitude of interacting scales. There is a high normality in disturbance with adaptability as a key function. If this feature cannot

BOX 8.4

CHAOS IN ECOSYSTEM MODELS

The prevailing conditions including the abundance of other species determine which growth rate is optimal. If the growth rate is too high, then the resources (food) will be depleted and the growth will cease. If the growth rate is too low, then the species does not utilize the resources (food) to the extent that it is possible. The optimal growth rate also yields the highest system exergy. If, in a well-calibrated and well-validated eutrophication model—state variables include phytoplankton, nitrogen, phosphorus, zooplankton, fish, sediment nitrogen, and sediment phosphorus—we vary the zooplankton growth rate, then exergy will show a maximum at a certain growth rate (which is frequently close to the value found by the calibration and approved by the validation). At both lower and higher growth rates, the *average* exergy is lower because the available phytoplankton is either not utilized completely or is overexploited. When overexploitation occurs the phytoplankton and zooplankton show violent fluctuations. When the resources are available the growth rate is very high, but the growth stops and the mortality increases, as soon as the resources are depleted, which gives the resources a chance to recover and so on. At a growth rate slightly higher than the value giving maximum exergy, the model starts to show deterministic chaos. Fig. 8.10 illustrates the exergy as function of the zooplankton growth rate in the model referred to above, focusing on the time when the model starts to show deterministic chaos. These results are consistent with Kauffman's (1993) statement: biological systems tend to operate at the edge of chaos to be able to utilize the resources at the optimum. In response, thermodynamic constraints move the system as far away from thermodynamic equilibrium as possible under the prevailing conditions, such that the system is operating close to chaos but has a high probability to avoid it. Considering the enormous complexity of natural ecosystems, and the many interacting processes, it is surprising that chaos is not frequently observed in nature, but it can be explained by an operation at *the edge* of chaos to ensure a high utilization of the resources—to move as far away as possible from thermodynamic equilibrium under the prevailing conditions. Keep in mind the idea of chaos in nature is a metaphor for abrupt system change due to bifurcations and other nonlinearities. However, in the absence of disturbances (and even in the face of many), the growth and development are largely linear. How often, when one visits a forest or meadow after an interval of a year or even many years, are the general characteristics of the ecosystem largely familiar, indicating a smooth transition from past to present? At a recent meeting of the International Society for Ecological Modeling held at Towson University in May 2016, one of the coauthors here (B. Patten) remarked in an ornery way, inviting bifurcation proponents to go

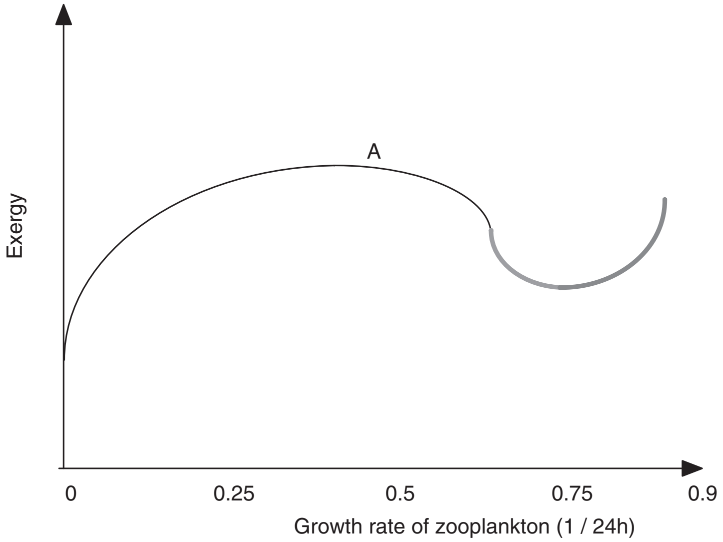

FIGURE 8.10 Exergy is plotted versus maximum growth rate for zooplankton in a well-calibrated and well-validated eutrophication model. The shaded line corresponds to chaotic behavior of the model, i.e., violent fluctuations of the state variables and the exergy. The shown values of the exergy above a maximum growth rate of about 0.65—0.7 day^{-1} are therefore average values. By a minor change of the initial value of phytoplankton or zooplankton in the model, significant changes are obtained after 2-month simulations as an indication of deterministic chaos.

BOX 8.4 *(cont'd)*

out into nature with him and show him this edge that everyone talks about. [It occurred later that one response could have been to go to the Grand Canyon, where there is a clear edge, but that is a slow spatial artifact not due to a fast temporal bifurcation.] Patten's comment was probably the most provocative one of the entire conference, which is exactly what science needs if it is to keep progressing, challenging, and advancing.

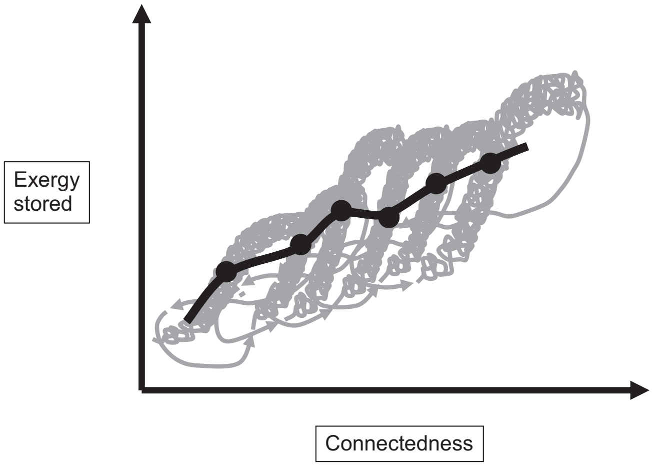

FIGURE 8.11 Long-term succession of ecosystems, indicated on different scales: small-scale disturbances may support the development of the overall system.

reach sufficient quantities by low-scale flexibility, then the breakdown on a higher hierarchical level enables the system to start a reset under the new prevailing conditions. Thus, in the end, disturbance really can be understood as a part of ecosystem growth and development on a higher scale, as indicated in Fig. 8.11; disturbance may even be extremely necessary to enable a continuation of the complexifying trajectory of the overall system.

8.6 A CASE STUDY: HUMAN DISTURBANCE AND RETROGRESSIVE DYNAMICS

Up to now, we have focused on "natural dynamics." Thus, in the end of this chapter, we demonstrate human disturbances using a wetland case study. In general, human activities influence disturbance regimes in several mechanisms, such as:

- the rescaling of natural disturbances,
- the introduction of novel disturbances,
- the modification of the reception mechanisms of the disturbed components,
- influences on disturbance rates and intensities,
- the suppression of natural disturbances to ensure the potential of aspired ecosystem services,
- the change of successional pathways due to irreversible changes.

As an example for human pressures and disturbance dynamics, Fig. 8.12 describes a case study from ecosystem research in the wetlands of the Bornhöved Lakes District in Northern Germany. Here a holistic indicator system, which has been developed on the base of the orientor theory (Müller 2005), has been used to demonstrate the steps of wetland retrogression as provoked by eutrophication and drainage.

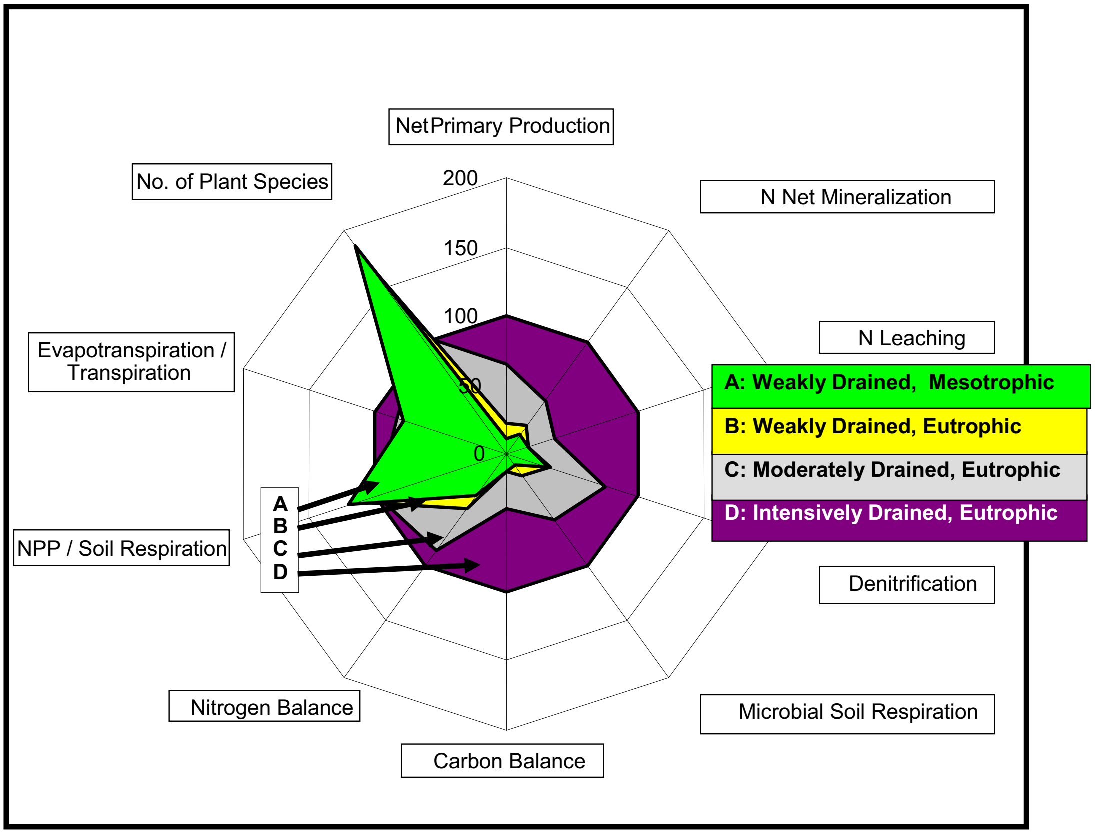

FIGURE 8.12 Retrogressive ecosystem features at different steps of human intervention. The figure shows a set of 10 holistic indicators which as a whole represent ecosystem integrity. Starting with the initial state A, drainage and eutrophication of the wet grassland ecosystems affect irreversible changes up to the degraded state D. During that development ecosystem structures (complexity) are reduced, energy and matter efficiencies decrease, and the originally sink ecosystem turns into a source for nitrogen and carbon compounds. *After Müller et al. (2006).*

Based on field measurement, mappings, and classifications, different ecosystem types have been analyzed with the computer-based "digital landscape analysis system" (Reiche, 1996) and the modeling system "Wasmod—Stomod" (Reiche, 1996) which was used to simulate the dynamics of water budgets and nutrient and carbon fluxes based on a 30-year series of daily data about meteorological and hydrological forcing functions. The model outputs were validated by measured data in some of the systems (Schrautzer, 2003). The model outputs were extended to include data sets concerning the ecosystem indicators by the following variables:

- Exergy capture: net primary production (NPP)
- Entropy production: microbial soil respiration
- Storage capacity: nitrogen balance, carbon balance
- Ecosystem efficiency: evapotranspiration/transpiration, NPP/soil respiration
- Nutrient loss: N net mineralization, N leaching, denitrification
- Ecosystem structures: Number of plant species (measured values)

The wet grasslands of the Bornhöved Lakes District are managed in a way that includes the following measures: drainage, fertilization, grazing, and mowing in a steep gradient of ecosystem disturbances. The systems have been classified due to these external input regimes, and in Fig. 8.12 the consequences can be seen in a synoptic manner: While the farmer's target (improving the production and the yield of the systems), the NPP, is growing by a factor of 10, the structural indicator is decreasing enormously throughout the retrogression. Also, the efficiency measures (NPP/soil respiration) are going down, and the biotic water flows get smaller. On the other hand, the development of the N and C balances demonstrates that the system is turning from a sink function into a source, the storage capacity is being reduced, and the loss of carbon and nitrogen compounds (all indicators on the right side of the figure) is rising enormously. With these figures, we can state an enormous decrease of ecosystem health, and as many of the processes are irreversible, the capacity for future self-organization is reduced up to a very small degree.

8.7 SUMMARY AND CONCLUSIONS

In this chapter we have discussed the role of destructive processes for ecosystem dynamics. After some examples of destructive events on the organism scale, the population scale, and the ecosystem scale and after a general integration of the disturbance concept into the orientor model, it is shown that especially mature states can suffer from the high risk of reduced adaptability. Therefore, breakdown is the consequent reaction if the living conditions of a community change strongly. Thereafter, new potentials can be realized and the orientor behavior will start again with renewed site conditions. Adopting this argumentation, natural disturbances seem to be crucial for the long-term self-organization, for the ecological creativity and for the long-term integrity of ecological entities. Destructive processes are focal components of the overall ecosystem adaptability, and they can be found on all relevant scales.

If we follow the ecosystem-based argumentation that integrity and health are relevant variables for ecological evaluation, then the potential for self-organizing processes becomes a key variable in environmental management. It is strictly related to the long-term ecosystem adaptability and its buffer capacity. Therefore, human disturbances in fact intervene the natural dynamics: They operate on artificial spatio1temporal scales, they introduce novel qualities and quantities of change, they modify the reception mechanisms of the ecosystems, they often reduce ecosystem adaptability, and—as shown in the case study—they set new constraints for successional pathways, thus suppressing the natural dynamics.

CHAPTER

9

Ecosystem Principles Have Broad Explanatory Power in Ecology

The best answer raises most questions

9.1 INTRODUCTION

There is a recurrent criticism that ecology as a whole lacks universal laws and predictive theory (Riera et al., 2018), and sometimes it is even argued that theoretical ecology related, for instance, with fitness and natural selection is not truly scientific (Murray, 2001). We argue in this chapter that the ecosystem principles outlined earlier in this book can drive the creation, understanding, and testing of ecological concepts.

Scientific observations carried out in nature usually give origin to possible explanations and, in a further step, intend to provide tentative generalizations that may comprehend the entire set of accessible information. Generalizations can be essentially descriptive and inductive, based on the observation of evident characteristics, or become deeper and convert into the base of deductive theories. In ecology, it must be recognized, there are essentially no universal laws, maybe because such laws cannot even be formulated in the same sense they are in other sciences, for instance, in physics. As a consequence, in ecology, most explanations constitute inductive generalizations, without any deductive theory supporting them. Therefore, we may find in ecology a large number of nonuniversal uncertain generalizations.

Ecology is more complex than physics, and it will therefore be much more difficult to develop an applicable, predictive ecological theory. The easiest way to test illustrative hypothesis is possibly doing it by verification, instead of doing it by falsification. Nevertheless, a more general integrative theory, that may help in explaining empirical observations and experimental results, is felt as necessary by many ecologists.

More than a few new ideas, hypotheses, and possible approaches emerged in the field of system's ecology in the last 20 or 30 years, which when analyzed more in detail appear to form a theoretical pattern able to explain the dynamics of ecosystems (Jørgensen, 1997). Considering the complexity of such dynamics, more than probably the science of ecology will indeed need a number of different complementary approaches to explain ecosystem structure and function (Jørgensen, 1994a). Such ecosystem theories were only used in a limited way in ecological modeling, namely in developing nonstationary models, able to take into account the adaptation of biological components (Jørgensen and de Bernardi, 1997, 1998; Jørgensen, 1986; 1992, 1994b, 1997). It has been argued that to improve substantially the predictive power of ecological models it will probably be necessary to apply theoretical approaches much more widely (Jørgensen and Marques, 2001). Nevertheless, a central question remains to be answered: Is it possible to develop a theoretical framework able to explain the numerous observations, rules, and correlations dispersed in the ecological literature during the last few decades (Jørgensen and Marques, 2001)?

There is no comprehensive or conclusive answer to this question, but it may be argued that it would at least be possible to propose a promising direction for ecological thinking (Jørgensen and Marques, 2001). The objective of this chapter is precisely to verify the possible compliance of ecosystem principles to evolutionary theory and also check if several other nonuniversal explanations, proposed by different authors in the ecological literature about various ecological problems, can be additionally enlightened in accordance with those ecological principles.

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9.2 DO ECOLOGICAL PRINCIPLES ENCOMPASS OTHER PROPOSED ECOLOGICAL THEORIES?

Evolutionary Theory

Through **evolution**, natural populations acquire and convey novel characteristics from generation to generation, a process that was first proposed by Darwin and Wallace (1858) and subsequently detailed by Darwin (1859) as the theory of evolution by natural selection. At first gradually accepted, subsequently the theory became definitively established within the scientific community. In the 1930s, the Darwin's natural selection theory was combined with the theory of heredity, originally proposed by Gregor Mendel and rediscovered by several geneticists, originating the modern evolutionary synthesis (Huxley, 1942). In this modern synthesis, the evolutionary process consists of changes in the frequencies of alleles within the genes pool of consecutive generations, which may be caused by natural selection, genetic drift, or changes in population structure (gene flow).

(a) *Natural selection* consists of the rate of success in survival and reproduction in a given environment. Selection takes place at the individual level, and individuals may exhibit differential mortality, expressed as their survival rate at the reproductive age, and differential fertility, expressed as their total genetic contribution to the next generation. Natural selection, due to its central role in evolutionary theory, allows establishing a strong connection between that and ecology.

We may therefore consider two categories of natural selection:

- *Ecological selection* takes place when the frequency of genes of organisms able to survive and reproduce increases in the population gene pool, in comparison with those of individuals that do not survive.
- *Sexual selection* takes place when the frequency of genes of organisms that are more attractive to the opposite sex, as a function of their greater reproductive success, increases in the population gene pool, in comparison with those of individuals with less attractive features.

Additionally, regarding mutations, natural selection also works in several different ways by:

- Eliminating harmful mutations from a population (purifying or background selection).
- Increasing the frequency of advantageous mutations (positive selection).
- Maintaining variation within a population (balancing selection) through mechanisms such as:
  Overdominance of heterozygous individuals that occurs when they have advantage in terms of fitness when compared with either of the homozygous forms (e.g., human sickle cell anemia, which confers resistance to malaria);
  Frequency-dependent selection, which occurs when infrequent genetic variations exhibit a better fitness.
- Stabilizing selection, which favors average characteristics in a population and consequently reduces gene variation by retaining the mean.
- Directional selection, which favors one extreme of a characteristic, resulting in a shift in the mean in the direction of the extreme.
- Disruptive selection, which favors the two extremes and originates a bimodal distribution of genes frequency, while the mean may shift or not.

(b) *Genetic drift* is the process, originated by sampling variance that describes changes in allele in between generations. In the progeny, the frequency of a given allele will fluctuate in accordance to a probability distribution of its frequency in the parental generation.

In many ways, genetic drift depends on how big the population is, which is particularly relevant in small mating populations because random fluctuations in allele frequency between generations can be large. Actually, such fluctuations between successive generations may cause the disappearance of some alleles from the population, and therefore two populations starting with the same allele frequency may diverge through genetic drift, with alleles being lost in one of them and remaining in the other.

Natural selection and genetic drift determine the destiny of new mutations, but their relative importance in influencing the process depends on the size of the population (N) and the force of selection (s), being given by N times s. If the strength of selection is small, or N times s is small, then genetic drift prevails, while if N times s is large, then selection dominates. This means that genetic drift is stronger in small populations, whereas natural selection acts more efficiently in large populations. Lastly, the time necessary for all individuals in a population to carry a given allele (gene fixation) by genetic drift for an allele to become fixed in the population by genetic drift also depends on the size of populations, being shorter in the smaller ones.

The theory underlying the modern synthesis has three major aspects:

1. The common descent of all organisms from a single ancestor.
2. The manifestation of novel traits in a lineage.
3. The mechanisms that cause some traits to persist while others perish.

The novelty of neo-Darwinism was connecting genes, as evolution units, and natural selection, as mechanism of evolution, and concurrently contributing to the unification of different fields in biology, such as systematics, genetics, paleontology, cytology, botany, zoology, etc.

In 1910, Morgan's work with *Drosophila melanogaster*, the fruit fly, established a crucial connection between experimental biology and evolution studies, illustrating the compliance Mendelian genetics, natural selection, and the chromosome theory of inheritance (Allen, 1978). Succeeding to Morgan's work, Dobzhansky applied his chromosome theory to natural populations (e.g., of *Drosophila pseudoobscura*), combining it with the mathematics of population genetics. His work *Genetics and the Origin of Species*, published in 1937, contributed to consolidate neo-Darwinism, being later followed by other authors in different fields, such as systematics and evolution (Mayr, 1942; Huxley, 1940, 1942), paleontology (Simpson, 1944), botany (Stebbins, 1950), and cytology (Darlington, 1943, 1953).

To summarize, according to neo-Darwinism, evolution is explained by changes in the frequencies of alleles in between generations, between one generation and another as a function of genetic drift, gene flow, and natural selection. Genetic variation in populations results from random mutations, caused by errors in DNA replication, and recombination, consisting of crossing over of homologous chromosomes during meiosis. Speciation takes place gradually when populations become reproductively isolated by geographic barriers.

The modern evolutionary synthesis suffered many refinements, but the most important paradigm shift occurred only when Williams (1966) proposed a gene-centric view of evolution, which extended Darwin's natural selection theory to include the later knowledge and concepts about DNA and genetics, allowing a more rigorous (e.g., mathematical) analysis of, for instance, speciation, altruistic behavior, and kin selection.

Examples

Example 1: Industrial Melanism in the Peppered Moth

According to Wallace (1858), we should expect that insects exhibiting colors that look like the trunks of the trees where they find shelter will have longer survival because of the camouflage from predators. Rapid changes in the frequency of the allele responsible for the mutation-based melanism in populations of *Biston betularia*, the peppered moth (Fig. 9.1), which occurred simultaneously in Europe and North America, constitute a splendid example of fast microevolution caused by mutation and natural selection. The more than probable explanation for the observations for industrial melanism is that in habitats darkened by industrial fumes birds will rather eat noticeable insects (Majerus, 1998; Cook, 2000; Coyne, 2002; Grant, 2002).

Example 2: Warning Coloration and Mimicry

Warning coloration was one of the most interesting topics analyzed by Wallace (1889), elegantly illustrated by Lepidoptera. A good example is provided by *Opthalmis lincea* (Agaristidae) and *Euproctis subnobilis* Snellen, 1881

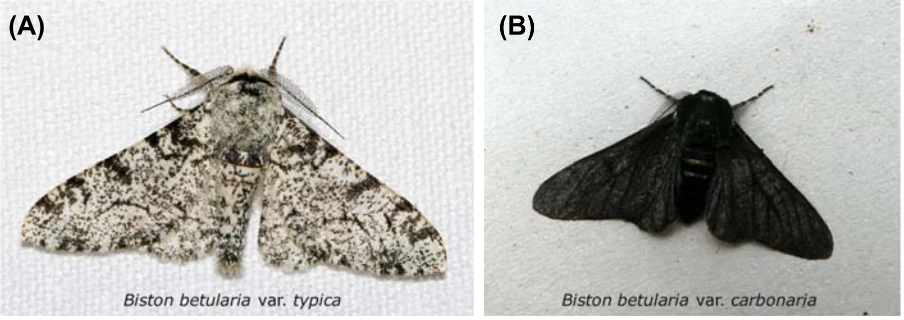

FIGURE 9.1 Industrial melanism in populations of the peppered moth (*Biston betularia*). Before 1850, white moths peppered with black spots (typica) dominated in England (A). With the increase of heavy industries fumes, between 1850 and 1920, typica was largely replaced by a black form (carbonaria) (B), produced by a single allele. Later, between 1950 and 1995, in response to a decrease in smoke emissions, the carbonaria form became rare, while the typica one became common again. *(Adapted from Kettlewell, 1965.)*

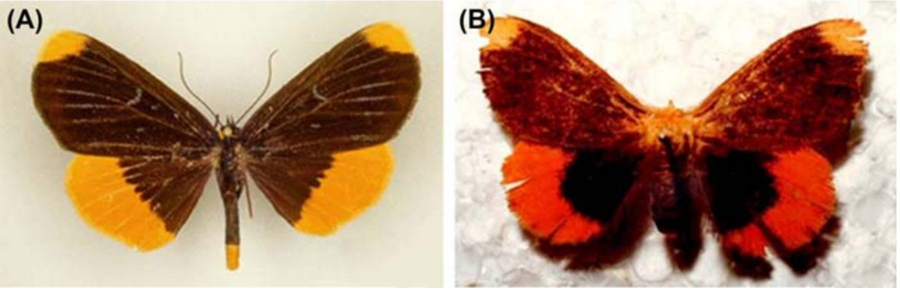

FIGURE 9.2 Wallace (1889) described several insect survival mechanisms in detail. *Opthalmis lincea* (A), which developed chemical repellents that make them repugnant to predators (Mullerian mimetics), is mimicked by *Euproctis subnobilis* (= *Artaxa simulans*) (B) that like succeeds being also avoided by predators.

(syn. *Artaxa simulans*) (Liparidae). *O. lincea* (Fig. 9.2A) is a brightly colored day-flying moth, very common in the Eastern tropics, which developed chemical repellents that make them repugnant to predators (Mullerian mimetics). *E. subnobilis* (= *A. simulans*) (Fig. 9.2B) mimics *O. lincea*, being also avoided by predators (Batesian mimetics) (Kettlewell, 1965).

Example 3: Darwin's Finches

Darwin's observations on finches illustrated how species' gene pools may adapt via offspring to improve long-term survival. The Darwin's finches diagram below illustrates how each finch species adapts to optimize feeding performance in different ecological niches (Fig. 9.3).

Through time, finches' beaks suffered evolution to adapt to their feeding function. For instance, finches eating grubs have a tinny and long beak to extract it from holes in the ground, while finches eating buds and fruit have clawlike beaks that allow grinding down the food, which shows to be advantage when buds represent the only food resource available.

Example 4: The Role of Size in Horses' Lineage

One of the best illustrative examples on the role of size is provided by the horses' lineage, which is very well known through the fossil record horses' ancestors from the early Eocene (50–55 million years ago) were mostly small species around the size of cats, although a few could be bigger, weighing 35 kg. In the Oligocene (30 million years ago), equine ancestral species were already bigger, maybe weighing up to around 50 kg, and in the middle Miocene (17–18 million years ago), the size would be often about 100 kg. More recently, horses could easily reach 200 kg (approximately 5 million years ago), and about 500 kg 20,000 years ago. This increase in size obviously offered a selective advantage. Why?

Fig. 9.4 shows a model in form of a STELLA diagram that has been used to answer this question. The model equations are shown in Table 9.1.

The model has been used to calculate the efficiency for different maximum weights. The heat loss is (Peters, 1983) proportional to the weight with an exponent 0.75. The growth rate also follows the surface but is proportional to the

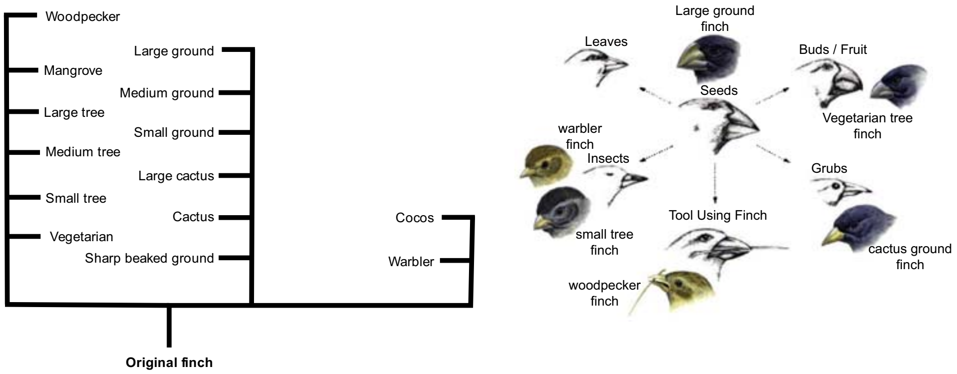

FIGURE 9.3 Darwin's finches' adaptive radiation diagram.

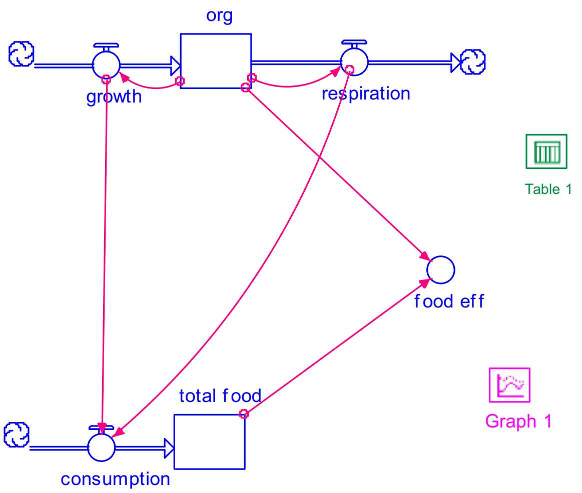

FIGURE 9.4 Growth and respiration follows allometric principles (Peters, 1983). The growth equation describes logistic growth with a maximum weight. The food efficiency is found as a result of the entire life span, using the β-values for mammals and grass (mostly Gramineae). The equations are shown in Table 9.1.

TABLE 9.1 Model Equations.

$d(\mathrm{org}(t))/dt = (\mathrm{growth} - \mathrm{respiration})$
INIT org = 1 kg
Inflows:
Growth = 3*org^(0.67)*(1 − org/upper maximum size)
Outflows:
Respiration = 0.5*org^(3/4)
$d(\mathrm{total\_food}(t))/dt = (\mathrm{consumption})$
INIT total_food = 0
Inflows:
Consumption = growth + respiration
Food_eff % = 2127*100*org(t)/(200*total_food(t))

See the Conceptual Diagram Fig. 9.4.

weight with an exponent 0.67 (see equations in Table 9.1). The results are shown in Table 9.2 and the conclusion is clear: the bigger the maximum weight, the better the eco-exergy efficiency (see Chapter 2 for eco-exergy definition). This is not surprising because a larger weight means that the specific surface that determines the heat loss by respiration decreases. As the respiration loss is the direct loss of free energy, relatively more heat is lost when the body weight is smaller. Notice that the maximum size is smaller than the upper maximum size that is a parameter to be used in the model equations (see also Table 9.2).

TABLE 9.2 Eco-Exergy Efficiency for the Life Span for Different Maximum Sizes.

Maximum Size	Eco-exergy Efficiency %	Upper Maximum Size Parameter
35 kg	1.41%	45 kg
50 kg	1.55%	65 kg
100 kg	1.84%	132 kg
200 kg	2.20%	268 kg
500 kg	2.75%	690 kg

2127 is the beta-value for mammals and 200 for grass.

9.3 EVOLUTIONARY THEORY IN THE LIGHT OF ECOSYSTEM PRINCIPLES

Although living systems constitute very complex systems, they obviously comply with physical laws (although they are not entirely determined by them), and therefore ecological theory should conform to basic laws of physics. One needs to understand the implications of the three generally accepted laws of thermodynamics in terms of understanding organisms' behavior and ecosystems' function. Nevertheless, although the three laws of thermodynamics are effective in describing system behavior close to thermodynamic equilibrium, in far from equilibrium systems, such as ecosystems, it has been recognized that although the three basic laws remain valid, there must be some more basic physics beyond them that is of ultimate importance for ecosystems' functioning. This is the purpose of "irreversible thermodynamics" or "nonequilibrium thermodynamics." A tentative Ecological Law of Thermodynamics was proposed by Sven Erik Jørgensen (1997) as *If a system has a throughflow of Exergy, it will attempt to utilize the flow to increase its Exergy, moving further away from thermodynamic equilibrium; If more combinations and processes are offered to utilize the Exergy flow, the organization that is able to give the highest Exergy under the prevailing circumstances will be selected.* This hypothesis can be reformulated, as proposed by De Wit (2005) as *If a system has a throughflow of free energy, in combination with the evolutionary and historically accumulated information, it will attempt to utilize the flow to move further away from the thermodynamic equilibrium; if more combinations and processes are offered to utilize the free energy flow, the organization that is able to give the greatest distance away from thermodynamic equilibrium under the prevailing circumstances will be selected.*

Both formulations mean that to ensure the existence of a given system, a flow of energy, or more precisely exergy, must pass through it: the system cannot be isolated. Exergy may be seen as energy which can do work (Jørgensen, 1997; Jørgensen and Marques, 2001). A flow of exergy through the system is sufficient to form an ordered structure, or dissipative structure (Prigogine, 1980). If we accept this, then questions arise: Which ordered structure among the possible ones will be selected? Which factors influence how an ecosystem will grow and develop?

Jørgensen (1992, 1997) proposed a hypothesis to interpret this selection, providing an explanation for how growth of ecosystems is determined, the direction it takes, and its implications for ecosystem properties and development. Growth may be defined as the increase of a measurable quantity, which in ecological terms is often assumed to be the biomass. But growth can also be interpreted as an increase in the organization of ordered structure or information. From another perspective, Ulanowicz (1986) makes a distinction between growth and development, considering these as the extensive and intensive aspects, respectively, of the same process. He argues that growth implies increase or expansion, while development involves increase in the amount of organization or information, which does not depend on the size of the system.

According to the tentative Ecological Law of Thermodynamics, when a system grows it moves away from thermodynamic equilibrium, dissipating part of the exergy in catabolic processes and storing part of it in its dissipative structure. We shall refer to this exergy as eco-exergy, in accordance to the definition provided in Chapter 2, which can be seen as a measure of the maximum amount of work that the ecosystem can perform when it is brought into thermodynamic equilibrium with its environment. In other words, if an ecosystem were in equilibrium with the surrounding environment, its eco-exergy would be zero (no free energy), meaning that it would not be able to produce any work, and that all gradients would have been eliminated.

Structures and gradients, resulting from growth and developmental processes, will be found everywhere in the universe. In the case of ecosystems, during ecological succession, eco-exergy is used to build biomass, which is eco-exergy storage. In other words, in a trophic network, biomass and exergy will flow between ecosystem compartments, supporting different processes by which exergy is both degraded and stored in different forms of biomass belonging to different trophic levels.

Biological systems are an excellent example of systems exploring a plethora of possibilities to move away from thermodynamic equilibrium, and thus it is most important in ecology to understand which pathways among the possible ones will be selected for ecosystem development. In thermodynamic terms, at the level of the individual organism, survival and growth imply maintenance and increase of the biomass, respectively.

From the evolutionary point of view, it can be argued that adaptation is a typically self-organizing behavior of complex systems, which may explain why evolution apparently tends to develop more complex organisms. On one hand, more complex organisms have more built-in information and are further away from thermodynamic equilibrium than simpler organisms. In this sense, more complex organisms should also have more stored eco-exergy (thermodynamic information) in their biomass than the simpler ones. On the other hand, ecological succession drives from simple to more complex ecosystems, which seem at a given point to reach a sort of balance between keeping a given structure, emerging for the optimal use of the available resources, and modifying the structure, adapting it to a permanently changing environment. Therefore, an ecosystem trophic structure as a whole will be a continuous evolution of the structure as a function of changes in the prevailing environmental conditions, during which the combination of the species that contribute the most to retain or even increase eco-exergy storage will be selected.

This constitutes a translation of Darwin's theory into thermodynamics because survival implies maintenance of the biomass, and growth implies increase in biomass. Eco-exergy is necessary to build biomass, and biomass contains eco-exergy, which may be transferred to support other eco-exergy (energy) processes.

The examples of industrial melanism in the peppered moth and warning coloration and mimicry are compliant with the Ecological Law of Thermodynamics, illustrating at the individual and population levels how the selected species are able to improve survival and maintenance or increase in biomass under the prevailing conditions. Also, the Darwin's finches adapt to take advantage of feeding in different ecological niches, which constitute another good illustration at the individual and population levels. Depending on the food resources available at each niche, the beaks evolved throughout time to adapt their function under the current conditions, improving survival and biomass growth capabilities. Finally, the horses' lineage increase in size illustrates very well how a bigger weight determines a decrease in body specific surface and consequently a decrease in the direct loss of free energy (heat loss by respiration). From the thermodynamic point of view, we may say that the solutions able to give the highest eco-exergy under the prevailing circumstances were selected, maintaining or increasing gradients and therefore keeping or increasing the distance to thermodynamic equilibrium.

Island Biogeography

We may easily corroborate that there are, in principle, many more bird species on a large island than on a small one. A possible explanation is related with the area of the island, since the number of species normally augment as a function of the available space. Nevertheless, this does not explain why sometimes small island assemblages, having together approximately the same area of isolated bigger islands, may host many fewer species and, in other cases, many more species than the last.

MacArthur and Wilson (1967) proposed and elaborated a theory of "island biogeography" in order to elucidate irregular distributions like the ones referred above. According to the theory, the number of species found on an island will reflect an equilibrium between the rate of colonization by new species and the rate of extinction of species previously established (Fig. 9.5). For instance, if a new volcanic island forms at a given distance from mainland and becomes habitable, then some bird species will start to immigrate across that distance and establish on the island. If X species exist in the adjacent mainland, then the rate of new species establishment in the island will gradually decrease because for each new species established the pool of possible new invaders diminishes by one. The species that became resident on the new island are not potential invaders anymore.

On the other hand, the rate of species extinction on the island is related to the number of species that became residents. At the beginning of the island colonization, the extinction rate is obviously low because there are few species and therefore only few candidates to become extinct. But as the island resources are limited, the increase in the number of resident species determines, as counterpart, that their individual populations will tend to be smaller and have a higher probability to become extinct. So, when the island is still almost unoccupied, new species will establish resident populations at a higher rate, while the rate of extinction of these populations will be higher as the island becomes almost fully colonized. It is assumed that there will a point between 0 and X (the number of species existent

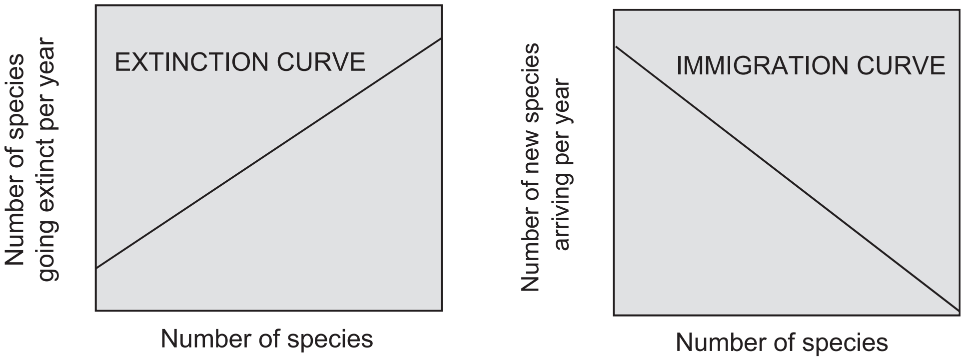

FIGURE 9.5 Extinction and Immigration curves.

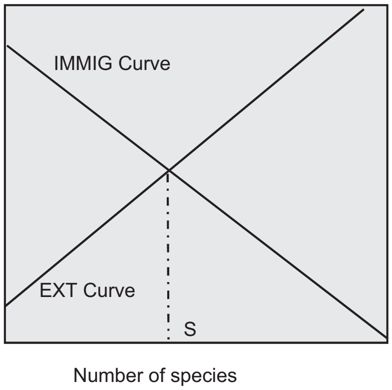

FIGURE 9.6 The equilibrium number of species: For each island, there will be a point where the extinction (EXT curve) and immigration curves (IMMIG curve) intersect. At this point, the rate of immigration of new species to the island will be equal to the rate at which species are going extinct.

on the mainland) for which the two rates will be equal, balancing the colonization and extinction processes and thus stabilizing the number of species on the island. That number of species (Fig. 9.6) may remain stable if the factors controlling the two rates do not suffer alterations, although the composition of the faunal community may vary continuously as a function of the dynamics of the different species invasions and extinctions.

Example

Krakatau Island

The island of Krakatau, between Java and Sumatra, was devastated by a volcanic explosion in 1883, which caused the complete annihilation of the fauna and flora. The island remnant and two adjacent islands, also distressed by the explosion, became a natural laboratory to test the island biogeography theory. Observations carried out after the catastrophe showed that in 1908, 25 years later, 13 bird species had recolonized what remained from the island, by 1921 28 species were established, and by 1934 this number raised to 29. Actually, from the moment of the explosion up to 1934, the number of species that colonized the island was 34, but 5 became extinct. Subsequently, during the next half century, by 1952 33 species were recorded, and by 1985 35 species, but again the faunal composition varied dynamically, as 14 new species established populations, but 8 species became extinct. These observations showed that, in accordance with theory, the rate of colonization declined as the number of species established on the island increased. Also, although the number of species more or less stabilized, the faunal composition gradually changed. Additionally, again in agreement with the theoretical predictions, if all other factors are equal, the rate of immigration to islands more distant from the mainland was lower than to closer islands, and thus the equilibrium was reached with a smaller number species established (Fig. 9.7). Finally, larger islands, providing more abundant resources than the small ones had comparatively lower extinction rates and thus more species established.

The Island Biogeography Theory can also be applicable in other contexts, for instance, to predict faunal changes in biodiversity as a function of habitat fragmentation. In fact, the remaining patches of previously continuous habitats, such as large forests, will largely behave like islands. Depending on their dimensions and on the difficulties in crossing the gaps between them, such patches will exhibit variable immigration and extinction rates, and the approach to predict their biodiversity is comparable to what we could utilize regarding islands with different sizes and at different distances from the mainland.

Island Biogeography Theory in the Light of Ecosystem Principles

In general terms, the Island Biogeography Theory explains therefore why, if everything else is similar, distant islands will have lower immigration rates with fewer species than those close to a mainland, while close islands will have high immigration rates and support more species. It also explains why large islands, presenting lower extinction rates, will have more species than small ones. This theory has been applied, for instance, in forecasting the effects of fragmenting previously continuous habitat, considering that fragmentation leads to both lower immigration rates (gaps between fragments are not crossed easily) and higher extinction rates (less area supports fewer species).

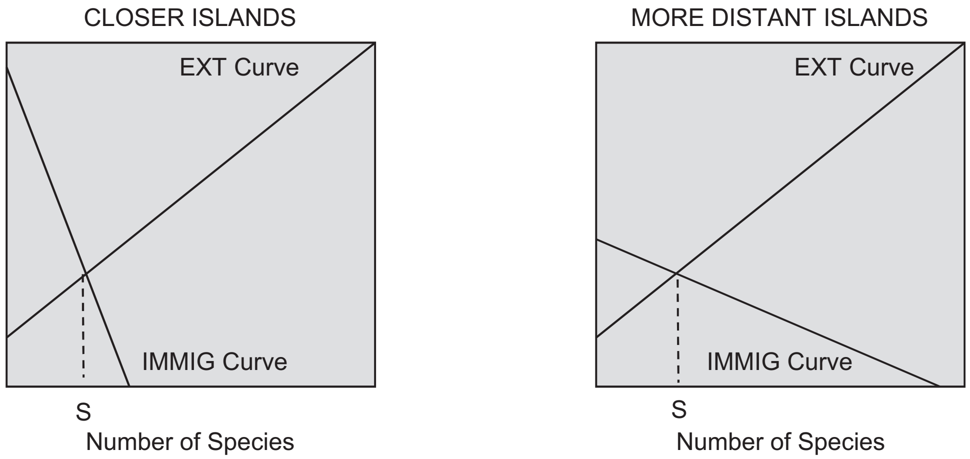

FIGURE 9.7 The influence of distance of an island from the source on the equilibrium number of species. *EXT curve*, extinction curve; *IMMIG curve*, immigration curve.

The Ecological Law of Thermodynamics equally provides a sound explanation for the same observations. Let us look in the first place to the problem of the immigration curves. In all the three examples, the decline in immigration rates as a function of increasing isolation (distance) is fully covered the concept of openness introduced by Jørgensen (2000). Once accepted the initial premise that an ecosystem must be open or at least nonisolated to be able to import the energy needed for its maintenance, islands' *openness* will be inversely proportional to its distance to mainland. As a consequence, more distant islands have lower possibility to exchange energy or matter and decreased chance for information inputs, expressed in this case as immigration of organisms. The same applies to fragmented habitats, the smaller the plots of the original ecosystem the bigger the difficulty in recovering (or maintaining) the original characteristics. After a disturbance, the higher the openness, the faster information and network (which may express as biodiversity) recovery will be.

The fact that large islands present lower extinction rates and more species than small ones, as well as less fragmented habitats in comparison with more fragmented ones, also complies with the Ecological Law of Thermodynamics. All three examples can be interpreted in this light. Provided that all the other environmental are similar, larger islands offer more available resources. Under the prevailing circumstances, solutions able to give the highest eco-exergy will be selected, increasing the distance to thermodynamic equilibrium not only in terms of biomass but also in terms of information (i.e., network and biodiversity). Moreover, after a disturbance, such as in the case of Krakatau Island, the rate of recolonization and ecosystem recovery will be a function of the system's openness.

Latitudinal Gradients in Biodiversity

Observations have noted that at a global scale species diversity typically declines as a function of increasing latitudes, from the equator to poles (Rosenzweig, 1995; Stevens and Willig, 2002). Nevertheless, although this pattern of variation of biodiversity with latitude is more than conspicuous, the dynamics behind it are not well understood. The observed gradient is generally thought as the result of species in situ origination and extinction, and in this context the tropics are seen as either generating biodiversity (the tropics-as-a-cradle hypothesis), or accumulating biodiversity (the tropics-as-museum hypothesis), eventually both.

The possible causes for latitudinal gradients in biodiversity (www.ecology.info/gradients-biodiversity.htm).

The variation of biodiversity according to a gradient from the equator to the poles (Fig. 9.8) is not determined by the latitude per se, but by the environmental factors correlated with it. Many different mechanisms, actually more than 25, have been proposed to explain how latitudinal diversity gradients may be generated, but in fact there is no consensus about it (Gaston, 2000).

The area of the different climatic zones is considered as one of the possible factors responsible for latitudinal diversity gradients. In fact, the area of land masses with similar climate characteristics, namely small temperature fluctuations, is larger at the tropics than at higher latitudes (Rosenzweig, 1992). Eventually, this might be connected to higher levels of speciation and lower levels of extinction in the tropics (Rosenzweig, 1992; Gaston, 2000; Buzas et al., 2002). Additionally, the present higher diversity found in the tropics may, at least partially, be explained by

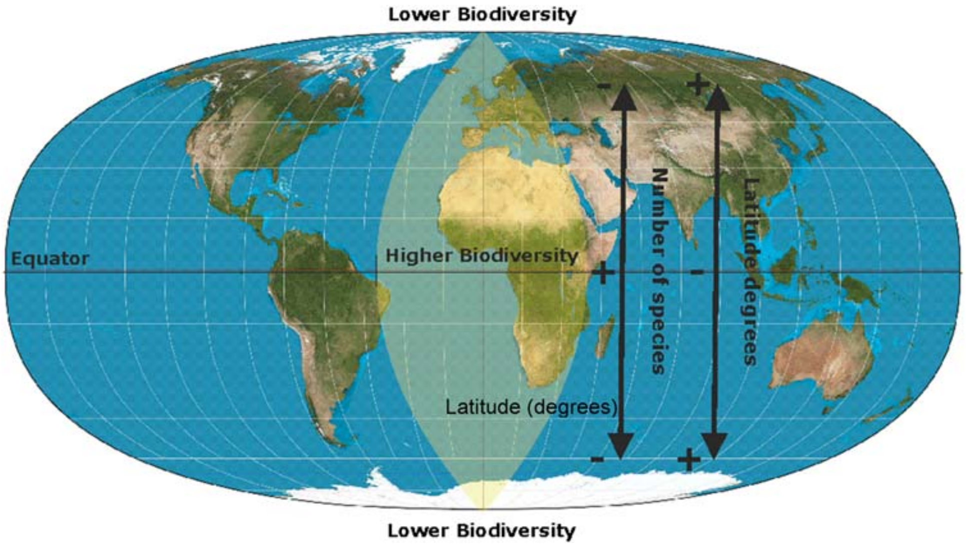

FIGURE 9.8 Latitudinal trends of biodiversity variation, exhibiting a decreasing gradient from the equator to the poles. *Reproduced from Roy K, Jablonski D, Valentine JW, Rosenberg G. 1998. Marine latitudinal diversity gra tests of causal hypothesis. Proc. Natl. Acad. Sci. USA 95, 3699–3702. Copyright (1998) National Academy of Sciences, U.S.A.*

the historical evolutionary process, since the land surface of the Earth was for the most located in tropical or subtropical zones during a long period in the Cenozoic (Ricklefs, 2004).

More intense solar radiation in the tropics will in principle increase primary productivity, which subsequently might augment biological diversity. Nevertheless, such relation is not evident, since an increase in primary productivity may indeed explain a surge of total biomass, but is not a sufficient condition to explain why that biomass should be allocated into more individuals belonging to more species (Blackburn and Gaston, 1996). In fact, both population density and individual body sizes tend to be lower in the tropics, which appears correlated to the occurrence of more species, but the reasons for such interactions are complex (Blackburn and Gaston, 1996). One explanation is that higher temperatures in the tropics determine shorter generation times and larger mutation rates, and thus faster speciation (Rohde, 1992). Maybe speciation is also hastened by the tropical higher habitat complexity, although this explanation cannot really apply to freshwater and marine ecosystems. Maybe higher speciation rates in the tropics results from a combination of several factors, each factor affecting differently distinct groups of organisms, areas (e.g., northern vs. southern hemisphere), and ecosystems, creating the observable patterns diversity.

Examples

Example 1: Latitudinal Distribution of Hyperiid Amphipods Diversity in the Atlantic Ocean

Burridge et al. (2016) published a very interesting paper analyzing the distribution and diversity of hyperiid amphipods along a latitudinal gradient in the Atlantic Ocean. Although their diversity and biogeographical distribution is not well known, it is recognized that marine hyperiid amphipods, as commensals or as parasites of gelatinous plankton, play a very important role in marine pelagic food webs.

Having collected hyperiids from epipelagic and upper mesopelagic depths, these authors could identify a total of 70 species belonging to 36 genera and 17 families. Additionally, they observed the occurrence of maxima in species and genus richness in the equatorial upwelling region (induced by Coriolis force), with species richness showing a significant positive correlation to sea surface temperature. The analysis allowed identifying different main assemblages of hyperiid species, respectively, gyral, equatorial, transitional, and sub-Antarctic, actually matching with the biochemical provinces proposed by Longhurst (2010). Although hyperiids are part of the zooplankton, mechanisms controlling hyperiids diversity appear to be different from other zooplankton taxa. In fact, while most zooplankton groups reach maxima in diversity in subtropical waters, hyperiids show a maximum diversity of species and genus in the equator. This might depend on the distribution and diversity of gelatinous plankton species that host hyperiids, which are not well characterized at the global ocean scale.

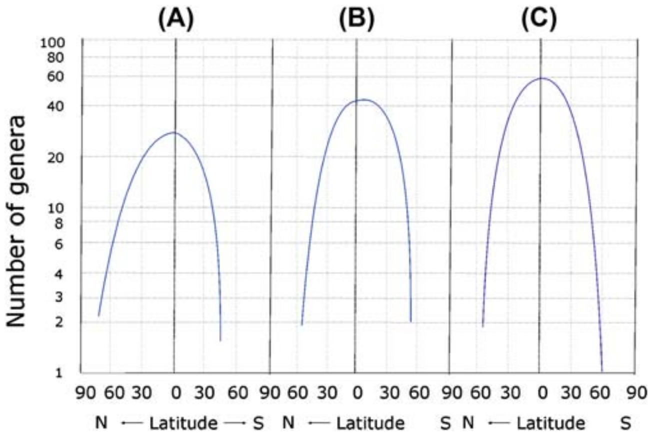

FIGURE 9.9 Diversity versus latitude plots for (A) genera of amphibians; (B) genera of lizards; (C) genera of snakes, showing that the highest number of genera occurs in 5° latitude classes.

Example 2: **Latitudinal Trends in Vertebrate Diversity (http://www.meer.org/chap3.htm)**

Amphibians are not present in the arctic regions but, on the other hand, are common in the mid-latitudes (Fig. 9.9A) (Jenkins et al., 2013). Amphibians are not able to regulate body temperature and therefore find their preferential habitats and reach their highest diversity in the tropics, where the climate is warmer and humid. Actually, the distribution of one of the three orders of Amphibian, the Gymnophiona or Apoda (represented by less than 200 species), is restricted to the tropics.

Reptiles, for similar reasons, are also represented by many more species in low latitudes. For instance, both lizards (Fig. 9.9B) and snakes (Fig. 9.9C) peak in diversity in the tropics. Nevertheless, in some cases, in low latitudes between 15° and 30°, where most of the deserts are located, their diversity may decrease (Laudenslayer and Grenfell, 1983). As a pattern, these two major groups of reptiles are represented by far more species in the tropics than in higher latitudes, which is even more evident for turtles.

Birds also present more species in the tropics. Although homeothermic, the group also presents a high diversity in temperate latitudes. For example, at least 88 bird species breed on the Labrador Peninsula of northern Canada (55°N.), 176 species breed in Maine (45°N.), and more than 300 species can be found in Texas (31°N.; Peterson, 1963), and 540 in California, while the total number of species reaches approximate 700 for all of North (Welty, 1975).

Mammalian higher species diversity is also recognizable at low latitudes. This was illustrated by Simpson (1964), who analyzed the latitudinal trend of mammals' diversity for continental North American mammals, although he also identified a secondary pattern of variation superimposed to the latitudinal trend. Simpson refers the occurrence of more mammal species in mountainous regions than in lowlands.

Fish also present much higher diversity in tropical water, where most of the marine and freshwater species can be found. Coral reefs and tropical reefs, for instance, present one of the most amazingly diverse fish communities, encompassing something like 30%–40% of all marine fish species, which is illustrated by the fact that in a single large reef complex, or in association with it, 2200 species could be found (Moyle and Cech, 1996). Another excellent example is the Amazon River, 3700 miles long, which drains one quarter of South America. This huge tropical river presents more than 2400 fish species, while its tributary, the Rio Negro, has alone more fish species than all the rivers of the United States taken together.

Example 3: ***Trends* within Plant Communities and Across Latitude**

The way plant species richness (expressed as the number of species) and species-specific plant density (expressed as number of individuals per species) vary within community size frequency distributions across latitude was examined in an interesting work published by Niklas (2003), based on data sets from 226 forested plant communities from Asia; Africa; Europe; and North, Central, and South America available at the Gentry database. Species richness and species-specific plant density exhibited an opposite variation as a function of the latitudinal gradient. Species richness showed a clear increase toward the tropics, while species-specific plant density showed the inverse trend.

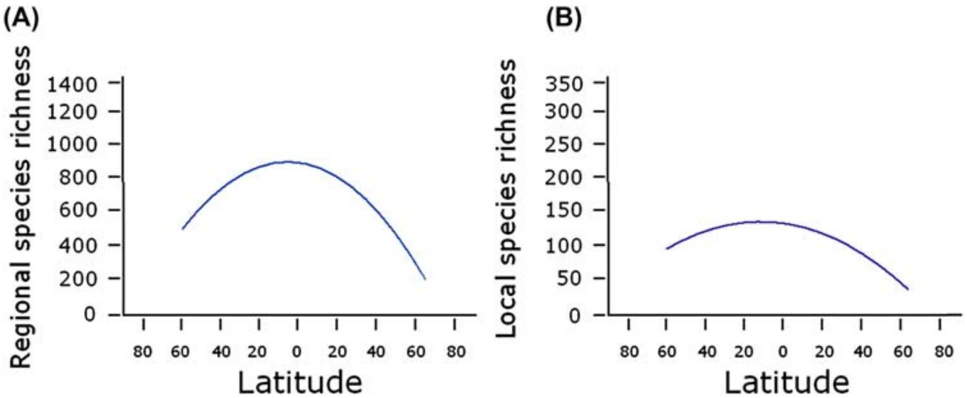

FIGURE 9.10 variation of marine invertebrate epifauna species richness as a function of latitude. (A) Regional species richness. (B) Local species richness.

Example 4: **Trends within Marine Epifaunal Invertebrate Communities**

The influence of latitude on local and regional pools of marine invertebrate epifauna species richness was analyzed by Witman et al. (2004), based on data provided by samples carried out in 12 independent biogeographic regions from 62ºS to 63ºN. Both regional and local species richness varied as a function of latitude, exhibiting the highest values at low latitudes and decreasing toward high latitudes (Fig. 9.10).

9.4 LATITUDINAL GRADIENTS IN BIODIVERSITY IN THE LIGHT OF ECOSYSTEM PRINCIPLES

Latitudinal gradients in biodiversity are easily interpretable in the light of the Ecological Law of Thermodynamics. Obviously, the higher solar radiation in the tropics increases productivity, which in turn is thought to increase biological diversity. In fact, Blackburn and Gaston (1996) found that one parameter that correlated significantly with diversity in both oceans was solar energy input, as represented by average sea surface temperature. Moreover, these authors claim that if that correlation was causal, sea surface temperature is probably linked to diversity through some aspect of productivity. However, they could not establish the causal nexus, considering that productivity could only explain why there is more total biomass in the tropics, not why this biomass should be allocated into more individuals, and these individuals into more species.

This apparent inconsistency can nevertheless be explained within the frame of ecosystem principles. In fact, Jørgensen et al. (2000), proposed that ecosystems show three growth and development forms:

I. Growth and development of physical structure (biomass), which is able to capture more of the incoming energy in the form of solar radiation but also requires more energy for maintenance (respiration and evaporation).
II. Growth and development of the network interactions which provides more cycling of energy or matter.
III. Growth and development of information (more developed plants and animals with more genes), from r-strategists to K-strategists, which waste less energy.

This was experimentally confirmed by Debeljak (2002) examining managed and virgin forest in different development stages (e.g., pasture, gap, juvenile, optimum forest). Accordingly, these growth and development forms may be considered an integration of E.P. Odum's (1969) attributes, which describe changes in ecosystems associated with successional development from the early stage to the mature stage. Clearly, Blackburn and Gaston (1996) were considering only growth form I.

Keystone Species Hypothesis

The keystone species concept was introduced by Paine (1969, 1980) and since then has been playing a central position in conservation biology. According to Paine, keystone species are understood as those whose importance in their environments with regards to ecosystems function is much greater than their representativeness in terms of abundance or biomass. In other words, they play, in ecological terms, the same role that a keystone does in the apex of an arch, by maintaining the structure and integrity of ecological communities.

This means that although the collapse of dominant species, in terms of abundance and biomass, will also have dramatic effects on ecosystems, such effects will be proportional to their importance, and therefore such species could not be considered as keystone. Nonetheless, the keystone species concept is theoretically young and still under development, and the term as originally proposed by Paine to predator species has been extended to include prey species, plants, and even habitat resources. This might be controversial; definitions of keystone species are many and eventually not always consensual. But, in any case, keystone refers to species that play critical roles, whose disappearance will result in dramatic alterations in their communities' structure and functioning, which has been observed in many ecosystems and for an extensive variety of organisms.

Independently from controversies, regarding a certain oversimplification of complex systems, the keystone species concept has been largely applied as a model to understand the drivers controlling ecological communities, allowing an easier communication between scientists and politicians and influencing managers and decision makers in establishing priorities in terms of species and habitats conservation.

Examples

Example 1—Sea Stars' Predation on Mussels

Paine's (1969a) work provides a classical example of a keystone predator species, *Pisaster ochraceus*, a sea star that usually preys on intertidal mussels and other bivalves, limpets, barnacles, chitons, etc. (Fig. 9.11), which have no other natural predators. In case *P. ochraceus* disappears from the intertidal zone, the mussels' populations tend to increase out of control and exclude many other species, damaging the whole community and decreasing biodiversity.

Example 2—Sea Otters' Predation on Sea Urchins

The same applies to sea otters that predate sea urchins and protect kelp forests. Without such predation, sea urchins' populations would increase excessively and consume kelp uncontrollably, destroying the habitat that kelp forests represent for many species, and therefore decreasing the system's productivity and biodiversity.

Example 3—Gray Wolves' Predation on Elks

Other well-know example is the control exerted by gray wolves (*Canis lupus*) on elk (*Cervus canadensis*) populations. The wolves' eradication to protect farmers' livestock (Grooms, 1993; Breck and Meier, 2004; Outland, 2010) (a classical example of an absurd economic-driven management decision) triggered an uncontrolled growth of elk populations, since their primary predators disappeared, and a consequent overgrazing of plants, namely in riparian zones, causing the loss of habitat for many other wild animal species, such as beavers and songbirds, and influencing other ecological factors, such as the stability of stream banks, the deposition of organic matter and fine particles sediments, nutrients cycling, water temperature via changes in shading (Smith and Bangs, 2009).

Example 4—Elephants in Savannas

Keystone species are frequently predators because even small populations of these may exert a strong influence on the distribution, behavior, and abundance of prey species. Nevertheless, species other than predators, herbivores for example, may also play the role of keystone species. That is the case of elephants in savannas. By eating trees'

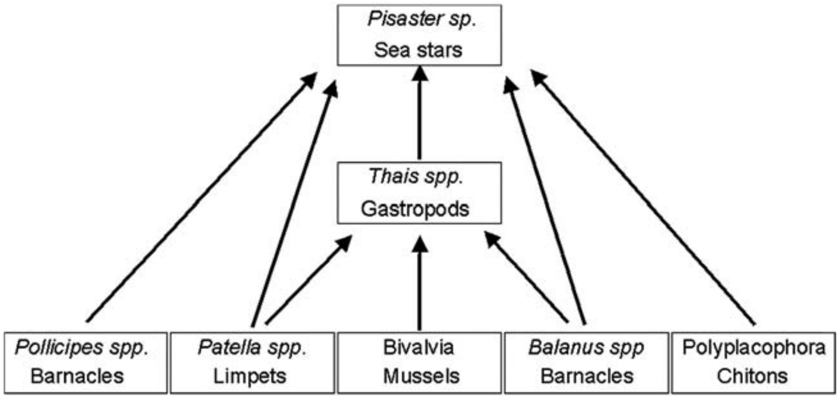

FIGURE 9.11 Food web of species that can be found in intertidal temperate rocky shores ecosystems illustrating the keystone species hypothesis.

sprouts, the elephants prevent these habitats from gradually becoming a woodland. Such vegetation management by elephants ensures grasses' abundant growth in savannas, which benefits other herbivores populations, such as small rodents, zebras, gnus, antelopes, etc.

9.5 THE KEYSTONE SPECIES HYPOTHESIS IN THE LIGHT OF ECOSYSTEM PRINCIPLES

All the examples illustrate that the keystone species hypothesis is clearly within the Ecological Law of Thermodynamics. In fact, ecosystems constitute dissipative, ordered, open structures, whose change in entropy depends on an external exogenous contribution from the environment and an internal endogenous contribution due to the system state (see Chapter 2 of this book). The origin of the ecosystem's ordered structure is therefore its openness and a flow of energy, which drives biogeochemical cycles. Biological systems may explore different possibilities to increase their eco-exergy (or work energy) and move away from thermodynamic equilibrium (Jørgensen, 1997), and therefore it is necessary to understand through which pathways among the possible ones the system will develop.

In general terms, to move away from thermodynamic equilibrium ecosystems may apply the growth and development forms listed above, which are utilized to store more work energy, or eco-exergy. In a trophic network, biomass and exergy will therefore flow between ecosystem compartments, supporting different processes by which eco-exergy is both degraded and stored in different forms of biomass belonging to different trophic levels. When a keystone disappears from the ecosystem, for natural or other causes, the pathways of the system's dissipative structure change, and biomass growth (form I) becomes predominant in moving away from thermodynamic equilibrium, while growth and development forms II and III become less important, with a concomitant decrease in the systems' network complexity and information (biodiversity).

Optimal Foraging Theory

Researchers have pursued theories to explain species' diversity since Charles Darwin's publication of *The Origin of Species* in 1859. Different approaches often focused on the observation of animals' feeding behavior, having as first concern quantifying adaptation, fitness, and natural selection. The assumption has been that feeding behaviors reflect these processes, and thus will encompass adaptation mechanisms, which will act in a feedback loop to create an interactive system between an animal's phenotypes and their environment.

In this context, the Optimal Foraging Theory was proposed by MacArthur and Pianka (1966), based on the argument that successful foraging is a crucial requisite to individual's survival, and therefore the use of decision theory should allow predicting the individual foraging behavior that would allow maximizing food intake. In their seminal paper, based on cost—benefit analysis, these authors developed a graphical model allowing predictions of animal feeding activities once a forager's optimal diet is specified. The degree to which a predator could be selective in choosing its preys was dependent on prey abundance and therefore on the time spent to search and capture each food item eaten. So, diets tend to be broad when prey are scarce (longer search time) and narrow when food items are abundant (shorter search time), meaning that predators can only afford to disdain mediocre preys if they have a reasonably high chance to find a superior food item in a period equivalent to what it would have taken to consume the previous one. Likewise, predators having larger available areas can be more specialized than those having smaller ones because travel time between preferred food items will be lower.

Summarizing, the Optimal Foraging Theory allowed to approach three main concepts: (1) the period that a predator will forage in a given area, which depends (2) on the influence of prey density on the time spent by the predator foraging in the area and (3) on the influence of the variety of prey on the predator's choice regarding preys captured.

The predator's behavior to optimize foraging could be described as a function of its relationships with the prey consumed, taking into account the time spent to capture and eat them and prey availability, and consequently encompassing the study of differential land and resources use.

Examples

Example 1: Rufous Hummingbirds

A study on Rufous hummingbirds carried out by Carpenter et al. (1983) allowed testing the Optimal Foraging Theory. Hummingbirds perform long migrations between the north-western Pacific, where they breed, and southern Mexico, where they spend the winter. During their migratory stops, they establish feeding territories, which they guard very actively, expulsing other hummers, hawk moths, butterflies, and even bees competing for the nectar. Moreover, to compete even more successfully with other nectar consumers, they exhaust the nectar resources in areas adjacent to their territories as early in the day as they can.

Experimentally, Carpenter and coworkers, covered one-half of the flowers in a territory with a fabric and observed that, being unable to drain those flowers, the resident bird increased his territory. This simple experiment illustrated that hummers' territoriality was connected to the availability of nectar, and also that the birds were able to appraise the amount of nectar they had under control. In order to calculate the bird's weight each time it rested, the usual perch used by the territory holder was replaced by a false one connected to a sensitive scale. Using this technique, it was possible to conclude that the birds optimized their territory by trial and error, dimensioning for the size that allowed maximizing their daily weight increase. Regarding Rufous hummingbirds, as a whole, the theory successfully predicted the birds' behavior in nature.

Example 2: Optimal Clam Selection by Predator Crows in North-Western Pacific

Another good illustration of the Optimal Foraging Theory is provided by clam selection by predator crows (Richardson and Verbeek, 1986). The authors observed that crows in the Pacific Northwest frequently did not eat littleneck clams after having located them. In fact, crows digging the sediments looking for food usually only care for capturing the larger clams, which they break by dropping them on the rocks before eating it. Crows acceptance rate increases as a function of the prey size, disdaining the smaller clams and consuming all the larger ones. Although bigger clams can be broken more easily when they are dropped on the rocks, the authors did not think this was the reason why crows preferred them. In accordance with the theory, they explained instead that the most profitable clams were the largest because they contained more calories than smaller ones, providing superior caloric benefits in exchange of the work necessary for searching, digging up, opening, and feeding on them. A mathematical model was built based on the assumption that crows would optimize their diet in terms of maximizing caloric ingestion. This model was able to predict successfully the crows' behavior in selecting clams as a function of the prey size, with simulations matching empirical observations carried out in the field (Fig. 9.12).

The Optimal Foraging Theory in the Light of Ecosystem Principles

The Optimal Foraging Theory clearly complies with the Ecological Law of Thermodynamics. The fact that prey abundance influences consumers' selectivity and that diets are broad when preys are scarce and narrow if food is abundant, as a function of search for food time, is clearly translated by …*If more combinations and processes are offered to utilize the exergy flow, the organization that is able to give the highest exergy under the prevailing circumstances will be selected* or *by if more combinations and processes are offered to utilize the free energy flow, the organization that is able to give the greatest distance away from thermodynamic equilibrium under the prevailing circumstances will be selected.* Both examples can therefore be easily explained by the same ecosystem principles.

Niche Theory

Hutchinson's Fundamental Niche Theory (Hutchinson, 1957, 1965) proposes that the ecological niche of an organism can be assumed as an abstract multidimensional mapping of population dynamics onto an environmental space, the axes of which are biotic and abiotic factors influencing reproduction and survival. In other words, niche can be

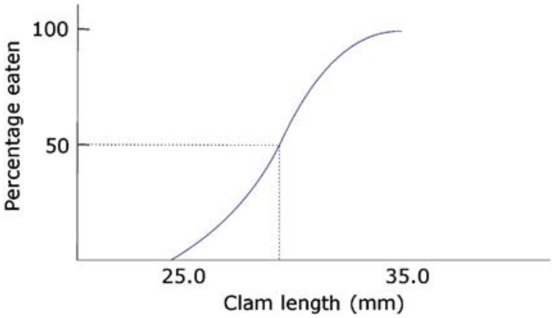

FIGURE 9.12 Model based on the Optimal Foraging Theory showing an optimal relationship between clams' size and their predation rate by crows, which assumes that birds will tend to maximize the rate of energy gain per unit of time spent foraging for clams. The *curve* corresponds to the predicted percentages; *Solid circles* correspond to empirical observations (Richardson and Verbeek, 1986).

interpreted as an "*n*-dimensional hypervolume" enclosing the total range of environmental conditions under which the individual (or population) can successfully live and replace itself.

The "fundamental niche" concept can be defined as the maximum inhabitable hypervolume where competitors and predators do not exist (biotic interactions such as competition, predation, and parasitism are absent), i.e., where the entire set of optimal conditions under which an organism can thrive are present. It can be distinguished from the concept of "realized niche," which designates a smaller part of hypervolume occupation by the species which is under biotic constraints, i.e., restricted due to competition. For single specific environmental variables, "niche breadth" can be thought of as the habitable range for an organism, i.e., the extent of the hypervolume projected onto each individual environment.

After Hutchinson's distinction, "niche" denotes the requirements of the species and "habitat" in the physical place in the environment where those requirements can be met. A clear understanding of Hutchinson's emphasis on the fundamental importance of competition as a force influencing the distribution of species in nature is required when interpreting the distribution of the species A and B in Fig. 9.13.

According to Hutchinson, a species will not use its whole fundamental niche when facing competition. Instead, a smaller realized niche comprising those portions of the fundamental niche where the species is competitively dominant will be actually utilized. In this sense, the realized niche is thus smaller than the fundamental niche, meaning that a species can often be absent from portions of its fundamental niche as a consequence of competitive exclusion. Competition will obviously be greater with the increase in resemblance of the species niches thus, when two populations are sharing limited resources.

Niche has been used to describe and analyze different aspects:

1. Forms of species interaction (including competition, resource portioning, exclusion, or coexistence);
2. To explain patterns of species abundance (dominance and rarity);
3. Factors responsible for governing species geographical distribution;
4. Factors determining structure and stability of multispecies communities.

Considering a hypothetical example, corresponding to an extreme situation:

> Can two populations occupying the same resource niche coexist in the same environment? (http://courses.washington.edu/anth457/nichelec.htm).
>
> By definition, if two populations occupy the same resource niche, it means they utilize the same resources and in the same way.
>
> Commonly thinking, three possible results could be expected: (1) resources are shared equally (neither population changes niche); (2) one or both populations may change niche to reduce overlap (*niche partitioning*); (3) one population totally fails (*competitive exclusion*). Which result is most probable to occur?

Answer from niche theory would consider options 2 or 3, but not 1. This somewhat counterintuitive result has been named as *competitive exclusion principle* (CEP) (Gause, 1934), a central tenet of modern niche theory. In essence, this states that two species with identical niches cannot coexist indefinitely—either the niches will differ or one will be excluded by the other (with "exclusion" meaning it has been replaced by differential population growth, not necessarily by fighting or territoriality). A complete niche overlapping (100%) is, however, very unlikely if not impossible; such an extreme case is unnecessary for competitive exclusion or other forms of niche change.

Predicting what happens when there is niche overlap and competition has been central to ecology in theory development and in advancing research. Questions that have been addressed, include the following: When does exclusion result, when coexistence? How much overlap is possible (a question treated by the "theory of limiting similarity")? How do environmental fluctuations affect this? Why are some species generalists, and others specialists?

Competitive exclusion and coexistence via reduction in niche overlap are two responses to niche competition which have often been observed, with their determinants and features being investigated using three main procedures: laboratory experiments, field observations, and mathematical models/simulations. The first response is frequently observed when a species colonizes a habitat and outcompetes indigenous species (probably linked to absence of parasites and predators adapted to exploit the colonizer) (e.g., introduced placentals vs. indigenous marsupials in Australia). The second, coexistence through niche partitioning, can hardly be directly observed, but it is often inferred from traces left by "the ghost of competition"." It can be achieved through inspection of the two populations that partially overlap in space, by comparing the niches of each population in the area of overlap and nonoverlap. Most of the time, in areas where competitors coexist, one or both present narrower niche range (e.g., diet breadth) compared to areas without competitors; this can be explained if we consider that competition compels each population toward specialization in resources (or other niche dimensions) which give them competitive advantage, and conversely, to

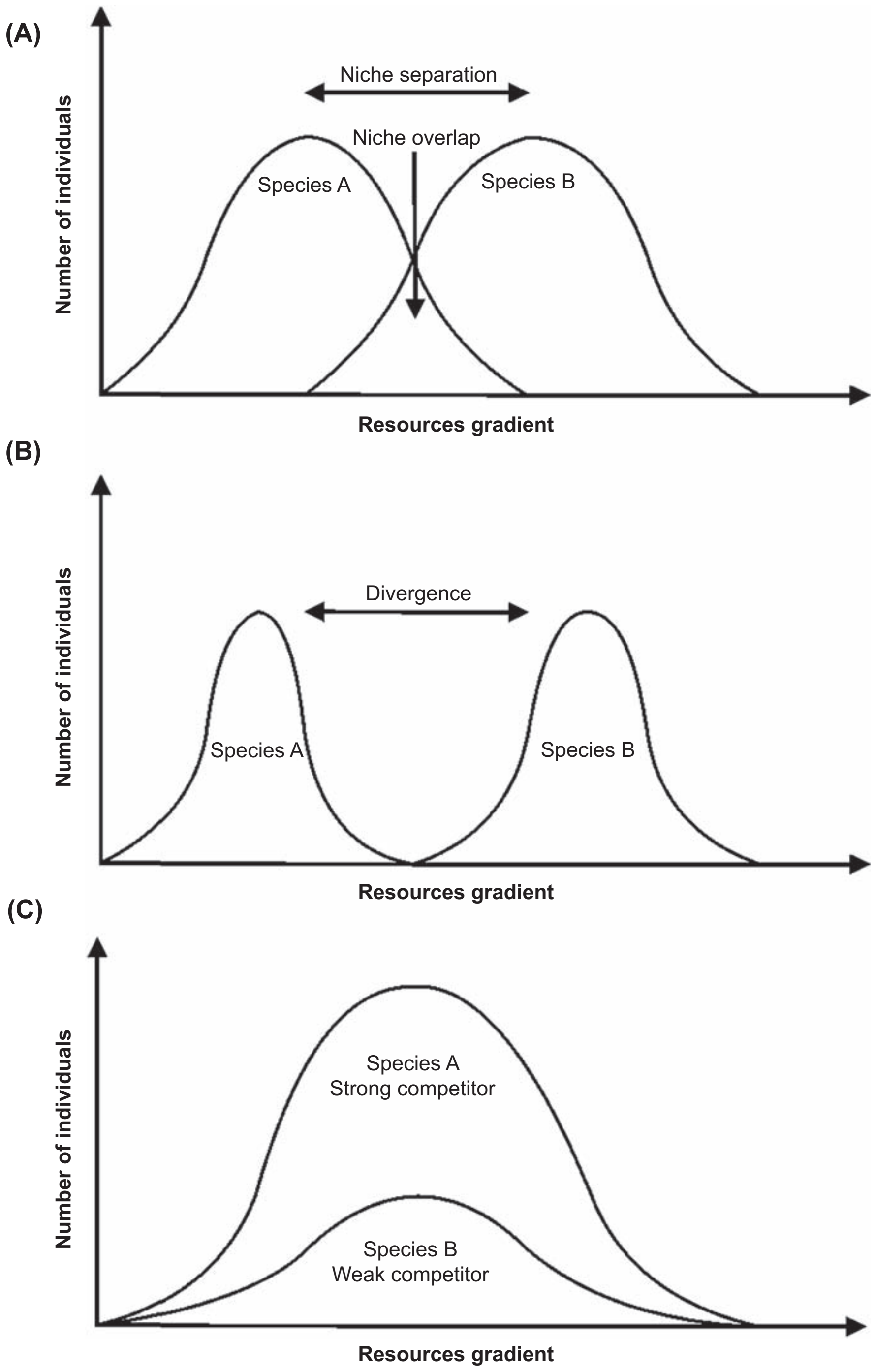

FIGURE 9.13 If two populations occupy the same resource, they utilize all the same resources, and in the same manner. Theoretically, there are three possible outcomes to this situation: (A) Share resources more or less equally (neither population changes niche); (B) One or both populations change niche to reduce overlap (*niche partitioning*); (C) One will be excluded by the other. ***Competitive exclusion principle***: N*o two species can permanently occupy the same niche*, and either the niches will differ, or one will be excluded by the other. *Reproduced from G. F. Gauze. 1934. The struggle for Existence. Williams and Wilkins, Baltimore.*

abandon those in which the other population surpasses it. Thus, "competitive release" occurs when a certain species has the ability to use a broader range of resources in the absence of competitors (closer to its fundamental niche), i.e., to utilize the resource more fully than it could in the presence of the competitor.

The phenomenon termed *character displacement* implies an evolutionary change in attributes ("characters") of competing populations when niches shift. It constitutes the best evidence for the role of competition in shaping

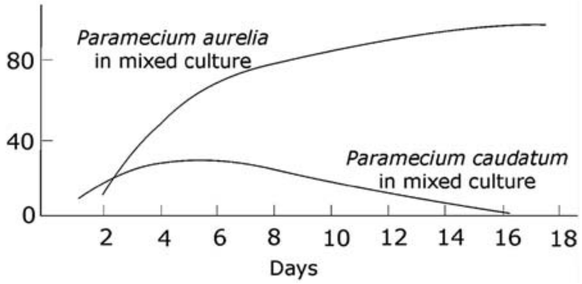

FIGURE 9.14 Experimental competition in laboratory between two populations of *Paramecium* having comparable necessities, illustrating the CEP. *Maps prepared by the Biological Records Centre at the Centre for Ecology & Hydrology, from records collated by the Mammal Society and others; drawn using Dr Alan Morton's DMAP software.*

niches as other explanation is unlikely. The change in length or shape of beaks in ecologically similar bird species that overlap geographically is a typical example of character displacement.

Example 1 of the Competitive Exclusion Principle or Gause's Principle: two species of Paramecium

Two species of *Paramecium* were placed into flasks with a bacterial culture used as food source (Gause, 1934). Both species were thus forced to share the same niche in this microcosm. Through a daily count of the *Paramecium* number, a pattern became evident to Gause: a few days after, one species always became extinct, as apparently it was unable to compete with the other species for the single food resource (Fig. 9.14).

Yet, other results can be observed for two species sharing the same niche, extinction is not the only possible. There is a chance that when two competing species coexist for a long time, they will evolve differences to minimize competition, i.e., they can develop different niches.

Example 2 of the Competitive Exclusion Principle or Gause's Principle: **Geospiza** *spp.*

Revisiting Darwin's finches of the Galapagos Islands, we can see examples of character displacement. The genus *Geospiza* has a widespread distribution among the islands. For instance, *Geospiza fortis* is found only on Daphne Island and *Geospiza fulginosa* on Crossman Island. Both are ground-feeding birds and have similar size. In turn, the species coexist on Charles and Chatham Islands. Here, *G. fortis* is similar in size to their relatives from Daphne, but *G. fulginosa* is smaller than their relatives from Crossman. This size modification allows the *G. fulginosa* to avoid competition with the larger *G. fortis* on Charles and Chatham Islands by feeding on smaller seeds. In this way, competition is important in shaping ecosystems as suggested in the abovementioned example of character displacement. Displacement is interpreted as evidence of historical competition.

Example 3 of the Competitive Exclusion Principle or Gause's Principle: Squirrels in England (www.saburchill.com/IBbiology/chapters02/035.html)

Due to competitive exclusion, disease, and the disappearance of hazel coppices and mature conifer forests in lowland Britain, the native population of red squirrels (*Sciurus vulgaris*) has declined. On the other hand, the gray squirrel (*Sciurus carolinensis*) introduced to Britain between 1876 and 1929 in only 30 sites easily adapted to parks and gardens replacing the red squirrel. The current distribution is shown below in Fig. 9.15.

The Niche Theory in the Light of Ecosystem Principles

In general terms, Hutchinson's niche theory considers that the fundamental niche (theoretical) of a given species comprises all the combinations of environmental conditions which permit an individual of that species to survive and reproduce indefinitely. But from all these possible combinations, only the ones where the species is competitively dominant will in fact be utilized, constituting the realized niche. There will be of course limits of tolerance (maximum and minimum) of the organisms regarding each environmental variable, which constitute the niche breadth.

This formulation, designed to be used at the species and individual level, is clearly compliant with the Ecological Law of Thermodynamics. In fact, what is said can be translated as under the prevailing circumstances the organisms *will attempt to utilize the flow to increase its Exergy, moving further away from thermodynamic equilibrium* (Jørgensen, 1997), or alternatively *in combination with the evolutionary and historically accumulated information, it will attempt to utilize the flow to move further away from the thermodynamic equilibrium* (Wit, 2005).

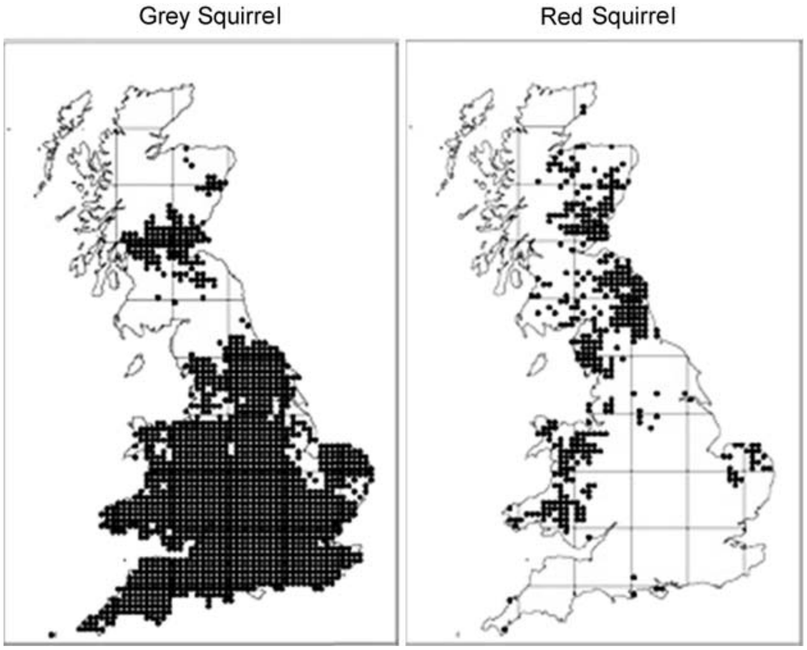

FIGURE 9.15 Present geographic distribution of two squirrel species (*Sciurus vulgaris* and *Sciurus carolinensis*) in Britain.

In accordance with the CEP (Gause, 1934), if the populations of two species occupy the same niche, then one of the two will become outcompeted. In trophic terms, in the absence of competitors, a given species will probably specialize less than it will in competitor's presence (competitive release). This also clearly complies with the Ecological Law of Thermodynamics and can be translated as

If more combinations and processes are offered to utilize the Exergy flow, the organization that is able to give the highest Exergy under the prevailing circumstances will be selected (Jørgensen, 1997) or alternatively as *if more combinations and processes are offered to utilize the free energy flow, the organization that is able to give the greatest distance away from thermodynamic equilibrium under the prevailing circumstances will be selected* (Wit, 2005).

All the three examples illustrating the CEP can be explained in the light of the Ecological Law of Thermodynamics.

9.6 LIEBIG'S LAW OF THE MINIMUM

Many different environmental factors have the potential to control the growth of a population. These factors include the abundance of preys or nutrients that the population consumes and also the activities of predators. A given population will usually interact with a multitude of different prey and predator species, and ecologists have described these many interactions by drawing food webs. Although a given population may interact with many different species in a food web and also interact with many different abiotic factors outside the food web, not all of these interactions are of equal importance in controlling that population's growth. Experience shows that "only one or two other species dominate the feedback structure of a population at any one time and place (Berryman, 1993)." The identity of these dominating species may change with time and location, but the number of species that limits a given population (i.e., actively controls its dynamics) is usually only one or two. Liebig's Law (Liebig, 1840), in its modern form, expresses this idea. It says that of all the biotic or abiotic factors that control a given population, one has to be limiting (i.e., active, controlling the dynamics) (Berryman, 1993, 2003). Time delays produced by this limiting factor are usually one or two generations long (Berryman, 1999). Moreover, Liebig's Law stresses the importance of limiting factors in ecology. "A factor is defined as limiting if a change in the factor produces a change in average or equilibrium density (Krebs, 2001)."

To summarize, "the functioning of an organism is controlled or limited by that essential environmental factor or combination of factors present in the least favorable amount. The factors may not be continuously effective but only at some critical period during the year or only during some critical year in a climatic cycle."

The Liebig's Law of the Minimum in the Light of Ecosystem Principles

The Liebig's Law of the minimum may be seen as a deductive consequence of the principle of increasing ascendency (Ulanowicz and Baird, 1999). Let us see why.

Increasing ascendency also implies greater exergy storage, as can be demonstrated by two propositions in sequence:

Proposition 1: Longer biomass retention times contribute to increasing ascendency.

Let B_i represent the amount of biomass stored in the ith compartment of the ecosystem. Similarly, let T_{ij} be the amount of biomass that is transferred from compartment i to compartment j within a unit of time.

Information is now the measure of change in a probability assignment (Tribus and McIrvine, 1971). The two distributions in question are usually the a priori and a posteriori versions of a given probability, which in the present case is the probability that a quantum of biomass will flow from i to j. As the a priori estimate that a quantum of biomass will leave i during a given interval of time, one may use an analogy from the theory of mass action that the probability can be estimated as ($B_i/B.$), where $B.$ represents the sum of all the B_i. In a strictly similar manner, the probability that a quantum enters some other compartment j should be proportional to the quotient ($B_j/B.$). If these two probabilities were completely independent, then the joint probability that a quantum flows from i to j would become proportional to the product (B_iB_j/B^2).

Of course, the exit and entrance probabilities are usually coupled and not entirely independent. In such case the a posteriori probability might be measured by empirical means in terms of the T_{ij}. That is the quotient ($T_{ij}/T_{..}$) would be an estimate of the a posteriori joint probability that a quantum leaves i and enters j.

Kullback (1959) provides a measure of information that is revealed in passing from the a priori to the a posteriori. This is called the Kullback–Leibler information measure, which is given by

$$I = \sum_{i,j} p(a_i, b_j) \log\left(\frac{p(a_i, b_j)}{p(a_i)p(b_j)}\right),$$

where $p(a_i)$ and $p(b_j)$ are the a priori probabilities of event a_i and b_j, respectively, and $p(a_i,b_j)$ is the a posteriori probability that a_i and b_j happen jointly. Substituting the probabilities as estimated in the preceding paragraphs, one obtains the form for the Kullback–Leibler information of biomass flow in a network as

$$I = \sum_{i,j} \frac{T_{ij}}{T_{..}} \log\left(\frac{T_{ij}B_.^2}{T_{..}B_iB_j}\right).$$

Following the lead of Tribus and McIrvine, as in Ulanowicz (1980), one may scale this information measure by the total activity ($T..$) to yield the storage-inclusive ascendency (Ulanowicz and Abarca, 1999) as

$$A = \sum_{i,j} T_{ij} \log\left(\frac{T_{ij}B_.^2}{T_{..}B_iB_j}\right).$$

Biomass Storage

Eugene Odum (1969) proposed 24 properties as indicators of maturity in ecosystems. These could be grouped under increases in species richness, trophic specificity, cycling, and containment. It happens that, other things being equal, an increase in any of these attributes will result in an increase of systems ascendency. As a result, Ulanowicz (1980, 1986) proposed as a phenomenological principle describing ecosystem development that "in the absence of major perturbations, ecosystems exhibit a tendency to increase in ascendency." Those factors which lend to an increasing ascendency, therefore, should be considered as significant contributors to ecosystem development.

From a mathematical point of view, one can elucidate how a system gains in magnitude by calculating what contributes to positive gradients in ascendency. So, for example, if one wishes to know what changes in the B_k foster increases in ascendency, one would want to study the partial derivatives ($\partial A/\partial B_k$). After rather tedious algebraic manipulation, the results reduce to

$$\frac{\partial A}{\partial X_k} = 2\left(\frac{T_{..}}{B_.} - \frac{1}{2}\,\frac{T_{k.} + T_{.k}}{B_k}\right).$$

This formula has a straightforward meaning. The first term in parentheses is the overall throughput rate. The second quotient is the average throughput rate for compartment k. That is, the sensitivity of the biomass-ascendency is proportional to the amount by which the overall throughput rate exceeds that of the compartment in question. If the throughput of compartment is smaller than the overall rate, then ascendency is abetted. In other words, increasing ascendency is favored by slower passage (longer storage) of biomass through compartment $k_{.}$, i.e., biomass storage favors increased ascendency.

Proposition 2: When several elements flow through a compartment, that element flowing in the least proportion (as identified by Liebig (1840)) is the one with the longest retention time in the compartment.

We begin by letting $T_{ij}k$ be the amount of element k flowing from component i to component j. We then consider the hypothetical situation of ideally balanced growth (production). In perfectly balanced growth, the elements are presented to the population in exactly the proportions that are assimilated into the biomass. This can be stated in quantitative fashion: For any arbitrary combination of foodstuff elements, p and q, used by compartment j,

$$\frac{T^{*}_{.jp}}{T^{*}_{.jq}} = \frac{B_{jp}}{B_{jq}}$$

where an asterisk is used to indicate a flow associated with balanced growth. Now we suppose that one and only one element, say p without loss of generality, enters j in excess of the proportion needed. That is, $T_{.jp} = T_{.jp}{}^{*} + e_p$ where e_p represents the excess amount of p presented to j. Under these conditions we have the inequality

$$\frac{T_{.jp} + e_p}{T_{.jp}} > \frac{B_{jp}}{B_{jq}}$$

Multiplying both sides of this inequality by the ratio $T_{.jq}{}^{*}/B_{jp}$ yields

$$\frac{T_{.jp} + e_p}{B_{jp}} > \frac{T^{*}_{.jq}}{B_{jq}}$$

In words, this latter inequality says that the input rate of p into j is greater (faster) than that of any other element by the "stoichiometric" amount e_p/B_{jp}. Over a long-enough interval, inputs and outputs must balance, and so we can speak about the input rate and throughput rate as being one and the same. (This does not weaken our argument, as there is an implied steady-state assumption in the Liebig statement as well.)

Now we suppose that only two of the elements flowing into j are supplied in excess. Again, without loss of generality, we call the second element q. It is immediately apparent that if $e_p/B_{jp} > e_q/B_{jq}$, then the throughput rate of p exceeds that of q, and vice versa. That is, a slower throughput rate indicates that one is closer to stoichiometric proportions. This last result can be generalized by mathematical induction to conclude that the element having the slowest throughput rate is being presented in the least stoichiometric proportion, i.e., it is limiting in the sense of Liebig.

The River Continuum Concept

The River Continuum Concept (RCC) was proposed by Vannote et al. (1980) (Fig. 9.16) to describe the variation of physical conditions and environmental variables within a river ecosystem, according to a continuous gradient from the source to the mouth. The gradient causes a set of differential responses within the river biological populations (e.g., benthic communities), reflected in a continuum of biotic adjustments and constant patterns of organic matter loading, transport, utilization, and storage along a river. Starting from the theory on energy equilibrium formulated by fluvial geomorphologists, Vannote et al. (1980) conjectured that the structural and functional features of stream communities will be fitted to the most likely position or middling state of the system's physical component. They argued that the characteristics of the biological communities (producers, consumers, and decomposers) in a given river section will establish in compliance with the channel's dynamic physical conditions, and consequently, along natural river ecosystems, there will be a consistent temporal continuum of species substitutions.

This incessant replacement of performers works to allocate the consumption of energy inputs through time, with the biological system moving to an equilibrium between a propensity for using efficiently those inputs through resource partitioning (food, substrate, etc.), and an opposite tendency for an even rate of energy processing throughout the year. In this context, Vannote et al. (1980) hypothesized that, in natural rivers, biological communities will optimize their performance by adopting processing strategies involving a minimal loss of energy. For instance, there are always predictable processing inefficiencies in upstream communities, and downstream communities will also predictably adjust alongside, becoming specialized in using wastes resulting from that inefficient processing. In general, the RCC offers an elegant framework that allows integrating both predictable and observable biological characteristics of river ecosystems.

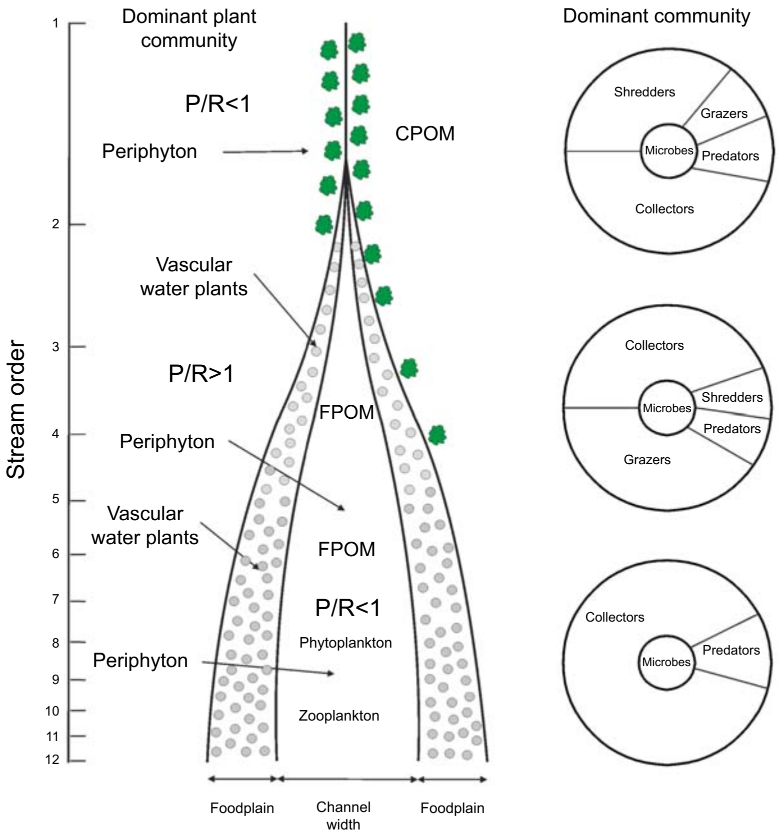

FIGURE 9.16 A possible relationship between the size of a stream and the gradual shift in the structure and functional characteristics of the dominant plant and benthic communities. *Based on the concept proposed by Vannote et al. (1980).*

9.7 THE RIVER CONTINUUM THEORY IN THE LIGHT OF ECOSYSTEM PRINCIPLES

The river continuum theory can almost be seen as a different verbalization of the Ecological Law of Thermodynamics applied to rivers, since it is fully compliant with it. Along a continuous gradient of changing environmental conditions, river communities *attempt to utilize the flow to increase its Exergy, moving further away from thermodynamic equilibrium*. Changing conditions along the gradient determine different constraints and therefore other processing strategies because *If more combinations and processes are offered to utilize the Exergy flow, the organization that is able to give the highest Exergy under the prevailing circumstances will be selected* (Jørgensen, 1997) or alternatively as *if more combinations and processes are offered to utilize the free energy flow, the organization that is able to give the greatest distance away from thermodynamic equilibrium under the prevailing circumstances will be selected* (Wit, 2005).

Hysteresis in Nature

Numerous examples in nature show that there are combinations of environmental factors (external constraints) that may give rise to two equally viable community structures, i.e., they may provide the same degree of support (possibilities to grow and develop) to different sets of internal constraints. In such cases, a hysteresis relationship exists between the dominant external constraining factors and the community structure (internal constraints relieving the external constraints). For instance, in freshwater shallow lakes ecosystems there are references to such type of scenarios:

1) For concentrations between approximately 50 μg P/L and 120−140 μg P/L a plankton community structure dominated by zooplankton and carnivorous fish has the same probability to occur than structure dominated by planktivorous fish and phytoplankton (de Bernardi and Giussani, 1995);
2) For concentrations between approximately 100 and 250 μg P/L shallow lakes can be dominated either by submerged vegetation or by phytoplankton (Scheffer, 1998).

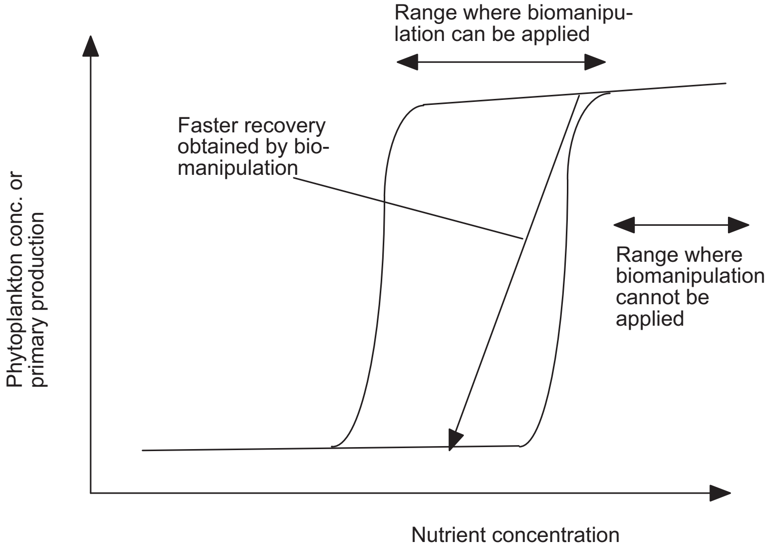

FIGURE 9.17 The hysteresis relation between nutrient level and eutrophication measured by the phytoplankton concentration is shown. The possible effect of biomanipulation is shown. The biomanipulation gives the expected results in the range where two different structures are possible. The range for a change from zooplankton—carnivorous fish control to planktivorous—phytoplankton control is about 50—120/140 μg P/L and for a change from dominance by submerged vegetation—phytoplankton is about 100 μg P/L to about 250 μg P/L.

In both cases, the system history will determine which one of the two possible community structures occurs. Once the community installed, within the indicated ranges, a shift in its structure will only take place in case the community (the internal constraints) is changed by external factors (forcing functions). In the first case, this might mean that the planktivorous fish are physically removed and replaced by more carnivorous fish, and in the second case that phytoplankton are removed and submerged vegetation planted. In fact, such interventions are called biomanipulation, and the experience has shown that it only works in the indicated ranges of nutrient concentrations. It can furthermore be shown in the two referred cases that the relief (indicated as the growth measured by eco-exergy) (Jørgensen et al., 2000) is the same for the two possible community structures within the indicated ranges (Fig. 9.17) (Jørgensen and de Bernardi, 1997, 1998). The occurrence of hysteresis can thus be explained in the light of the maximum eco-exergy principle.

9.8 CONCLUSIONS

The objective of this chapter was to explore common ecological concepts alongside the principles of the Ecological Law of Thermodynamics proposed herein. The observed compliance between them shows that the same principles can provide explanations to different ecological problems usually addressed by different approaches. The Ecological Law of Thermodynamics is a more general and integrative theory. Does this mean that the other theories have no explanatory power? Definitely no. This just means that they are not universal, and therefore they can only be used to explain a relatively narrow number of observations, being in most cases specific for a given type of system. We have demonstrated that the ecosystem principles of a new ecology are fully compliant with evolutionary theory and can cover some of the most well-known nonuniversal ecological theories.

CHAPTER

10

Ecosystem Principles Have Ecological Applications

Tempus item per se non est, sed rebus ab ipsis
consequitur sensus, transactum quid sit in aevo,
tumquae res instet, quid porro deinde sequantur.

Time per se does not exist: the sense of what
has been done in the past, what is in the present
and what will be is embodied in things themselves. **Lucretius, De Rerum Natura, I, 459–461.**

10.1 INTRODUCTION

Orientors, being holistic ecological indicators, can give further information on the state of an ecosystem than can simply reductionistic indicators. Information coming from systematic or analytical approaches should never be neglected, but holistic indicators allow us to understand if the system under study is globally following a path that takes the system to a “better” or to a “worse” state. And, we can also compare macroscopic state of different systems, which is impossible to do with isolated reductionistic information. So, advantages of holistic indicators are additional aggregate information without losing information, ability to compare, ability to compare states of the same system at different times, and possibility of understanding what new data types are needed for this approach.

With indicator concepts like ecosystem health, ecosystem integrity can find operational values, using information coming from approaches like Network analysis, Eco-exergy, Ascendency, Emergy evaluation, and other related indicators. Here, we present several examples in which the systems perspective in ecology has been applied. The types and locations of systems in which they have been applied are very diverse: terrestrial and aquatic ecosystems in Europe, North and South America, and Asia, as are the goals of the research and management questions involved. Regardless of the setting or objective, at its core, holistic indicators always give a broader understanding of the amalgamation of the ecosystem parts into a context of the whole.

10.2 ENTROPY PRODUCTION AS AN INDICATOR OF ECOSYSTEM TROPHIC STATE

References where entropy production has been used as indicator:

Aoki, I., 1987. Entropy balance in lake Biwa. Ecol. Model. 37, 235–248.
Aoki, I., 1995. Entropy production in living systems: from organisms to ecosystems. Thermochim. Acta 250, 359–370.
Aoki, I., 2000. Entropy and Exergy principles in living systems. In: Thermodynamics and Ecological Modeling. Lewis Publishers, New York, pp. 165–190.
Ludovisi, A., Poletti, A., 2003. Use of thermodynamic indices as ecological indicators of the development state of lake ecosystems. 1. Entropy production indices. Ecol. Model. 159, 203–222.

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Entropy flow and entropy production (see Chapter 2) can be quantitatively estimated using physical modeling or calculated from observed energy flow data of biological systems. Here entropy production in lake ecosystems is examined in detail for three ecosystems located in Japan, the United States, and Italy.

Case Studies

Lake Biwa is located at 34°58′–35°3′ N, 135°52′–136°17′ E (near Kyoto, Japan) and consists of a northern basin (the main part) and a southern basin (the smaller part). The former is oligotrophic and the latter is nearly eutrophic. Only the northern basin is considered. Data for this study were collected in the 1970s. The annual adsorbed solar energy was 4153 MJ, while the mean depth of the lake is of 44 m. It is possible to identify two zones in the column water: a light one (20 m) and a dark one (24 m). The average amount of suspended solid (SS) in the light zone was 1.3 [g m^{-3}] (National Institute for Research Advancement, 1984), while the average amount of dissolved organic carbon (DOC) was 1.6 [gC m^{-3}] (Mitamura and Sijo, 1981). The average amount of total plankton plus zoobenthos in the whole water column was 0.16 [gC m^{-3}] (Sakamoto, 1975).

Lake Mendota is located at 43°04′ N, 89°24′ W (near Madison, Wisconsin, USA) and is a eutrophic lake. Its energy budget was investigated by Dutton and Bryson (1962) and Stewart (1973). The annual adsorbed solar energy was 4494 MJ, while the mean depth of the lake is 12.2 m. Two zones of the water column were identified: the euphotic one (until 9 m) and the aphotic one (the lasts 3.2 m). The average amount of SS in the light zone was 1.9 [g m^{-3}] (National Institute for Research Advancement, 1984), while the average amount of DOC was 3.3 [gC m^{-3}] (Brock, 1985). The average amount of total plankton plus zoobenthos in the whole water column was 0.62 [gC m^{-3}] (Brock, 1985).

Lake Trasimeno is the largest lake in peninsular Italy (area 124 km^2); it is shallow (mean depth 4.7 m, maximum 6.3 m), and accumulation processes are favored. The water level of the lake showed strong fluctuations with respect to meteorological conditions; hydrological crises occur after several years with annual rainfall <700 mm. Lake Trasimeno can be considered homogeneous for chemical and physical parameters (MARU, 1994) and very sensitive to meteorological variability or human impact. According to the Vollenweider–OECD classification (Giovanardi et al., 1995), Lake Trasimeno is mesotrophic, whereas by using the annual phosphorus loading estimation method (MARU, 1994) and the Hillbrich–Ilkowska method (Hamza et al., 1995), the lake is classified as eutrophic.

Entropy production Indices for Waterbodies

The quantities necessary to estimate entropy production (see Aoki, 1989, 1990) can be obtained from experimentally observed data. Entropy production plotted against adsorbed solar radiation energy for Lake Biwa and Lake Mendota are shown in Figs. 10.1 and 10.2, respectively. The monthly entropy production per unit of volume (S_p)

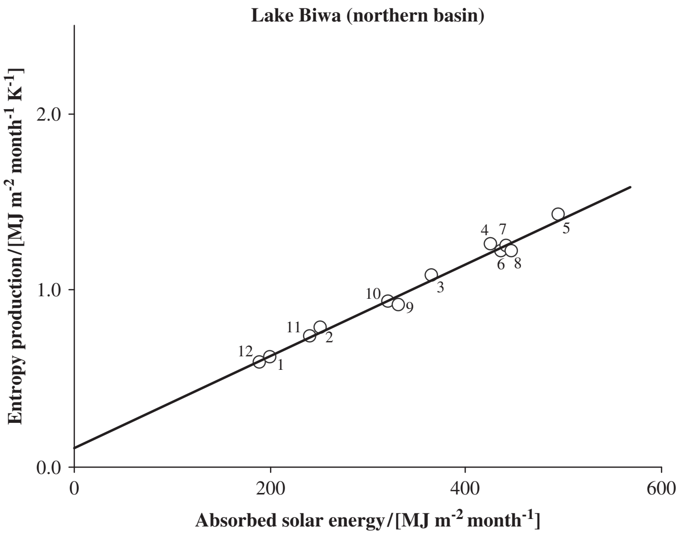

FIGURE 10.1 Monthly entropy production in the northern basin of Lake Biwa per m^2 of the lake surface plotted against monthly solar radiation energy absorbed by 1 m^2 of the lake surface. The numbers near the circles are the months.

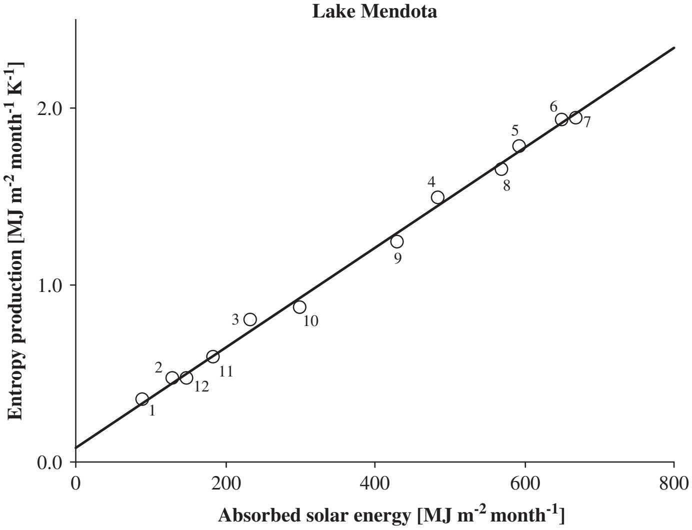

FIGURE 10.2 Monthly entropy production in Lake Mendota per m^2 of the lake surface plotted against monthly solar radiation energy absorbed by 1 m^2 of the lake surface. The numbers near the circles are the months.

of the Trasimeno lake was calculated by simple division of S_{prod} by monthly mean values of water depth; the annual values were calculated as the sum of monthly values and is given in Table 10.1.

Entropy production is expressed in MJ m^{-2} month^{-1} K^{-1}, while solar radiation in MJ m^{-2} month^{-1}. According to Aoki, entropy production in month j (denoted as $(\Delta_i S)_j$) is a linear function of the absorbed solar radiation energy in month j (denoted as Q_j):

$$(\Delta_i S)_j = a + bQ_j \tag{10.1}$$

According to Ludovisi (2003) the definition of the b index as a ratio of S_p (in units MJ m^{-3} year^{-1} K^{-1}) and annual Q_s (MJ m^{-2} year^{-1} K^{-1}) is not proper because entropy and energy flows do not refer to the same spatial unit. This fact introduces an artificial dependence on the water depth. Partially following Aoki's indices, a set of new ones (c, d, d') analogous to the a, b, and b' were proposed by Ludovisi and Poletti (2003) on the basis of the relationship between the entropy production per surface units (S_{prod}) and the solar energy absorbed by the lake surface (Q_s). The index d' does not demonstrate any significant trend during the years 1988–96 (Table 10.1).

A good linear correlation between the monthly entropy production (S_{prod}) per surface unit of Lake Trasimeno and the monthly solar energy absorbed by the lake (Q_s) has been found on a monthly time scale (Fig. 10.3) and the

TABLE 10.1 Annual Values of S_{prod} (MJ m^{-2}year^{-1} K^{-1}), S_p (MJ m^{-3} year^{-1} K^{-1}) and of the Indices b' (10^{-4} m^{-1} K^{-1}), d' (10^{-4} K^{-1}), Calculated for Lake Trasimeno in the Years 1988–96.

Year	S_{prod}	S_p	b'	d'
1988	16.02	3.20	6.2	31.0
1989	15.60	3.34	6.4	29.9
1990	15.72	3.65	7.3	31.4
1991	15.57	3.74	7.4	30.8
1992	15.42	3.54	7.1	30.8
1993	15.62	3.68	7.1	30.1
1994	16.40	3.91	7.4	30.8
1995	15.60	3.93	7.6	30.2
1996	15.62	4.17	8.0	29.8
Average	15.73	3.69	7.2	30.6

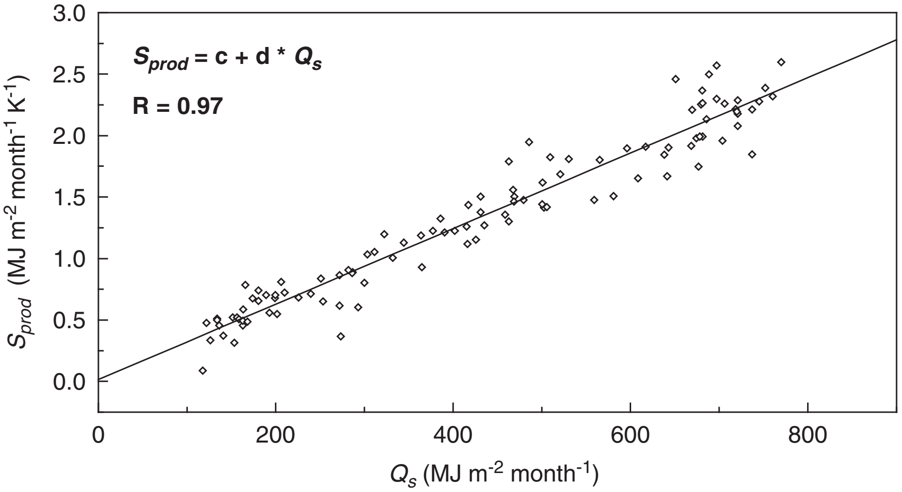

FIGURE 10.3 Linear regression between the monthly entropy production (S_{prod}) per surface unit of Lake Trasimeno and the monthly solar energy absorbed by the lake (Q_s).

regression coefficients of the curve (*c*, intercept and *d*, slope) can be compared with the analogous Aoki's indices *a*, *b* (Table 10.2).

The comparison of *c*, *d* (regression coefficients of the curve Fig. 10.3 intercept and slope), *d*′ (the ratio between the annual S_{prod} and Q_s) values (Table 10.2) calculated for Lake Mendota and the northern basin of Lake Biwa, significantly distinguishes the eutrophic Lake Mendota from the oligotrophic Lake Biwa, and attributes to Lake Trasimeno higher values of *d* and *d*′ than both other lakes.

TABLE 10.2 Environmental Parameters, TSI Values and Values of Trophic Indices Proposed by Aoki (*a*, *b*, *b*′) and Those of the New Set of Indices *c*, *d*, *d*′ for Lake Mendota, Lake Biwa, Lake Trasimeno.

Parameter	Lake Biwa	Lake Mendota	Lake Trasimeno
Mean depth (m)	44	12.2	4.7
Residence time (year)	5.5	3.1–8.8	>20
Transparency (Secchi depth (m))	5.2	2.9	1.2
Chlorophyll α (μg L^{-1})	5	32	8
Total phosphorus (mg L^{-1})	0.01	0.07	0.05
TSI (SD)[a]	36	45	58
TSI (Chlα)[a]	46	65	51
TSI (TP)[a]	37	65	59
TSI (average)[a]	39	58	56
Trophic classification[b]	Oligotrophic	Hypereutrophic	Eutrophic
a (MJ m^{-3} month^{-1} K^{-1})	0.002	0.006	
b (10^{-4} m^{-1} K^{-1})	0.6	2.3	
b′ (10^{-4} m^{-1} K^{-1})	0.6	2.4	7.2[c]
c (MJ m^{-2} per mese K^{-1})	0.070	0.0070	0.014
d (10^{-4} K^{-1})	26.7	27.9	31.0
d′ (10^{-4} K^{-1})	26.4	29.3	30.7[c]

[a] *Trophic state index calculated by using Carlson (1997) equations.*
[b] *Based on the Kratzer and Brezonik (1981) classification system.*
[c] *Average value of the years 1988–96.*

Regarding Eq. (10.1), the second term on the right-hand side is the entropy production dependent on solar radiation energy that is caused by the conversion in heat of the solar energy absorbed by water, by dissolved organic matter, and by SS (negligible are the contributions from photosynthesis and light respiration of phytoplankton). The first term on the right-hand side of Eq. (10.1) is the entropy production independent of solar radiation energy and it is caused by respiration of organisms in the lake.

For Lake Biwa and Lake Mendota total and solar energy—dependent entropy productions (per year per MJ of absorbed solar radiation energy per m^3 of the lake water) and entropy productions independent of solar radiation energy (per year per m^3 of the lake water) are shown in Table 10.3. The values of entropy production dependent on solar radiation in the light zone (eutrophic zone) are related to the amount of dissolved organic matter and SS per m^3 of lake water in the light zone. The ratio of the amount of SS in Lake Mendota to that in Lake Biwa (1:5) and the ratio of DOC in Lake Mendota to that in Lake Biwa (2:1) are consistent with the ratio of entropy production dependent on solar radiation between Lake Mendota and Lake Biwa (Table 10.3). Thus, the greater the amount of SS and DOC, the more the entropy production is dependent on solar radiation. The entropy production dependent on solar radiation gives a kind of physical measure for the amount of dissolved organic matter and SS in the lake water by means of reactions to incident solar radiation.

The entropy production independent of solar radiation energy (Table 10.3) is the measure of activity of respiration of organisms distributed over the whole water column. The ratio of the amount of plankton plus zoobenthos in Lake Mendota with respect to Lake Biwa is 3:9 and is consistent with the ratio of entropy production independent of solar radiation (3:6). The larger the amount of organisms, the more the entropy production is independent of solar radiation. The entropy productions in eutrophic Lake Mendota are larger than those in oligotrophic Lake Biwa in any of the categories considered (i.e., due to light absorption, respiration, and total).

Fig. 10.4 reports the linear regression curves between d and TSI, TSI(SD) (Carlson, 1977) and the mean depth (because of the little data available, the regression curves cannot be considered highly significant). As can be seen, d' is positively correlated to TSI, although the relation is not very sharp because of the similarity of TSI for Lake Trasimeno and Lake Mendota. The index d' shows a good negative linear correlation with the lake's mean depth: the intercept value given by the linear regressions ($30.9 \times 10^{-4}\ K^{-1}$) could approach the higher values for d' at the limits of existence of an aquatic ecosystem, which is reached at a rate of $0.1 \times 10^{-4}\ K^{-1}\ m^{-1}$.

The indices d and d' could be considered measures of the ability of the ecosystems to dissipate the incoming solar energy into the system; the positive correlation between these indices and the trophic state of the lakes indicates that they could account for the influence of the biological productivity on the whole entropy production of the system. As high nutrient concentrations increase the whole biological production as well as the energy flow through an ecosystem, an increase in d and d' values with eutrophication is expected because of the irreversibility of the biological processes.

Furthermore, the efficiency of the energy transfer between the trophic levels in eutrophic systems was found to be lower than in oligotrophic systems (Jonasson and Lindegaard, 1988). In ecological terms, this should mean that a higher nutrient availability in more eutrophic systems induces the achievement of a biological community possessing a better ability to dissipate energy, following a development strategy based on the maximization of the productivity, rather than optimization of the energy exploitation.

Conclusions

The entropy production of the three categories (total entropy production, dependent entropy production, and independent entropy production) can be proposed to be larger in a eutrophic lake than in an oligotrophic lake. Natural

TABLE 10.3 Comparison of Entropy Productions in Lake Biwa and in Lake Mendota.

Lake	Total (in Whole Water Column)	Solar Energy Dependent (in Light Zone)	Solar Energy Independent (in Whole Water Column)
Lake Biwa	0.07	0.13	19
Lake Mendota	0.24	0.31	69
Lake Mendota/Lake Biwa	3:7	2:3	3:6

Total and solar energy dependent entropy productions (per year per MJ of absorbed solar radiation energy per m^3 of the lake water) are shown, respectively, in the first and in the second column, and entropy productions independent of solar radiation energy (per year m^3 of the lake water) are in the third column units are [$kJ\ K^{-1}\ m^{-3}\ year^{-1}$]. Ratios of the values for the two takes are shown in the last row.

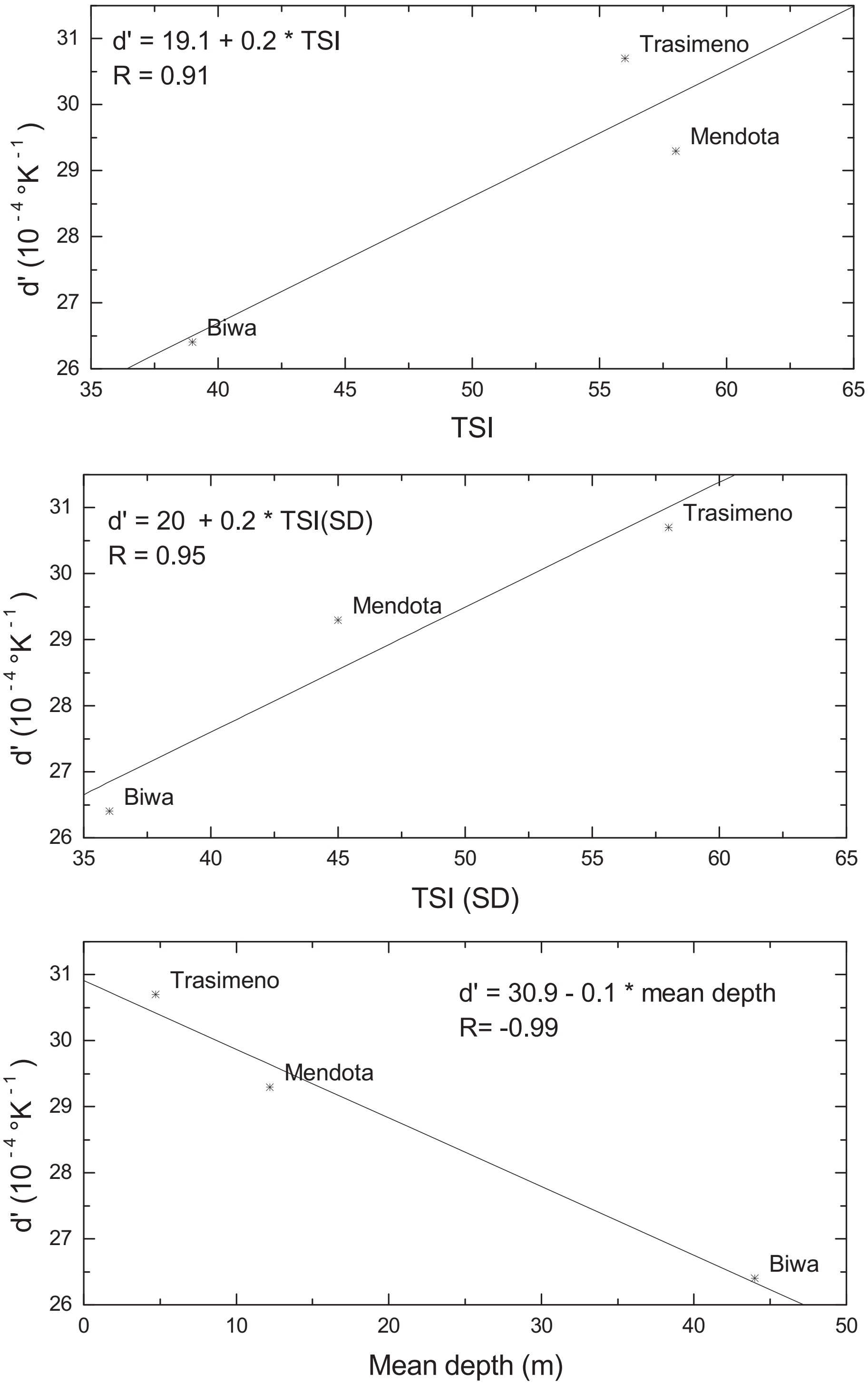

FIGURE 10.4 Linear regression between the entropy production index d' and TSI, TSI(SD), the mean water depth for Lake Biwa, Lake Mendota, and Lake Trasimeno.

processes tends to proceed with time from oligotrophy to eutrophy in most of present lake ecosystems surrounded by the environment full of organic matter; the entropy production of the three categories in a lake will increase with time accompanying the process of eutrophication (Aoki, 1989, 1990).

These entropy production indices can be useful tools for characterizing the trophic status of a water body; however, their ecological interpretation might need more investigation as they depend on the successional stage (Margalef, 1977; Reynolds, 1984) or on the "prevailing condition" the system is following.

10.3 THE USE OF ECOLOGICAL NETWORK ANALYSIS FOR THE SIMULATION OF THE INTERACTIONS BETWEEN AMERICAN BLACK BEAR AND ITS ENVIRONMENT

Reference where ecological network analysis has been applied to show the importance of indirect effects:

Patten, B.C., 1997. Synthesis of chaos and sustainability in a non stationary linear dynamic model of the American black bear (*Ursus americanus* Pallas) in the Adirondack Mountains of New York. Ecol. Model. 100, 11−42.

Here an application of a dynamic model is used to show the importance of indirect effects even within a linear approach.

There are many examples of indirect relationships in natural systems, some of them involving the global one—the biosphere. The majority of these relationships remain either overlooked or poorly understood (Krivtsov et al., 2000). To model such systems requires the use of many integrated submodels due to the complexity of processes involved.

The knowledge that all species in nature are complexly interconnected directly and indirectly to all other biotic and abiotic component of their ecosystems is slow in being translated into models and even more in management practice.

An example for such a synthesis is the simulation model of a wildlife population, the American black bear (*Ursus americanus* Pallas) on the 6000 ha Huntington Wildlife Forest in the central Adirondack Mountain region of upper New York State, USA (Costello, 1992). The model was designed to be conceptually complex but mathematically simple so its behavior would derive more from biology and ecology than from mathematics. The STELLA II (High Performance Systems, Hanover NH) model of the Adirondack black bear is linear, donor-controlled, nonstationary, and phenomenological (Patten, 1983).

The model's purposes are to express black bear biology as a population system inseparable from its ecosystem and to demonstrate how chaos and sustainability can be realistically incorporated into models, minimizing the use of inappropriate mathematics that, though traditional or classical, may not be well chosen due to an inadequate rationale.

If *envirograms* for all the taxa and significant abiotic categories of the Huntington Wildlife Forest could be formed, then the centrum of each would account for one row and one column of an $n \times n$ interconnection matrix for the whole ecosystem. The centrum of each black bear envirogram for a life history stage would then represent one such row and column within the ecosystem matrix and from these indirect connections between bear and ecosystem compartments could be determined. Of course the forest ecosystem model does not exist, but the rationale for embedding the bear subsystem within it is clear, and the purpose of the envirograms was to implement this in principle by way of organizing relevant information for modeling.

A further criterion was that all the direct interactions between the bear compartments and the environment would be by mass energy transactions, enabling the conservation principle to be used in formulating system equations. The envirograms prepared for this model are depicted in Simek (1995) and were then used to construct a quantitative difference equation model employing STELLA 11.

Quantification of the model is still approximate, based on general data and knowledge of the bear's life history, reproductive behavior, environmental relationships, and seasonal dynamics as known for the Huntington Forest and the Adirondack region. The equations are all linear and donor-controlled, with details of temporal dynamics introduced by nonstationary (time-varying) coefficients rather than by nonlinear state variables and constant coefficients.

The model's behavior is here described in detail only for the cub compartment and selected associated parameters (Fig. 10.5). The other compartments behave with similar realism.

A baseline simulation was achieved which generated 33−64 individuals 6000 ha^{-1} during a typical model year; this is consistent with a mean of about 50 animals typically considered to occur on the Huntington property. Yearling M/F sex ratios generated by the model varied slightly around 0.85, compared to 0.6 observed during 1989−94. Besides the baseline simulation, model parameters were manipulated to investigate sensitivity relationships. The compartments were indicated to be more sensitive to inputs and less sensitive to outputs. The sensitivity relationships described below for cubs generally hold true also for the other age classes in the model.

Conclusion

In descending order, the most sensitive inputs were maternal milk (cubs), fruit production, and plant food availability (Fig. 10.6); relatively insensitive inputs were immigration, animal food, and recruitment (to yearlings and adults). Sensitivities to outputs, lower than for inputs, were, in descending order, respiration, egestion, accidental

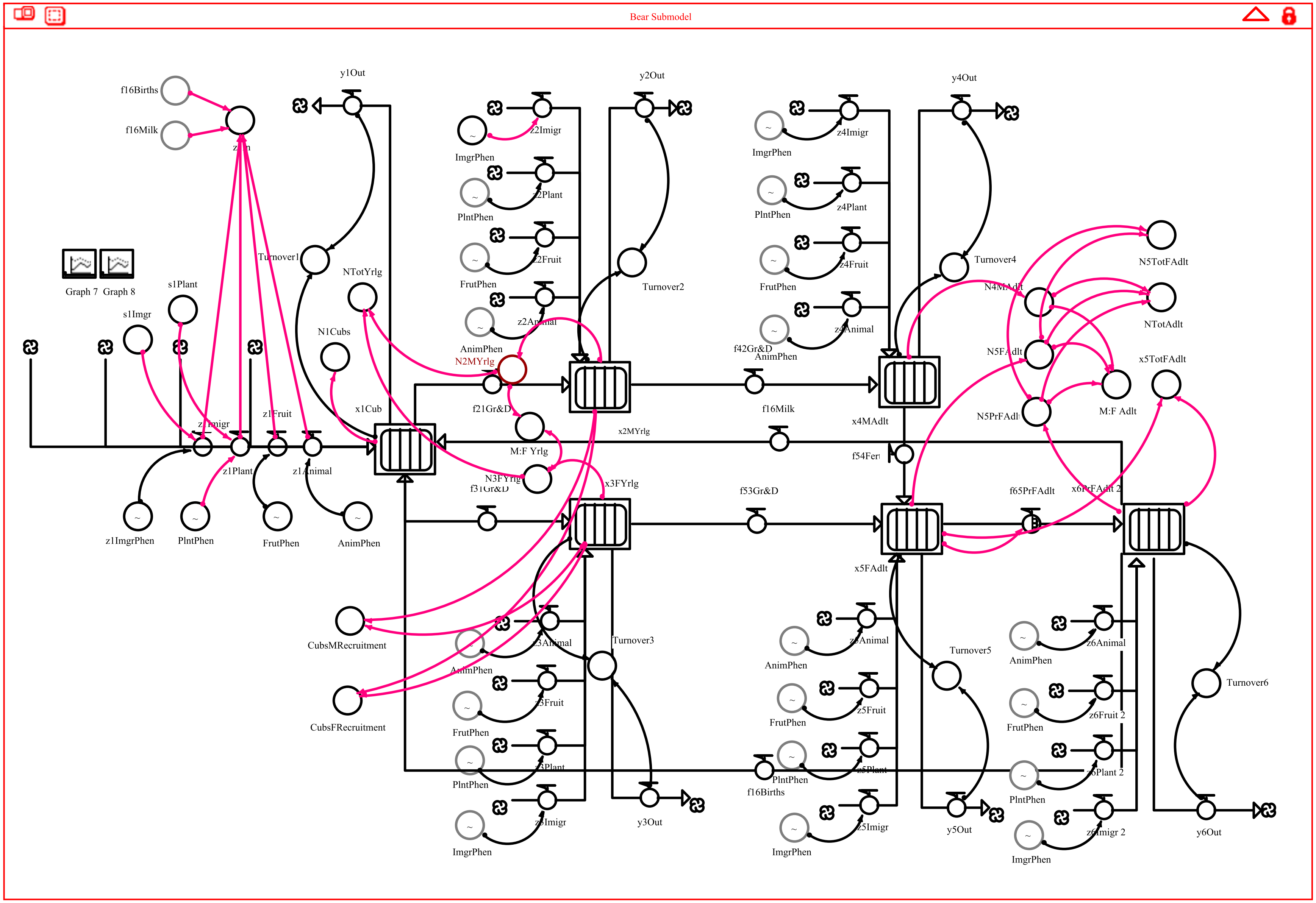

FIGURE 10.5 Submodel layer depiction of the cub compartment of the black bear model.

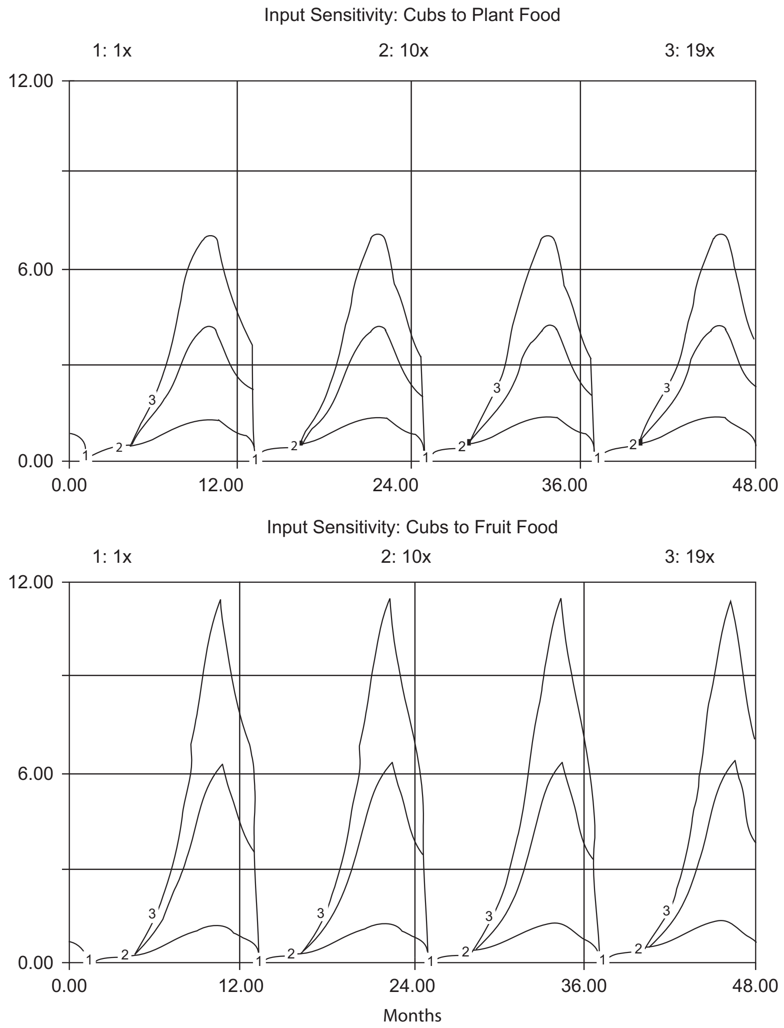

FIGURE 10.6 Sensitivity of cubs to plant food and fruit. Plant food, principally leaves, fruits, and tubers, comprise 90% of their diets. Fruit is a late season resource (after July) whereas plant food availability began in May—June. Fruit production occurs when they are approaching going into negative energy balance.

mortality, emigration, parasitic infection, predation (on cubs), harvest, and sickness. Since the model is linear, it can be considered to represent near steady-state dynamics, but its realism suggests that the neighborhood of applicability may actually be very broad around steady state.

10.4 APPLICATIONS OF NETWORK ANALYSIS AND ASCENDENCY TO SOUTH FLORIDA ECOSYSTEMS

Reference where ascendency has shown its practical applicability:

Heymans, J.J., Ulanowicz, R.E., Bondavalli, C., 2002. Network analysis of the South Florida Everglades graminoid marshes and comparison with nearby cypress ecosystems. Ecol. Model. 149, 5—23.

Ascendency (see Chapter 6) is used to compare a cypress system and a graminoids one and to discern the degree of maturity shown by the two systems.

Case Studies

The Everglades ecosystem in South Florida occupies a 9300 km^2 basin that extends from the southern shore of Lake Okeechobee south and southwest to the Gulf of Mexico (Hoffman et al., 1990). Currently, the basin can be divided into three sections: Everglades Agricultural Area, Water Conservation Areas, and the Southern Everglades, the latter of which includes the marshes south of Tamiami Trail and the Shark River Slough. There are two distinct communities in the graminoid system that are differentiated according to short and long hydroperiod areas (Lodge, 1994) and occur in areal ratio of approximately 3:1. Short hydroperiod areas flank both sides of the southern Everglades and are occupied by a low sawgrass community of plants with a high diversity (100 species) (Lodge, 1994). Typically, vegetation in the short hydroperiod marsh is less than 1 m tall (Herndorn and Taylor, 1986). Long hydroperiod, deeper marsh communities are developed over peat soil (Goodrick, 1984). The long hydroperiod community occurs more commonly in the central Everglades where they typically are straddled between sawgrass marshes and sloughs. These inundated areas are important for fish and aquatic invertebrates, such as prawns. Long hydroperiod areas provide an abundant reserve of prey for wading birds toward the end of the dry season (March—April).

The freshwater marshes of the Everglades are relatively oligotrophic and have been typified as not being very productive—averaging only about 150 g m^{-2} per year in wet prairie areas according to DeAngelis et al. (1998). Graminoid ecosystems provide valuable habitat for a wide range of animals, including species listed by the US Fish and Wildlife Service as endangered, threatened, or of concern.

The cypress system is a 295,000 ha wetlands of the Big Cypress Natural Preserve and the adjacent Fakahatchee Strand State Preserve. Both areas cover a flat, gently sloping limestone plain (Bondavalli and Ulanowicz, 1999) with many strands and domes of cypress trees. The cypress swamp does not have a distinct fauna but shares many species with the adjacent communities (Bondavalli and Ulanowicz, 1999).

The Network Models of the Ecosystems

A model of the freshwater graminoid marshes was constructed by Heymans et al. (2002) and consists of 66 compartments, of which three represent nonliving groups and 63 depict living compartments (*see reference for details*). The three nonliving compartments include sediment carbon, labile detritus, and refractory detritus, all of which are utilized mainly by bacteria and microorganisms in the sediment (living sediment) and in the water column (living POC—particulate organic carbon). The primary producers include macrophytes, periphyton, *Utricularia*, and other floating vegetation.

Lodge (1994) suggested that: "the Everglades does not have a great diversity of freshwater invertebrates due to its limited type of habitat and its nearly tropical climate, which many temperate species cannot tolerate." The source of most fauna in South Florida is from temperate areas further north. Accordingly, the invertebrate component of the graminoid marshes are broken down into eight compartments, consisting of apple snails (*Pomacea paludosa*), freshwater prawns (*Palaemonetes paludosus*), crayfish (*Procambarus alleni*), mesoinvertebrates, other macroinvertebrates, large aquatic insects, terrestrial invertebrates, and fishing spiders. Loftus and Kushlan (1987) described an assemblage of 30 species of fish in the freshwater marshes, of which 16 species are found in the sawgrass marshes.

The Everglades assemblage of herpetofauna consists of some 56 species of reptiles and amphibians. Nine compartments of mammals were identified for the graminoid marshes. Approximately 350 species of birds have been recorded within the Everglades National Park, and just slightly less than 300 species are considered to occur on a regular basis (Robertson and Kushlan, 1984). Sixty percent of these birds are either winter residents, migrating into South Florida from the north, or else visit briefly in the spring or fall. The remaining 40% breed in South Florida (Lodge, 1994), but of these only eight groups nest or breed in the graminoids. Various species of wading and terrestrial birds roost or breed in the cypress wetlands and feed in the graminoid marshes, including anhingas, egrets, herons, wood storks, and ibises. These birds are explicit components of the cypress network. They feed on the aquatic and terrestrial invertebrate members of the graminoid wetland; however, this capture of prey is represented as an export from the graminoid system and an import into the cypress swamp. Waders were not included as explicit components in the graminoid network.

The cypress swamp model consists of 68 compartments and similar to the graminoid system, the cypress model has three nonliving compartments (refractory detritus, labile detritus, and vertebrate detritus) and two microbial compartments (living POC and living sediment). Ulanowicz et al. (1997), Bondavalli and Ulanowicz (1999) give a breakdown of the construction of the model. The primary producers are more diverse than those found in the graminoids and are represented by 12 compartments, 7 of which are essentially terrestrial producers: understory, vines, hardwood leaves, cypress leaves, cypress wood, hardwood wood, and roots (Bondavalli and Ulanowicz, 1999).

These seven compartments ramify the spatial dimension of the ecosystem in the vertical extent—an attribute not shared by the graminoid marshes. Other primary producer compartments include phytoplankton, floating vegetation, periphyton, macrophytes, and epiphytes (Bondavalli and Ulanowicz, 1999).

According to Bondavalli and Ulanowicz (1999), cypress swamps do not possess a distinct faunal assemblage, but rather share most species with adjacent plant communities. Most fauna spend only parts of their lives in the swamp. Benthic invertebrates form the heterotrophic base of the food chain. A high diversity of invertebrates has been recorded in cypress domes and strands, but a lack of data at the species level mandated that they resolve the invertebrates into only five compartments (Bondavalli and Ulanowicz, 1999). Similarly, the fish component of this model could not be resolved into more than three compartments, two containing small fish and a third consisting of large fish (Bondavalli and Ulanowicz, 1999).

The herpetofauna compartments of the cypress model were similar to those of the graminoids. The bird community of the cypress swamps was much more diverse than that in the graminoids. The increased diversity can be traced to the inclusion of wading birds in the cypress model. The wading birds do not roost or nest in the graminoids, although they do feed there; therefore, it was assumed that an export of energy and carbon flowed from the graminoids into the cypress. The 17 bird taxa in the cypress include 5 types of wading birds, 2 passerine collections, and various predatory birds (Bondavalli and Ulanowicz, 1999). The mammals of the cypress include all the mammalian compartments of the graminoids, as well as some terrestrial mammals unique to the cypress (shrews, bats, feral pigs, squirrel, skunks, bear, armadillos, and foxes; Bondavalli and Ulanowicz, 1999). These species are found mostly in the cypress trees and cypress domes, which extend the spatial extent of the ecosystem into the third dimension.

Ascendency, Redundancy, and Development Capacity

Information theory is employed to quantify how well "organized" the trophic web is (expressed in terms of an index called the system's "ascendency"), how much functional redundancy it possesses (what is termed the "overhead"), what its potential for development is, and how much of its autonomy is encumbered by the necessary exchanges with the external world (Ulanowicz and Kay, 1991).

According to the "total system throughput (TST)," the graminoid system is far more active than the cypress system (Table 10.4). Its TST (10,978 gC m^{-2} per year) is fourfold that of the cypress system (2952 gC m^{-2} per year). The development capacity of an ecosystem is gauged by the product of the diversity of its processes as scaled by the TST. The development capacity of the graminoid system (39,799 gC bits m^{-2} per year) is significantly higher than that of

TABLE 10.4 Information Indices for Both the Graminoid and Cypress Systems.

	Cypress		Graminoids	
Index	**Index**	**% of C**	**Index**	**% of C**
Total system throughput (gC m^{-2} per year)	2952.3		10,978	
Development capacity = C (gC-bits m^{-2} per year)	14,659		39,799	
Ascendancy (gC-bits m^{-2} per year)	4026.1	34.3	20,896	52.5
Overhead on imports (gC-bits m^{-2} per year)	2881.6	19.7	3637	9.1
Overhead on exports (gC-bits m^{-2} per year)	75.4	0.5	606	1.5
Dissipative overhead (gC-bits m^{-2} per year)	2940	20.1	4932	12.4
Redundancy (gC-bits m^{-2} per year)	3735.8	25.5	9728	24.4
Internal capacity (gC-bits m^{-2} per year)	5443.4		18,122	
Internal ascendancy (gC-bits m^{-2} per year)	1707.5	31.4	8394	46.3
Redundancy (gC-bits m^{-2} per year)	3735.8	68.6	9728	53.7
CONNECTANCE INDICES				
Overall connectance		1.826		1.586
Intercompartmental connectance		3.163		1.807
Food web connectance		2.293		

the cypress (14,659 gC bits m^{-2} per year), a difference that one might be inclined to attribute to the disparity in the scalar factor (TST) between the systems. When one regards the normalized ascendency, however (ascendency is a measure of the constraint inherent in the network structure), one notices that the fraction of the development capacity that appears as ordered flow (ascendency/capacity) is 52.5% in the graminoids. This is markedly higher than the corresponding fraction in the cypress system (34.3%).

The graminoid system has been stressed by a number of modifications to the patterns of its hydrological flow, which have resulted in the loss of transitional glades, reduced hydroperiods, unnatural pooling, and overdrainage (Light and Dineen, 1994). In comparison with the cypress community, however, the system has exhibited fewer changes in its faunal community and is sustained by an abundance of flora and microbiota. The cypress ecosystem, like that of the graminoids, is limited by a dearth of phosphorus, which remains abundant in marine and estuarine waters and sediments. The graminoid system compensates for this scarcity of nutrients with a profusion of periphyton. Periphyton exhibits a high P/B ratio, even under oligotrophic conditions.

The natural stressors that affect the cypress ecosystem appear to have far greater impacts, in that they modulate the rates of material and energy processing to a far greater extent in that system. This analysis is phenomenological, and there is no clear reason why the modulation of rates of material and energy occur in the cypress. Thus, even though these systems are (1) adjacent to one another, (2) share many of the same species, and (3) some of the heterotrophs of the cypress feed off the graminoid system, the characteristic indices of the graminoid system remain distinct from those of the cypress community.

Calculating and ranking "relative sensitivities" proves to be an interesting exercise. For example, when the average trophic levels of the 66 compartments of the graminoid wetland ecosystem were calculated, lizards, alligators, snakes, and mink were revealed to be feeding at trophic levels higher than some of the "charismatic megafauna," such as the snail kite, nighthawk, Florida panther, or bobcat (Table 10.5).

The relative contributions to ascendency by the latter actually outweighed those of the former, however. The relative values of these sensitivities thus seemed to accord with most people's normative judgments concerning the specific "value" of the various taxa to the organization of the system as a whole (Table 10.5).

Similarly, in the cypress system, white ibis, large fish, alligators, and snakes feed at high effective trophic levels, but the system performance seemed to be enhanced more by the activities of the vultures, gray fox, bobcat, and panthers (Table 10.5).

In comparing the component sensitivities in the graminoid and cypress systems, one discovers numerous similarities between the taxa of the two systems (Table 10.5). For example, the avian and feline predators ranked high in both systems. The contributions of snail kites and nighthawks to the performance of the graminoid system were highest (at ca. 14 bits), while that of the bobcat and panther were highest in the cypress (at ca. 13 bits). Both bobcat and panther seem to be more sensitive in the cypress than in the graminoids.

The low sensitivity of crayfish (0.99 bits) in the graminoids was not repeated in the cypress, although aquatic invertebrates generally had a low sensitivity in that system, too (2.01 bits). The sensitivity of labile detritus was similar in both systems (around 1.5 bits), while refractory detritus was more sensitive in the graminoid (1.59 bits), indicating a greater importance in that system. The sensitivities of the primary producers are lower in the cypress (1.51 bits) than in the graminoids (1.66 bits) and are uniform within both systems, except for *Utricularia* in the graminoids. *Utricularia* are carnivorous plants, and, therefore, both its effective trophic level and its sensitivities are higher than those of the other primary producers (Table 10.5). *Utricularia* can exhibit an interesting example of positive feedback in ecosystems; indeed, it harnesses the production of its own periphyton via intermediary zooplankton grazers. This subsidy to the plant apparently allows it to drive in oligotrophic environments that would stress other macrophytes with similar direct uptake rates. As ambient nutrient level rise, however, the advantage gained by positive feedback wanes, until a point is reached where the system collapses (Ulanowicz, 1995).

The cypress system exhibits an additional spatial dimension in comparison with that of the graminoids. The third, vertical (terrestrial) dimension of cypress vegetation provides both additional habitat and food for the higher trophic levels. In the cypress, the appearance of terrestrial vegetation affords increased herbivory by terrestrial fauna such as mammals, birds, and terrestrial invertebrates. Furthermore, much of what is produced by the bacteria is consumed by the higher trophic levels, and less production is recycled back into the detritus. With the addition of the arboreal dimension in the cypress, one would expect that system to be more productive than its graminoid counterpart, and that the total systems throughput (and, consequently, other systems properties) would be higher in the cypress as well. This is not the case, however. In fact, the throughput of the graminoids exceeds that of the cypress by some fourfold. Although the total biomass in the cypress is three times greater than that in the graminoids, the cypress systems P/B ratio is four times lower there than in the graminoids, thereby yielding the greater throughput in the graminoids.

TABLE 10.5 Ascendency Sensitivity Coefficients (Sensitivity In Bits) and Effective Trophic Levels (ETLs) for Both the Graminoid and Cypress Systems.

	Graminoids			Cypress		
	Compartment	**ETL**	**Sensitivity**	**Compartment**	**ETL**	**Sensitivity**
1	Crayfish	2.14	0.99	Liable detritus	1.00	1.42
2	Mesoinvertebrates	2.15	1.12	Refractory detritus	1.00	1.45
3	Other macroinvertebrates	2.12	1.15	Phytoplankton	1.00	1.51
4	Flagfish	2.00	1.27	Floating vegetation	1.00	1.51
5	Poeciliids	2.20	1.47	Periphyton/macroalgae	1.00	1.51
6	Labile detritus	1.00	1.55	Macrophytes	1.00	1.51
7	Refractory detritus	1.00	1.59	Epiphytes	1.00	1.51
8	Apple snail	2.12	1.60	Understory	1.00	1.51
9	Tadpoles	2.03	1.63	Vine leaves	1.00	1.51
10	Periphyton	1.00	1.66	Hardwoods leaves	1.00	1.51
11	Macrophytes	1.00	1.66	Cypress leaves	1.00	1.51
12	Floating vegetation	1.00	1.66	Cypress wood	1.00	1.51
13	*Utricularia*	1.03	1.69	Hardwood wood	1.00	1.51
14	Lizards	3.83	1.79	Roots	1.00	1.51
15	Freshwater prawn	2.27	2.12	Aquatic invertebrates	2.20	2.01
16	Ducks	2.20	2.32	Tadpoles	2.16	2.29
17	Bluefin killifish	2.57	2.34	Anseriformes	2.05	2.38
18	Other small fishes	2.48	2.44	Crayfish	2.26	2.46
19	Sediment carbon	1.00	2.44	Terrestrial invertebrates	2.00	2.55
20	Living sediments	2.00	2.58	Living sediment	2.00	2.64
21	Mosquito fish	2.47	2.64	Squirrels	2.00	2.72
22	Living particulate organic carbon (POC)	2.00	2.80	Apple snail	2.26	2.74
23	Chub suckers	2.50	2.86	Prawn	2.26	2.91
24	Shiners and minnows	2.68	3.60	Rabbits	2.00	2.97
25	Gruiformes	2.01	3.76	White-tailed deer	2.00	2.97
26	Muskrats	2.00	3.83	Living POC	2.00	3.08
27	White-tailed deer	2.00	3.83	Black bear	2.26	3.30
28	Terrestrial inverts	2.00	3.91	Small herbivorous and omnivorous fish	2.60	3.48
29	Rabbits	2.00	5.10	Galliformes	2.33	3.58
30	Killifish	2.81	5.13	Mice and rats	2.37	3.77
31	Turtles	2.74	5.57	Wood stork	3.24	3.82
32	Large aquatic insects	2.96	5.63	Raccoon	2.74	3.84
33	Salamander larvae	2.57	5.64	Great blue heron	3.24	3.85
34	Grebes	2.63	5.79	Egrets	3.23	3.90
35	Other centrarchids	3.02	6.59	Hogs	2.44	3.96

Continued

TABLE 10.5 Ascendency Sensitivity Coefficients (Sensitivity In Bits) and Effective Trophic Levels (ETLs) for Both the Graminoid and Cypress Systems.—cont'd

	Graminoids			Cypress		
	Compartment	**ETL**	**Sensitivity**	**Compartment**	**ETL**	**Sensitivity**
36	Rats and mice	2.27	6.66	Other herons	3.21	4.10
37	Raccoons	2.59	6.72	White ibis	3.58	4.19
38	Opossum	2.45	6.77	Turtles	2.82	4.28
39	Pigmy sunfish	3.09	6.79	Woodpeckers	2.52	4.43
40	Bluespotted sunfish	3.09	6.83	Omnivorous passerines	2.53	4.45
41	Dollar sunfish	3.09	6.87	Hummingbirds	2.53	4.45
42	Seaside sparrow	2.57	7.10	Small carnivorous fish	3.07	5.56
43	Passerines	2.96	7.16	Opossum	2.35	5.61
44	Topminnows	3.10	7.47	Kites and hawks	3.37	6.10
45	Redear sunfish	3.13	9.09	Owls	3.36	6.10
46	Catfish	3.11	9.21	Mink	3.25	6.21
47	Spotted sunfish	3.16	9.32	Otter	3.25	6.23
48	Warmouth	3.21	9.42	Medium frogs	3.21	6.24
49	Mink	3.41	9.53	Small frogs	3.21	6.24
50	Snakes	3.32	9.66	Salamanders	3.28	6.32
51	Otter	3.34	9.71	Large frogs	3.32	6.38
52	Bitterns	3.25	9.75	Gruiformes	3.35	6.53
53	Alligators	3.39	9.96	Armadillo	2.90	6.54
54	Large frogs	3.29	10.19	Pelecaniformes	3.40	6.61
55	Small frogs	3.17	10.33	Large fish	3.42	6.99
56	Other large fishes	3.27	10.69	Lizards	3.00	7.64
57	Largemouth bass	3.24	10.92	Caprimulgiformes	3.00	7.64
58	Medium frogs	3.16	10.93	Bats	3.00	7.64
59	Gar	3.45	10.96	Predatory passerines	3.00	7.64
60	Cichlids	3.22	10.98	Shrews	3.00	7.65
61	Fishing spider	3.27	11.77	Alligators	3.78	8.30
62	Bobcat	3.02	12.01	Snakes	3.79	8.58
63	Salamanders	3.32	12.29	Salamander larvae	3.20	8.62
64	Panthers	3.17	12.33	Vertebrate detritus	1.00	8.82
65	Snail kites	3.13	14.38	Vultures	2.00	10.03
66	Nighthawks	3.00	14.69	Gray fox	3.41	10.29
67				Bobcat	3.03	12.96
68				Florida panther	3.36	13.48

The increase in throughput in the graminoids increases its development capacity and ascendency. The relative ascendency, which excludes the effects of the throughput, is perhaps a better index with which to compare these two systems. The relative ascendency of the graminoids is exceptionally high. For example, Heymans and Baird (2000) found that upwelling systems have the highest relative ascendency of all the systems they compared (which were mostly estuarine or marine in origin), but the relative ascendency of 52% for the graminoids is higher than any such index they had encountered. The relative ascendency of 34% reported for the cypress is lower than most of the relative ascendencies reported by Heymans and Baird (2000).

Some reasons behind the higher relative ascendency of the graminoids can be explored with reference to the relative contributions of the various components to the community ascendency (Table 10.5). The highest such "sensitivity" in the cypress is more than 1 bit lower than its counterpart in the graminoids, and, on average, most higher trophic level compartments that are present in both models exhibit higher sensitivity in the graminoids than in the cypress. It is noteworthy also that 41 compartments in the cypress show sensitivities of less than 5 bits, while only 28 compartments lie below the same threshold in the graminoids. The higher sensitivities in the graminoids owe mainly to the greater activity among the lowest trophic compartments, which causes the other compartments to seem rare by comparison. Thus, in the graminoids, community performance seems sensitive to a larger number of taxa, which accords with the analysis of dependency coefficients and stability discussed in Heymans et al. (2002). Pahl-Wostl (1998) suggested that the organization of ecosystems along a continuum of scales derives from a tendency for component populations to fill the envelope of available niche spaces as fully as possible. This expansive behavior is seen in the cypress system, where the arboreal third dimension of the cypress trees fills with various terrestrial invertebrates, mammals, and birds not present in the graminoids. The graminoid system, however, appears to be more tightly organized (higher relative ascendency) than the cypress in that it utilizes primary production with much higher turnover rates. This confirms the suggestion made by Kolasa and Waltho (1998) that niche space is not a rigid structure but rather coevolves and changes in mutual interaction with the network components and the dynamical pattern of the environment. The graminoid system is more responsive because it utilizes primary producers with higher turnover rates, and has, therefore, been able to track more closely environmental and anthropogenic changes. The cypress system, on the other hand, should have more resilience over the long term due to its higher overhead, especially its redundancy (Table 10.4).

Conclusions

According to Bondavalli et al. (2000) a high value of redundancy signifies that either the system is maintaining a higher number of parallel trophic channels in order to compensate the effects of environmental stress or that it is well along its way to maturity. Even though these authors suggest that the cypress system is not very mature, in comparison to the graminoids, one would have to conclude that the cypress is a more mature system. A slower turnover rate, as one observes in arboreal systems, such as the cypress, is indicative of a more mature ecosystem. Furthermore, the third dimension of terrestrial vegetation affords the system a greater number of parallel trophic channels to the higher trophic levels than exists among the mainly periphyton-dominated graminoid system. Although the graminoid system has a large throughput of carbon and a substantial base of fast-producing periphyton, it appears relatively fragile in comparison to the cypress system, which is more resilient over the long run and has more trophic links between the primary trophic level and the heterotrophs. In conclusion, according to ascendency indices, scale—in the guise of the vertical dimension of the cypress—makes that system more resilient as a whole and less sensitive with respect to changes in material processing by many of its composite species.

10.5 THE APPLICATION OF ECO-EXERGY AS ECOLOGICAL INDICATOR FOR ASSESSMENT OF ECOSYSTEM HEALTH

Reference where eco-exergy has been used as ecosystem health indicator:

Zaldívar, J.M., Austoni, M., Plus, M., De Leo, G.A., Giordani, G., Viaroli, P., 2005. Ecosystem health assessment and bioeconomic analysis in Coastal Lagoon. In: Handbook of Ecological Indicator for Assessment of Ecosystem Health. CRC Press, pp. 163–184.

In this paragraph is reported an application of eco-exergy (see Chapters 2 and 7) to assess the ecosystem health of a coastal lagoon.

Coastal lagoons are subjected to strong anthropogenic pressure. This is partly due to freshwater input rich in organic and mineral nutrients derived from urban, agricultural, or industrial effluent and domestic sewage, but also due to the intensive shellfish farming.

The Sacca di Goro is a shallow water embayment of the Po Delta. The surface area is 26 km^2 and the total water volume is approximately 40×10^6 m^3. The catchment basin is heavily exploited for agriculture, while the lagoon is one of the most important clam (*Tapes philippinarum*) aquaculture systems in Italy. The combination of all these anthropogenic pressures call for an integrated management that considers all different aspects, from lagoon fluid dynamics, ecology, nutrient cycles, river runoff influence, shellfish farming, macroalgal blooms, and sediments, as well as the socioeconomical implication of different possible management strategies. All these factors are responsible for important disruptions in ecosystem functioning characterized by eutrophic and dystrophic conditions in summer (Viaroli et al., 2001), algal blooms, oxygen depletion, and sulfide production (Chapelle et al., 2000). Water quality is the major problem. In fact from 1987 to 1992 the Sacca di Goro experienced an abnormal proliferation of macroalga *Ulva* spp. This species has become an important component of the ecosystem in Sacca di Goro. The massive presence of this macroalga has heavily affected the lagoon ecosystem and has prompted several interventions aimed at removing its biomass in order to avoid anoxic crises, especially during the summer, when the *Ulva* biomass start to decompose. Such crises are responsible for considerable damage to the aquaculture industry and to the ecosystem functioning.

To carry out such an integrated approach a biogeochemical model, partially validated with field data from 1989 to 1998, has been developed (Zaldívar et al., 2003). To analyze its results it is necessary to utilize ecological indicators, using not only indicators based on particular species or component (macrophytes or zooplankton) but also indicators able to include structural, functional, and system level aspects. Eco-exergy and specific eco-exergy are used to assess the ecosystem health of this coastal lagoon. Effects of *Ulva*'s mechanical removal on the lagoon's eutrophication level are also studied with specific exergy (Jørgensen, 1997) and cost—benefits analysis (De Leo et al., 2002). Three scenarios are analyzed (for a system with clam production and eutrophication by *Ulva*) using a lagoon model: (1) present situation, (2) optimal strategy based on cost—benefit for removal of *Ulva*, and (3) a significant nutrient loading reduction from watershed. The cost—benefit model evaluates the direct cost of *Ulva* harvesting including vessel cost for day and damage to shellfish production and the subsequent mortality increase in the clam population. To take into account this factor, the total benefit obtained from simulating the biomass increase was evaluated using the averaged prices for clam in northern Adriatic; therefore, an increase in clam biomass harvested from the lagoon will result in an increase of benefit.

The Sacca di Goro model has several state variables for which the exergy was computed: organic matter (detritus), phytoplankton (diatoms and flagellates), zooplankton (micro- and meso-), bacteria, macroalgae (*Ulva* sp), and shellfish (*Tapes philippinarum*). The exergy and the specific eco-exergy are calculated using the data from Table 10.6 on genetic information content and all biomasses were reduced to gDW/L.

Figs. 10.7 and 10.8 present the evolution of exergy and specific exergy under the two proposed scenarios: *Ulva* removal and nutrient load reduction, in comparison with the "do nothing" alternative. As it can be seen the eco-exergy and specific eco-exergy of both increase, due to the fact that in our model both functions are dominated by clam biomass.

However, the optimal result from the cost/benefit analysis will considerably improve the ecological status of the lagoon in terms of specific exergy.

TABLE 10.6 Parameters Used to Evaluate the Genetic Information Content.

Ecosystem Component	Number of Information Genes	Conversion Factor
Detritus	0	1
Bacteria	600	2.7 (2)
Flagellates	850	3.4 (25)
Diatoms	850	3.4
Microzooplankton	10,000	29.0
Mesozooplankton	15,000	43.0
Ulva sp.	2000[a]	6.6
Shellfish (bivalves)	—	287[b]

[a] *Coffaro et al. (1997).*

[b] *Marques et al. (1997), Fonseca et al. (2000).*

From Jørgensen, S.E., 2000a. Principles of Pollution Abatement. Elsevier, Oxford, UK, 520 pp.

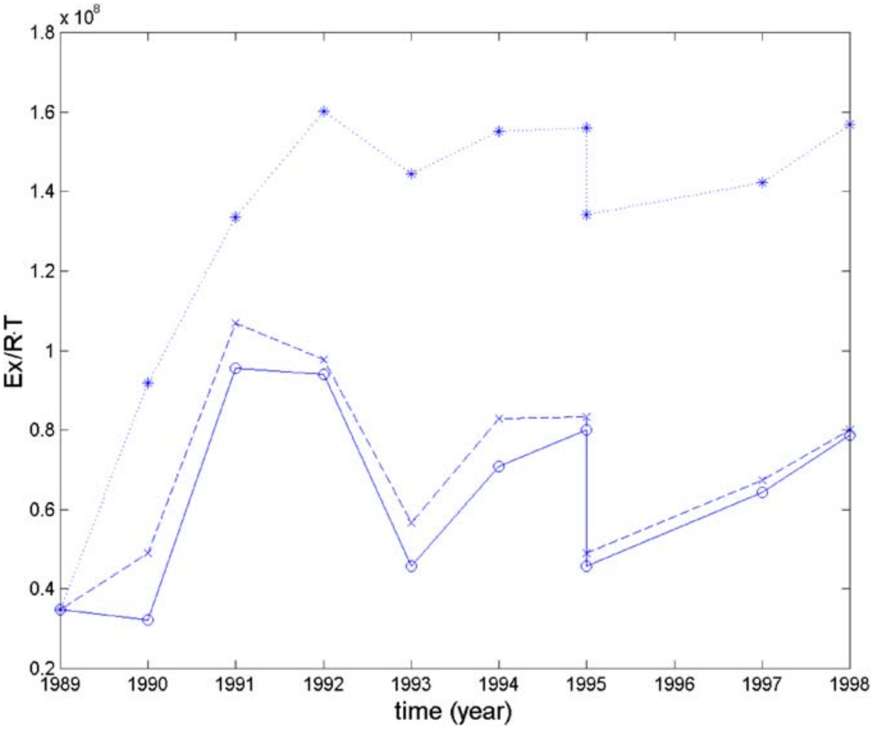

FIGURE 10.7 Eco-exergy mean annual values: Present scenario (*continuous line*), removal of *Ulva*, optimal strategy from cost–benefit point of view (*dotted line*) and nutrients load reduction from watershed (*dashed line*).

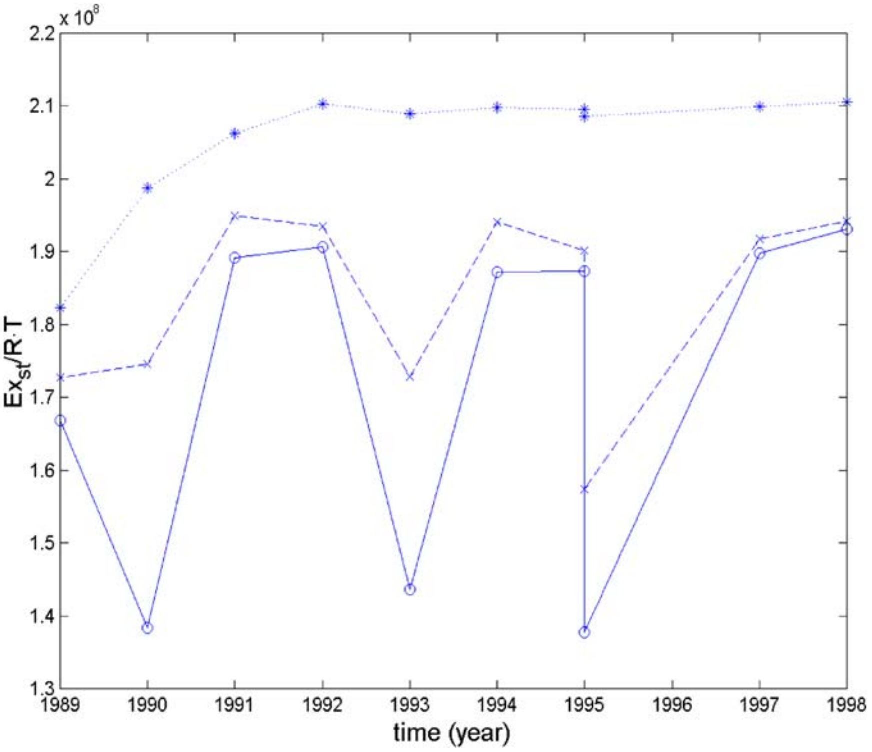

FIGURE 10.8 Specific eco-exergy mean annual values: Present scenario (*continuous line*), removal of *Ulva*, optimal strategy from cost–benefit point of view (*dotted line*) and nutrients load reduction from watershed (*dashed line*).

Conclusions

The results show that cost—benefit optimal solution for removal of *Ulva* has the highest eco-exergy and specific eco-exergy, followed by a significant removal of nutrients from the watershed. In the case for removal of *Ulva* specific exergy continues to increase as the number of vessels operating in the lagoon increase. The present situation had the lowest eco-exergy and specific eco-exergy. The result shows that it is a good sustainability policy to take care of natural resources, in this case the clams.

Eco-exergy expresses the system biomass and genetic information embedded in that biomass, while specific eco-exergy tells us how rich in information the system is. These indicators broadly encompass ecosystem characteristics and it has been shown that they are correlated with several important parameters such as respiration, biomass, etc. However it has been pointed out (Jørgensen, 2000a) that eco-exergy is not related to biodiversity, and, for example, a very eutrophic system often has a low biodiversity but high eco-exergy.

When the manager must select between different alternatives, it is difficult to evaluate the optimal solution from an ecological point of view. As eco-exergy and specific exergy are global parameters of the ecosystem, they give an idea of benefits that a measure will produce.

10.6 EMERGY AS ECOLOGICAL INDICATOR TO ASSESS ECOSYSTEM HEALTH

Reference where emery is applied as ecological indicator:

Howington, T.M., Brown, M.I., Wiggington, M., 1997. Effect of hydrologic subsidy on self-organization of a constructed wetland in Central Florida. Ecol. Eng. 9, 137—156.

Emergy (see Chapter 7) is used to study and explain theories concerning the effect of an external subsidy on a complex system (constructed wetland) seen by an holistic point of view.

Lake Apopka is a shallow (mean depth = 1.7 m) hypereutrophic lake in Central Florida, with an area of 124 km^2 (Lowe et al., 1989, 1992). In the early 1940s a hurricane removed most of the rooted macrophytes in the lake which led to the early stages of increased nutrient availability and subsequently increased algal productivity (Schelske and Brezonik, 1992). Addressing the nutrient status of this lake, the St. Johns River Water Management District (SJRWMD) constructed a 200 ha freshwater marsh on former agricultural lands with the goal of reducing the nutrient levels in the lake. It was suggested that by pumping enriched lake water through a constructed marsh, filtration of phosphorus and suspended sediments could be maximized. The pump system was turned on in early 1991. The subsidized and unsubsidized marsh maintained similar average water levels (0.76 m) throughout the study period varying yearly by no more than 0.2 m. Theory suggests that an external subsidy should increase the carrying capacity for wildlife of an ecosystem, all other things being equal. The increased capacity for wildlife may be an indirect result of certain self-organizational processes such as changes in vegetative cover. Other factors influencing the relationship between wetland productivity and hydroperiod include nutrient inputs, export, nutrient cycling, and decomposition (Carpenter et al., 1985).

This study tested theories concerning the effect of an external subsidy on ecosystem structure and organization. Two newly established marshes (one receiving nutrient enriched lake water and the other not receiving the subsidy) were the areas under study. The 63 ha subsidized marsh is the first of 2 cells that constitute the treatment wetland receiving lake water. The unsubsidized marsh, 46 ha, was created as a result of being a borrow pit for building berms around the treatment wetland. Vegetative cover richness and percent cover were determined using aerial photos and GIS, and was calculated using Margalef's index for species richness. Percent cover provided a further description of the changes in structural complexity of each marsh over time. Also avifauna surveys were conducted. Shannon diversity indexes were used to compare the avian communities found in the surveyed marshes. A synoptic study on the fish population of the subsidized and unsubsidized marshes was also conduced. A model of the marsh system (see Fig. 10.9 for energy symbols) was created to describe the role of the most important components and relationships (Fig. 10.10). An emergy analysis was performed to evaluate on a common basis (solar energy) the contributions of the various inputs (pumps, water, nutrients, human services, and renewable energies) driving the marshes ecosystems.

Emergy evaluation separates inputs on the basis of the origin (local or purchased) and of their renewability (see also Chapter 7). An environmental loading ratio (ratio of local and exogenous nonrenewable emergy to renewable emergy) and an investment ratio (ratio of exogenous to local emergies) were calculated to compare the quantities

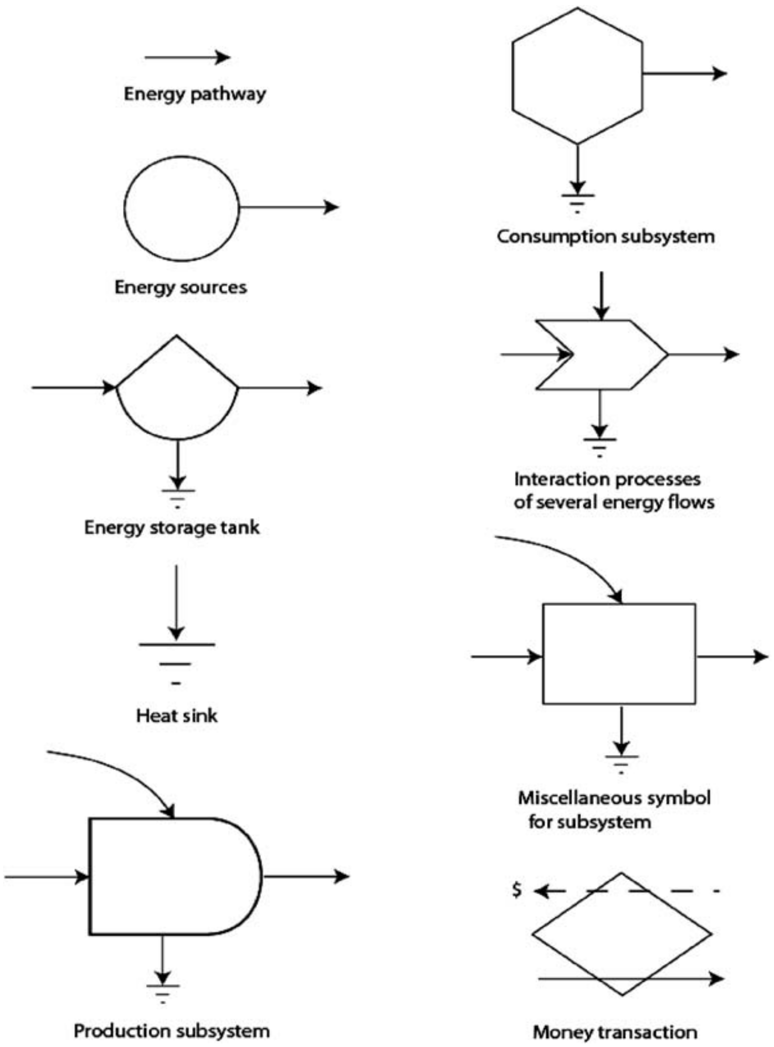

FIGURE 10.9 Energy symbols used to make an energy diagram.

and qualities of the energies entering each system. Emergy analysis tables were developed separately in Tables 10.7 and 10.8 for the subsidized and unsubsidized marshes.

The environmental loading ratio showed a large contrast between the two marshes. Investment ratios for the two marshes showed a large difference in the amount of purchased energy necessary to maintain the flows of environmental inputs.

Table 10.9 contains the ratios of free to purchased energy (environmental loading) and nonrenewable energy to renewable energy (investment ratio). Renewable energy sources for the subsidized marsh and the unsubsidized marsh were the same in both marshes. Lake water pumped into the subsidized marsh largely increased the emergy of total nitrogen and total phosphorus compared to that entering the unsubsidized marsh. This implies that the emergy flux of free nonrenewable energy sources influencing self-organization contributed 26% of the total emergy flow to the subsidized marsh. Liquid fuel used to operate the hydraulic pumps and the physical structure of the pump system itself are the two nonrenewable purchased energy sources that were included in the subsidized marsh system and that contributed 68% of its total emergy flow.

Vegetative community richness in the subsidized marsh was lower than that of the unsubsidized marsh. Fish biomass was also significantly different between marshes (Table 10.10).

A dynamic model was used to simulate situations in which the fuel use was increased (0% = unsubsidized marsh; 100% = subsidized marsh). Fig. 10.11 shows the changes in biomass carrying capacity with different levels of fuel used. Material and energy balances, as shown in the emergy analysis, were significantly different between the subsidized and unsubsidized marshes.

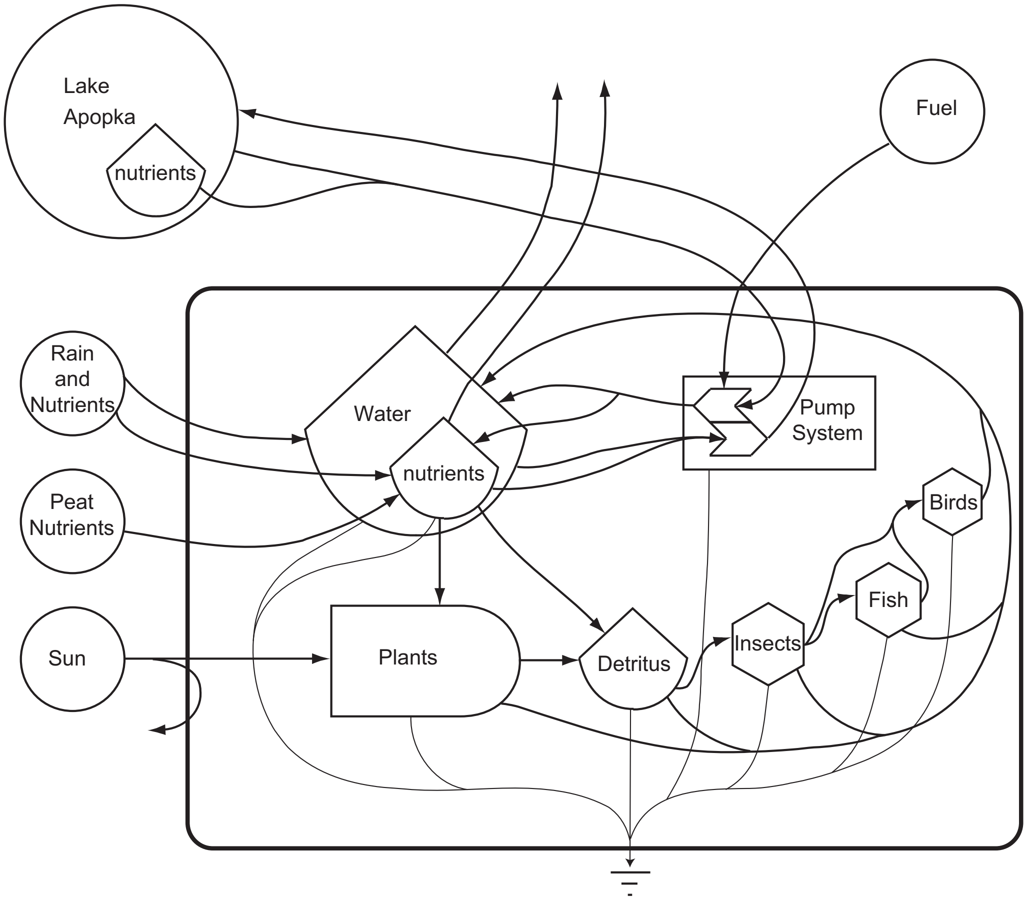

FIGURE 10.10 Diagram of constructed marsh. Removal of pump system simulated unsubsidized marsh.

TABLE 10.7 Annual Energy, Material, and Dollar Flows and Resulting Emergy Flows Supporting 1 Ha of the Subsidized Marsh.

Notes		Energy (J, g, $)	Transformity (sej/unit)	Emergy (E+14)
RENEWABLES				
1	Sun	5.41E+09 J	1.00E+00	0.00
2	Rain-chemical potential	6.27E+10 J	1.54E+04	9.66
NONRENEWABLES-FREE				
3	Total nitrogen	7.85E+05 g	4.21E+09	33.05
4	Total phosphorus	4.31E+04 g	6.88E+09	2.96
5	Phytoplankton	2.12E+09 J	1.00E+04	0.00
6	Pumped water-chemical potential	2.39E+09 J	2.35E+04	0.56
NONRENEWABLES-PURCHASED				
7	Liquid fuel	1.21E+11 J	6.60E+04	79.59
8	Construction-structure	5.11E+03 g	6.70E+09	0.34
9	Construction-services	9.34E+01 $	1.60E+12	1.49
10	Operation and maintenance	9.55E02 $	1.60E+12	15.28

TABLE 10.8 Annual Energy, Material and Dollar Flows and Resulting Emergy Flows Supporting 1 Ha of the Unsubsidized Marsh.

Notes		Energy (J, g, $)	Transformity (sej/unit)	Emergy (E+14 sej)
RENEWABLES				
1	Sun	5.41E+09 J	1.00E+00	0.00
2	Rain-chemical potential	6.27E+10 J	1.54E+04	9.66
3	Total nitrogen	1.54E+04 g	4.21E+09	0.65
4	Total phosphorus	6.35E+02 g	6.88E+09	0.04
NONRENEWABLES-PURCHASED				
5	Construction-services	3.76E+01 $	1.60E+12	0.60

TABLE 10.9 Environmental Ratio and Investment Ratio.

	Subsidized (E+15sej)	Unsubsidized Marsh (E+15sej)
EMERGY FLOWS		
Renewable emergy	9.7	9.7
Nonrenewable emergy		
Free	36.6	9.7
Purchased	96.7	0.6
Total emergy flux	142.9	19.9
EMERGY INDEX		
Environmental loading	13.8	0.1
Investment ratio	2.1	0.1

Due to the nonrenewable energy sources from the lake (e.g., nutrients, phytoplankton) and the pump system itself, the subsidized system had much higher flows of available resources. This is also clearly evident in the higher densities and biomass of the avian and fish communities. On the other hand, the complexity of the subsidized marsh as measured by diversity and community structure was lower. High emergy subsidies may compromise the complexity of the system in favor of high productivity. Community structure and dynamics are likely a result of many processes, including demographics, energy cycling, habitat disturbance, and the influence of other populations (Brown and Maurer, 1987; Maurer and Brown, 1988; Weins, 1989). In the case of the subsidized marsh, organization and community dynamics are also controlled by the availability of energy sources with high transformities. The importance of certain high emergy sources is their ability to facilitate the input of additional nonrenewable energies. The nutrient enrichment seemed to speed up self-organizational processes in the subsidized marsh increasing the rate of vegetative coverage of the marsh. Given the higher animal densities and biomass the

TABLE 10.10 Summary of Fish Community Structure.

Parameter	Subsidized	Unsubsidized Marsh	Significant Difference
Fish density	230 m^{-2}	165 m^{-2}	$n = 30, df = 5, P = .01$
Fish biomass	6.44 kg m^{-2}	4.29 kg m^{-2}	$n = 30, df = 5, P = .03$

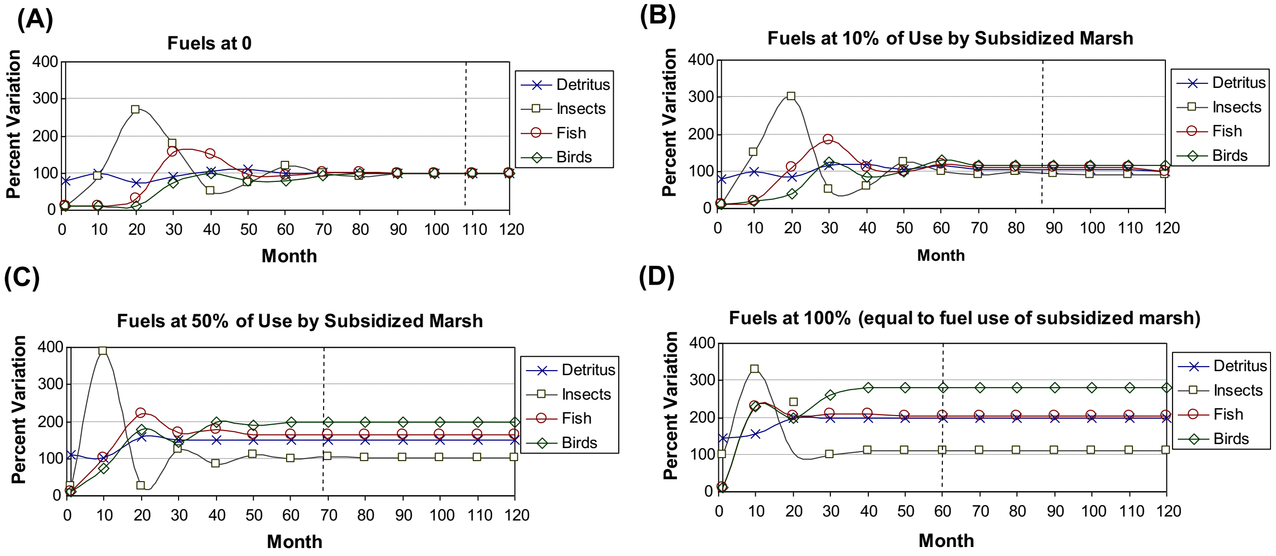

FIGURE 10.11 Percentage variation of biomass over time for different rates of fuel use showing: (A) 0 fuel usage represented by unsubsidized marsh; (B) 10%; (C) 50%; (D) 100%; (E) 500%; and (F) 1000% fuel usage relative to actual usage by subsidized marsh. (100% = biomass carrying capacity of unsubsidized marsh). Vertical dashed line marks appropriate time when marsh biomass reaches a steady state.

external subsidy may have also increased the rate that these components reached their respective carrying capacities.

This theory seemed to be validated by the computer model simulation; it suggests that carrying capacity varies with different levels of external subsidy.

The simulation in Fig. 10.12 of changing subsidy reveals that if the subsidy is pulsed, biomass will also pulse; the simulation model is sustained by studies in literature about the relationship between nutrients increase and biomass increase (Price, 1992; Kerekes, 1990). Overall, the external subsidy increased the emergy flux in the subsidized marsh

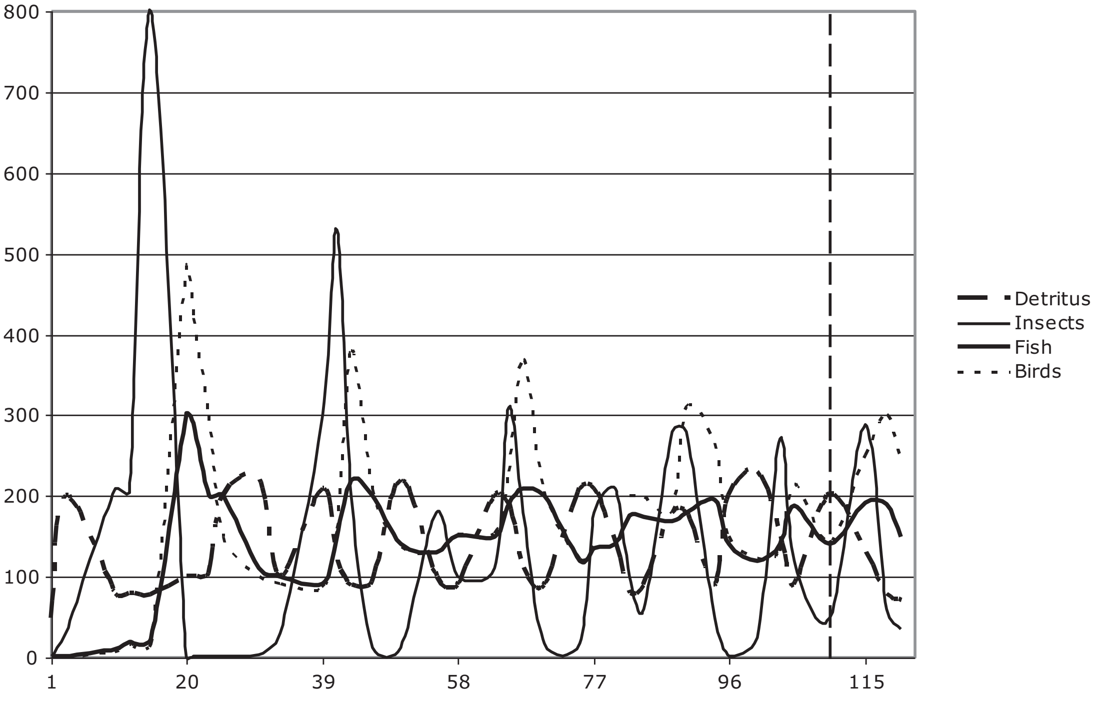

FIGURE 10.12 Percentage variation of biomass over time as fuel usage changes monthly as sine wave between 0% and 100% fuel usage relative to actual fuel usage of subsidize marsh.

by increasing the input of nonrenewable energy sources. As a result community parameters such as density and overall biomass also increased in the subsidized marsh, but at a cost of lowered richness, diversity, and evenness.

Conclusions

The emergy analysis reveals that the higher emergy flow in the subsidized marsh is caused by a higher input of nonrenewable energy sources. Community parameters (density and overall biomass) are also higher in the subsidized marsh, but at a cost of lowered richness, diversity, and evenness. Complexity of community structures is not influenced by the external subsidy. External subsidies increase the total emergy flow in an ecosystem and may increase the rate of successional processes in both the vegetative and wildlife communities.

10.7 THE ECO-EXERGY TO EMPOWER RATIO AND THE EFFICIENCY OF ECOSYSTEMS

Reference where the ratio eco-exergy to empower is used as ecological indicator:

Bastianoni, S., Marchettini, N., 1997. Emergy/exergy ratio as a measure of the level of organization of systems. Ecol. Model. 99, 33–40.

Bastianoni, S., 2002. Use of thermodynamic orientors to assess the efficiency of ecosystems: a case study in the lagoon of Venice. Sci. World J. 2, 255–260.

Bastianoni, S., 2006. Emergy, empower and the eco-exergy to empower ratio: a reconciliation of H.T. Odum with Prigogine? Int. J. Ecodynamics (in press).

The ratio of exergy to emergy flow (empower) has been used in order to assess the efficiency of an ecosystem in transforming available inputs in actual information and organization in eight aquatic ecosystems located in Argentina, Italy, and the United States.

The Case Studies

Eight aquatic ecosystems are used to understand the importance as an indicator of the eco-exergy to empower (emergy flow) ratio. Two of these ecosystems (called “Control Pond” and “Waste Pond”) are in North Carolina (USA) and are part of a group of similar systems built to purify sewage. Near the town of Morehead City, six artificial lakes were created: three control ponds fed with estuary water and “clean” water from the local sewage treatment plant, and three “waste” ponds fed with estuary water mixed with more “polluted” (i.e., richer in nutrients) effluent (Odum, 1989). Plant and animal species were introduced in and around the lakes to colonize the new areas and eventually produce new ecosystems by natural selection.

The third ecosystem is the Lagoon of Caprolace in Latium, Italy, at the edge of the Circeo National Park. The Lagoon of Caprolace is an ancient natural system fed by rainwater and farmland run-off rich in nitrogen, phosphorus, and potassium.

The fourth ecosystem is Lake Trasimeno. This is the largest lake in peninsular Italy (area 124 km^2), and it is shallow (mean depth 4.7 m, maximum 6.3 m) and accumulation processes are favored. The water level of the lake shows strong fluctuations with respect to meteorological conditions; hydrological crises occur after several years with annual rainfall <700 mm.

The fifth system is the Lagoon of Venice. With a surface area of about 550 km^2, it is the largest Italian lagoon. The sea and the lagoon are connected through three inlets. The average daily volume of water that enters the lagoon from the sea is about 400 million m^3, while 900 million m^3 of fresh water flow into the lagoon every year from the drainage basin.

The sixth system is an artificial one, located in the central part of the Lagoon of Venice, i.e., the Figheri basin. Fish farming basins consist of peripheral areas of lagoon surrounded by banks in which local species of fish and crustaceans are raised. Salt water from the sea and freshwater from canals and rivers are regulated by locks and drains. The fishes of highest demand raised in basins are *Dicentrarchus labrax* (bass) and *Sparus auratus*. Various types of mullet are also raised, as well as eels and mollusks.

Two ecosystems are located within the Esteros del Iberá (northeastern Argentina), one of the most pristine and largest wetlands of South America (13,000 km^2). This subtropical wetland is located between 27°36′ and 28°57′S and 58°00′–57°30′W. The macrosystem consists of a mosaic of marshes, swamps, and open water bodies. It is located between three large rivers, the Rio Paraná alto, the Rio Paraná medio, and the Rio Uruguay, with a single outlet to the Rio Corrientes that feeds into the Parana Medio (Bracchini et al., 2005; Loiselle et al., 2001).

The Galarza Lagoon is a mesotrophic, round-shaped lake with an area of 14 km^2 and averages 2 m in depth. The lagoon is fed by a small stream that originates in the large marsh area (200 km^2) directly above the lagoon and feeds into another small stream that leads to another large shallow lagoon. The water then flows out of this second lagoon into another large marsh area.

Laguna Iberá (area 58 km^2, mean depth 3.2 m) has a more irregular morphology and an eutrophic status. This lake is divided into two basins by a narrow passage that acts as a barrier reducing the interchange of wave energy and water masses. A small river (Rıo Miriñay) feeds the southern basin.

Emergy, Exergy and Their Joint Use

Why use emergy flow (empower) and eco-exergy together on the same systems? Emergy and eco-exergy are complementary concepts, the former based on the history of the system (Odum, 1988, 1996) and the latter examining the actual state (Jørgensen, 1992, 2006). When systems follow a process of selection and organization, we can use the ratio of exergy to emergy flow in order to assess the efficiency of an ecosystem in transforming available inputs in actual information and organization. The higher the ratio, the greater the efficiency of the ecosystem in transforming available inputs (as emergy flow) into structure and ecosystem organization (as eco-exergy). Its units are J yr sej^{-1}. Since dimensions are those of time, it cannot be regarded as a real efficiency (which is dimensionless), but more as an index of efficiency.

According to Svirezhev, this fact is normal, since this concept resembles that of a relaxation time, i.e., the time necessary to recover from disturbances, so that the exergy to empower ratio should be related with concepts like resilience and resistance of an ecosystem.

The *eco-exergy/empower* ratio indicates the quantity of external input necessary to maintain a structure far from equilibrium: if the eco-exergy/empower ratio tends to increase (apart from oscillations due to normal biological cycles), it means that natural selection is making the system follow a thermodynamic path that will bring the system to a higher organizational level.

As an efficiency indicator the eco-exergy to empower ratio enlarges the viewpoint of a pure exergetic approach as described in Fath et al. (2004), where the exergy degraded and the eco-exergy stored for various ecosystems are compared: using emergy there is a recognition of the fact that solar radiation is the driving force of all the energy (and exergy) flows on the Biosphere, important when also important "indirect" inputs (of solar energy) are present in a process.

To compare ecosystems different in size empower and eco-exergy densities were used. Table 10.11 shows empower and eco-exergy density values and the ratio of eco-exergy to empower. The emergy flow to Iberá Lagoon has been underestimated due to lack of data about the release of nutrients from the surrounding rice farms. In a sense this explains the highest value for eco-exergy to empower ratio, while the ecosystem does not seem to be in ideal conditions (Bastianoni et al., 2006). Nonetheless, the important fact is that all the natural systems that are better protected from human influence show very close figures. It seems that there is a tendency common to different ecosystems in different areas and of different characteristics to evolve toward similar thermodynamic efficiencies.

Figheri basin is an artificial ecosystem, but has many characteristics typical of natural systems. This depends partly on the long tradition of fish farming basins in the Lagoon of Venice, which has ""selected" the best

TABLE 10.11 Empower Density, Ecoexergy Density and Eco-exergy to Empower Ratio for eight Different Ecosystems.

	Control Pond	Waste Pond	Caprolace Lagoon	Trasimeno Lake	Venice Lagoon	Figheri Basin	Iberá Lagoon	Galarza Lagoon
Empower density (sej $year^{-1}$ L^{-1})	20.1×10^8	31.6×10^8	0.9×10^8	0.3×10^8	1.4×10^9	12.2×10^8	1.0×10^8	1.1×10^8
Eco-exergy density (J L^{-1})	1.6×10^4	0.6×10^4	4.1×10^4	1.0×10^4	5.5×10^4	71.2×10^4	7.3×10^4	5.5×10^4
Eco-exergy/ empower (10^{-5}J year sej^{-1})	0.8	0.2	44.3	30.6	39.1	58.5	73	50.0

Also the results on the entire lagoon of Venice confirm the general trend, showing figures in the range of Trasimeno and Caprolace, albeit the differences in the structure of the ecosystems and the huge inputs from the watershed.

management strategies (Bastianoni, 2002). The human contribution at Figheri basin manifests as a higher emergy density (of the same order of magnitude as that of artificial systems) than in natural systems. However, there is a striking difference in eco-exergy density, with values of a higher order of magnitude than in any of the other systems used for comparison: Man and nature are acting in synergy to enhance the performance of the ecosystem. The fact that Figheri can be regarded as a rather stable ecosystem (i.e., quite regular in its behavior) makes this result even more interesting and significant.

It was observed that the "natural" lagoon of Caprolace had a higher eco-exergy/emergy ratio than the control and waste ponds, due to a higher eco-exergy density and a lower emergy density (Bastianoni and Marchettini, 1997). These observations were confirmed by the study of Lake Trasimeno (Ludovisi and Poletti, 2003).

Conclusions

In general, in the more "natural" systems, where selection has acted relatively undisturbed for a long time, the ratio of eco-exergy to empower is higher, and decreases with the introduction of artificial inputs or stress factors that make higher the emergy flow and/or lower the eco-exergy content of the ecosystem.

10.8 APPLICATION OF ECO-EXERGY AND ASCENDENCY AS ECOLOGICAL INDICATOR TO THE MONDEGO ESTUARY (PORTUGAL)

The application of eco-exergy and ascendency as ecological indicators are presented in:

Jorgensen, S.E., Marques, J., Nielsen, S.N., 2002. Structural changes in an estuary, described by models and using exergy as orientor. Ecol. Model. 158, 233−240.

Marques, J.C., Pardal, M.A., Nielsen, S.N., Jorgensen, S.E., 1997. Analysis of the properties of exergy and biodiversity along an estuarine gradient of eutrophication. Ecol. Model. 102, 155−167.

Patrício, J., Ulanowicz, R., Pardal, M.A., Marques, J.C., 2004. Ascendency as an ecological indicator: a case study of estuarine pulse eutrophication. Estuar. Coast Shelf Sci. 60, 23−35.

The Mondego estuary has been used to benefit of the integration of the information derived from different ecological indicators: eco-exergy, specific eco-exergy (Chapter 2 and 7), and ascendency (Chapter 6).

Mondego Estuary: The Mondego River drains a hydrological basin of approximately 6670 km^2 at the western coast of Portugal. Urban wastewater is still discharged into the Mondego without treatment, and the estuary supports industrial activities, desalination ponds, and aquaculture. Additionally, the lower Mondego River valley has about 15,000 ha of farming fields (mainly rice paddies), with a significant loss of nutrients to the estuary (Marques, 1989). The Mondego estuary is located in a warm/temperate region with a basic Mediterranean temperate climate. It consists of two arms, north and south (Fig. 10.13), separated by an island. The two arms split in the estuarine upstream area about 7 km from the sea, and join again near the mouth. These two arms of the estuary present very different hydrographic characteristics. The north arm is deeper (5−10 m during high tide, tidal range about 2−3 m), while the south arm (two to four m deep, during high tide) is almost filled with silt in the upstream areas, directing most of the freshwater through the north arm. The water circulation in the south arm is controlled by tidal circulation and the relatively small fresh water input from the tributary, the Pranto River, which is controlled by a sluice located 3 km from the confluence with the south arm of the estuary. Due to differences in depth, the tidal excursion is longer in the north arm, causing daily changes in salinity to be much stronger, whereas daily temperature changes are highest in the south arm (Marques, 1989).

Seasonal intertidal macroalgae blooms (mainly of *Enteromorpha* spp.) have been reported in the south arm of the estuary for several years (Marques et al., 1993 a,b) and *Zostera noltii* beds, which represent the richest habitat with regard to productivity and biodiversity, are being drastically reduced in the south arm of the Mondego estuary, presumably outcompeted by *Enteromorpha* (Rafaelli et al., 1991). The physical data are listed in Table 10.12.

Nutrient loading into the south arm of the estuary was estimated, assuming that the major discharge is through the Pranto River, from the Armazens Channel (there is no freshwater discharge but, in each cycle, the tidal wave washes out the channel, where several industries discharge waste waters), and from the downstream communication of the south arm. The only way out of the system is the downstream communication (Fig. 10.13). The nutrient inputs from the Pranto River and Armazens Channel, and the exchanges (input vs. output) in the downstream communication of the south arm have been monitored from May 1993 to June 1994. The annual nitrogen loading to the south arm of the Mondego estuary was roughly estimated to 134 tons (126 tons of nitrate and 8 tons of nitrite),

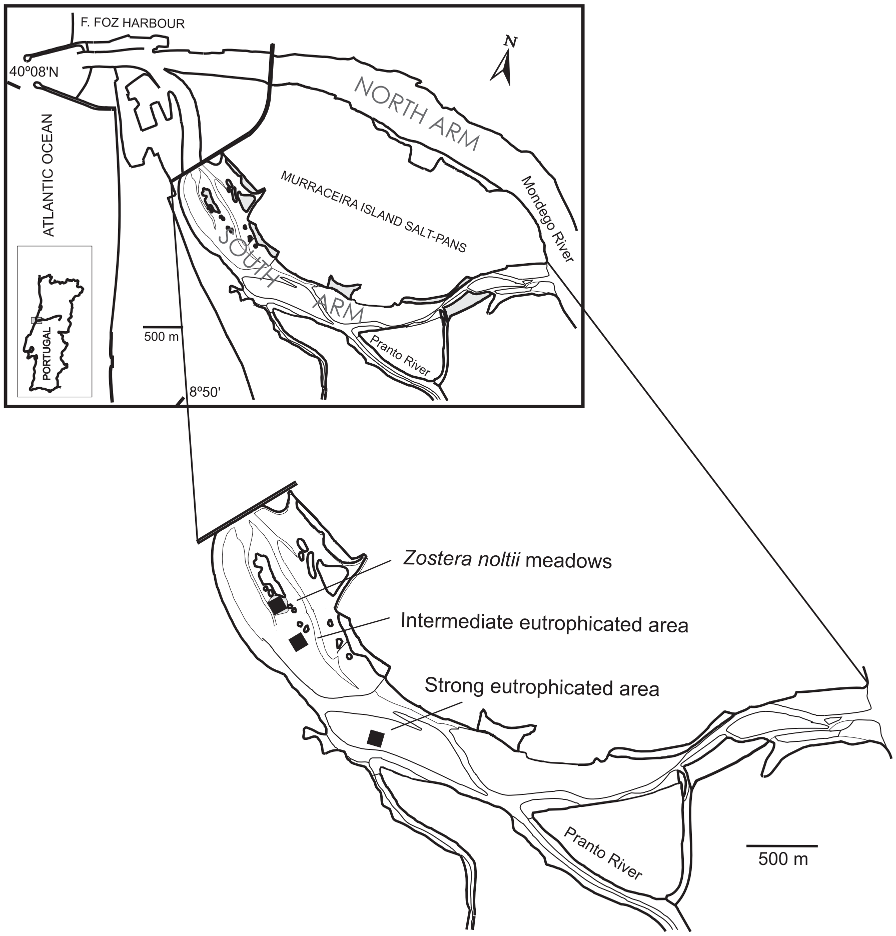

FIGURE 10.13 Map of Mondego River showing the field areas and the dividing of the river in the north and south arm.

TABLE 10.12 Physical Parameters of Mondego River.

Physical Parameters	Mondego River
Length and width of estuary (km^2)	10, 0.3
Area (km^2)	3.4
Volume (km^3)	0.0075
Mean depth (m)	1 and 2
Tidal range	0.35–3.3
Drainage area (km^2 excluding the estuary)	6670
Discharge (m^3 per year)	8.5 × 109
Mean residence time (days) (based on fresh water discharge)	North arm 2 South arm 9
Temperature range (min, max)	7–32
Mean Secchi depth in m (May–Sept.)	0.5–1.0
Annual insolation of PAR (400–700 nm) (mol. Fot. m^{-2} year^{-1})	3200–32,000

of which 14 tons are still in the system (18 tons of nitrate were imported and 4 tons of nitrite were exported) and 120 tons were transported to the sea. For phosphorus the loading was estimated to 14 tons (1 ton was imported to the system, while 15 tons were exported to the sea, which means that 14 tons were net released from the south arm of the estuary). In Table 10.13 are listed the chemical aspects of the area.

TABLE 10.13 Chemical Parameters of Mondego River.

Chemical Parameters	Mondego River	Inner Part	Outer Part
External N loading (tons N per year)	126		
External P loading (tons P per year)	1		
Salinity	Winter	10	10
	Summer	25	30
DIN (μg L^{-1})	Winter	300	200
	Summer	50	40
DIP (μg L^{-1})	Winter	30	25
	Summer	25	30
Tot-N (mg L^{-1})	Winter	0	0
	Summer	0.25	0.2
Tot-P (mg L^{-1})	Winter	0.30	0.25
	Summer	0.25	0.30
Sediment C (mg L^{-1})		350 gC m^{-2}	500 gC m^{-2}
Gross sedimentation (gC m^{-2} per year)			
Net sedimentation (gC m^{-2} per year)			
Sediment O_2 consumption (mg m^{-2} d^{-1})			

Maximization of Eco-exergy to Predict the Behavior of the System

It is often of interest to determine among several possibilities which structure of an ecosystem will prevail under given environmental circumstances. Here the thermodynamic variable, eco-exergy, was used as an orientor to describe adaptation and changes in the species composition. In the Mondego estuary two very different types of communities have been observed: (1) An *Enteromorpha* dominant community with the presence of *Cyathura carinata*, mollusca and crustacea. The algae community shows often a crash at early summer due to oxygen depletion. This community is found where the salinity is not too low and the nutrient concentration is high. (2) A *Zostera noltii* dominant community with the presence of oligochaeta, polychaeta, mollusca, and crustacea. This ecosystem is found where the nutrient concentration is lower. Mollusca are more abundant in ecosystem (2) than in ecosystem (1), while for crustacea the reverse is valid. From an ecological management point of view the *Zostera* dominated community is preferred because the oxygen concentration is higher, the water is clearer, and no crash due to anaerobic conditions takes place.

Starting from the hypothesis that the ecosystem structure having the highest eco-exergy among the possible ones would prevail, two models (one for an *Enteromorpha* dominant community and another one for A *Zostera noltii* dominant community) were developed to compare eco-exergy for several conditions, using STELLA. The growth was described as a function of internal concentrations of nutrients, temperature, light, and salinity (Duarte, 1995). If the hypothesis is correct, comparing the models for the two types of ecosystems the highest exergy under eutrophied and medium to high salinity conditions should be found for ecosystem (1), while the highest exergy should be found for ecosystem (2) under low nutrient and low salinity conditions. The models show that if the fresh water with high concentration of nutrients (particularly nitrogen) is discharged during the last part of the year, *Enteromorpha* will be dominant. The eco-exergy calculations show that the exergy is approximately the same for the two models, which may be interpreted as the initial value may be crucial for the final results. The results of the five simulations suggest that the ecological management of the freshwater discharge is a key factor for the prevailing of the two communities (*Enteromorpha*, *Zostera noltii*). From a management viewpoint at least two possibilities can be considered: artificial control of the freshwater discharges through the use of sluices, increasing the discharge during the first part of the year; or reduction of the nutrient input from fresh water (and if possible also from tide water). The joint use of these two alternatives should give the *Zostera* dominated community better conditions.

Eco-exergy, Specific Eco-exergy, and Diversity

The spatial and temporal variation of eco-exergy, specific eco-exergy, species richness, and heterogeneity were analyzed to examine in what extent these ecological indicators would capture changes in benthic communities along the gradient of eutrophication.

The benthic communities in the Mondego estuary (Portuguese western coast) were monitored during a yearly cycle. Samples of macrophytes, macroalgae, and associated macrofauna were taken fortnightly at three different sites, during low water, along an estuarine gradient of eutrophication in the south arm of the estuary, from the non-eutrophicated zone, where the *Zostera noltii* community is present, up to the heavily eutrophicated zone, in the inner areas of the estuary, where *Enteromorpha* spp. blooms have been observed. An overview of the major taxonomic groups contributing to the exergy in this system is provided in Table 10.14.

With regard to eco-exergy, values were consistently higher in the *Zostera noltii* community than in the eutrophicated areas. Also, eco-exergy values were higher in the most heavily eutrophicated area when compared with the intermediate eutrophicated area, especially during spring and early summer. This was related to the intensity of the *Enteromorpha* bloom, which gave rise to much higher values for total biomass in the most eutrophicated area. Specific eco-exergy was found to be consistently higher in the *Zostera noltii* community than in the eutrophicated areas until late spring when the picture changed completely and values became higher in the eutrophicated areas. This was due to a macroalgae crash in the eutrophicated areas, which determined not only a drastic reduction of the total biomass but also a change from a primary production—based situation toward a detritus-based food web. Therefore, since total biomass values after late spring consisted basically of animals (consumers), primarily deposit feeders and detritus feeders (e.g., annelid worms and crustaceans), it is clear that the abrupt increase of specific eco-exergy in the eutrophicated areas after the algae crash do not reflect any augmentation of the structural complexity of the community, but simply the different quality of the biomass involved in the calculations.

Regarding the *Zostera* community (data from after July 6), accounting for the primary producers and the consumers, specific exergy is lower than in the eutrophicated areas. But if we account only for the consumers, it is higher, following the same pattern from before the algae crash. Hence, specific eco-exergy may shift very drastically as a function of yearly dynamics (like in communities dominated by r-strategists), providing a spatial and temporal picture that may not be related with the long-term evolution and integrity of the system. With regard to biodiversity, the variation of species richness and of heterogeneity (species richness + evenness) along the gradient of eutrophication provided quite a different picture. Through time species richness was consistently higher in *Zostera* community, decreasing along the gradient of eutrophication. On the contrary, heterogeneity was always higher in the

TABLE 10.14 Major Contributors to the Exergy in the Mondego Estuary Benthic Communities Along the Gradient of Eutrophication.

Contributors	Noneutrophicated Area	Intermediate Eutrophicated Area	Eutrophicated Area—Before the Algae Crash	Eutrophicated Area—After the Algae Crash
Enteromorpha + Ulva	2.099	28.211	264.642	1.273
Other macroalgae	16.141	2.138	6.152	0.165
Zostera noltii leafs	128.368	0.000	0.000	0.000
Z. noltii roots	87.975	0.000	0.000	0.000
Z. noltii-total	216.343	0.000	0.000	0.000
Anthozoa	0.003	0.000	0.000	0.000
Sipunculida	0.001	0.001	0.001	0.002
Nemertinea	0.005	0.003	0.005	0.001
Oligochaeta	0.128	0.031	0.010	0.002
Polychaeta	1.254	0.709	0.569	0.846
Mollusca	63.950	14.192	31.195	13.240
Crustacea	1.3720	1.088	14.945	3.419
Insecta	0.007	0.006	0.009	0.001
Echinodermata	0.000	0.000	0.000	0.000
Pisces	0.000	0.006	0.034	0.000

For the noneutrophicated and intermediate eutrophicated areas, the average annual biomass (g m^{-2}) of each is given. For the eutrophicated area, the average biomass (g m^{-2}) of each group before and after the algae crash is given.

eutrophicated areas, except for the decrease observed in the most heavily eutrophicated area after an algae crash. The observed spatial variation of heterogeneity is due to the fact that the Shannon—Wiener's index integrates two components, the number of species (species richness), and their relative abundance (evenness). Therefore, although species richness decreased as a function of increasing eutrophication, as we expected, the dominance of a few species (e.g., *Hydrobia ulvae*, a detritus feeder and epiphytic grazer gastropod, and *Cerastoderma edule*, a filter feeder bivalve) in the *Zostera* community, probably due to the abundance of nutritional resources, decreased species evenness and consequently heterogeneity values. In this case, lower values of heterogeneity must be interpreted as expressing higher biological activity, and not as a result of environmental stress (Legendre and Legendre, 1984a,b). Taking into account the yearly data series for each site along the eutrophication gradient (noneutrophicated, intermediate eutrophicated, eutrophicated), eco-exergy and specific eco-exergy were significantly correlated ($P \leq .05$) providing a similar picture from the system. Values were consistently higher and more stable in the noneutrophicated area. The comparison of yearly data series (t-test, $P \leq .05$) showed that using eco-exergy values it was possible to distinguish between the three situations considered, even though differences between the intermediate and eutrophicated areas were not significant, which suggests that eco-exergy, an extensive function, might be more sensitive to detect subtle differences.

Species richness and eco-exergy were significantly correlated ($P \leq .05$), following a similar pattern, both decreasing from noneutrophicated to eutrophicated areas (Fig. 10.14B). On the contrary, heterogeneity and eco-exergy appeared negatively correlated (although not significantly), providing a totally distinct picture of the benthic communities along the eutrophication gradient (Fig. 10.14A). This obviously resulted from the properties of the heterogeneity measure, as explained above. Similar results were obtained comparing the patterns of variation of species richness, heterogeneity, and specific eco-exergy. Species richness and specific eco-exergy appeared clearly positively correlated ($P \leq .05$) (Fig. 10.14B), while the patterns of variation of heterogeneity and specific eco-exergy showed to be distinct (Fig. 10.14A). Moreover, from the comparison of yearly data series (t-test, $P \leq .05$), heterogeneity values were not significantly different in the intermediately eutrophicated and eutrophicated areas and therefore did not permit to discriminate relatively subtle differences. The hypothesis that eco-exergy and biodiversity would follow the same trends in space and time was validated with regard to species richness, but not for heterogeneity. Actually, eco-exergy, specific eco-exergy, and species richness responded as hypothesized, decreasing from noneutrophicated to eutrophicated areas, but heterogeneity responded in the opposite way, showing the lowest values in the noneutrophicated area. Their range of variation (eco-exergy and specific eco-exergy) through time was smaller in the noneutrophic area, expressing a more stable situation, while the magnitude of the variations was stronger in the other two areas, but especially in the intermediate eutrophic area (Marques et al., 2003). On the other hand, both eco-exergy and species richness were able to grade situations presenting relatively subtle differences, but specific eco-exergy and heterogeneity appeared to be less sensitive. Although biodiversity may be considered as an important property of ecosystem structure, the relative subjectivity of its measurements and their interpretation constitutes an obvious problem.

The spatial variation of species richness was significantly biodiversity and may be seen as the full range of biological diversity from intraspecific genetic variation to the species richness, connectivity, and spatial arrangement of entire ecosystems at a landscape level scale (Solbrig, 1991). If we accept this biodiversity concept, then eco-exergy, as system-oriented characteristic and as ecological indicator of ecosystem integrity, may encompass biodiversity.

Moreover, eco-exergy implies the existence of the transport information through scales, from the genetic to the ecosystem level, accounting not only for the biological diversity but also for the evolutionary complexity of organisms and ecosystem emergent properties arising from self-organization.

Ascendency Calculations

Eutrophication can be described in terms of network attributes as any increase in system ascendency (due to a nutrient enrichment) that causes a rise in TST that more than compensates for a concomitant fall in the mutual information (Ulanowicz, 1986). This particular combination of changes in variables allows one to distinguish between instances of simple enrichment and cases of undesirable eutrophication. Three sampling stations representative of the noneutrophic area, of the intermediate eutrophic area, and of the strongly eutrophic area were chosen. Estuarine food webs were constructed at the three sites and these quantified food webs were examined using network analysis. Taken together with Table 10.15 these provide the measures that were used to characterize the trophic status of the three estuarine ecosystems. Although the three habitats are clearly distinct in physical appearance, network analyses revealed both differences and similarities among their trophic structures that had not been apparent at first glance.

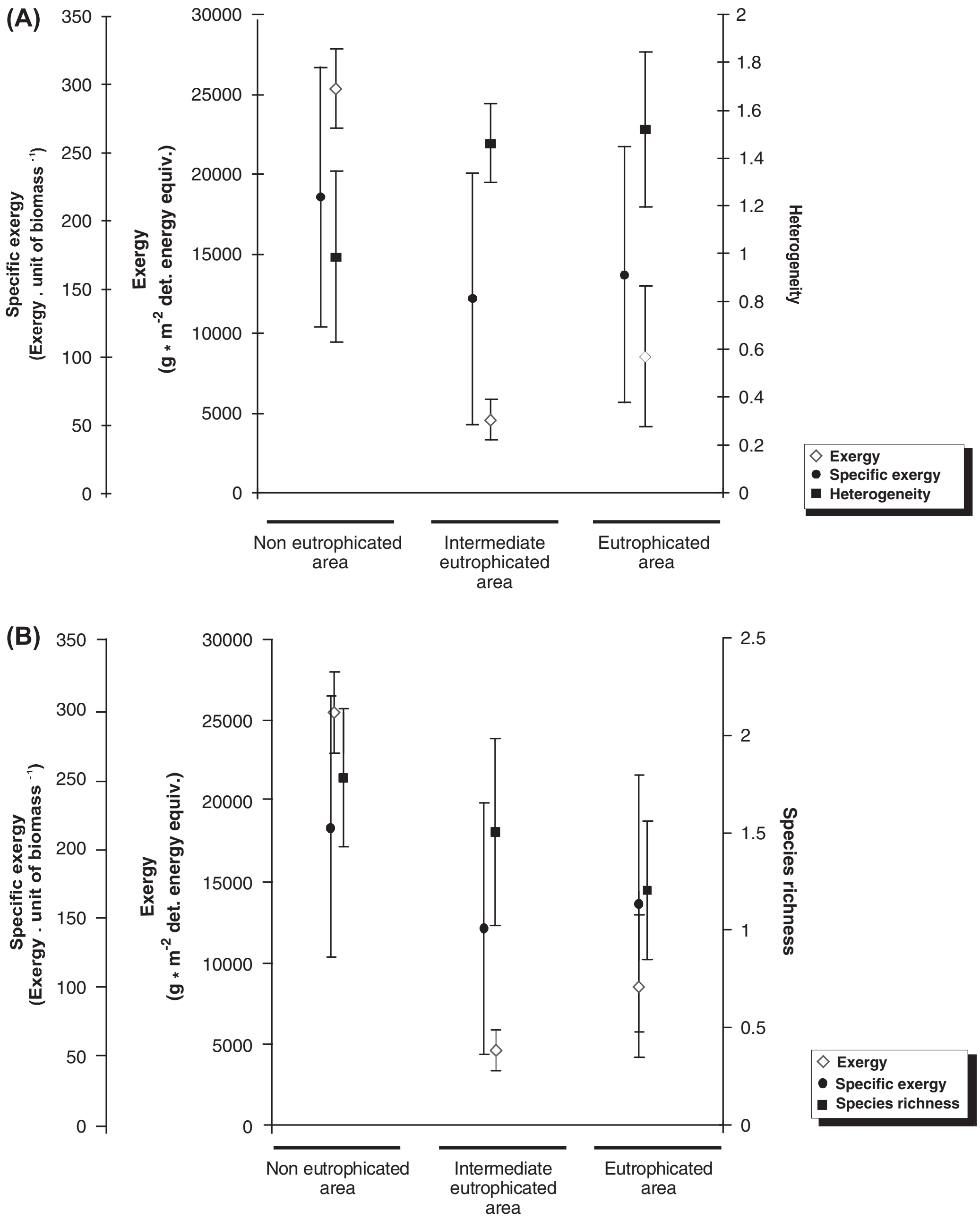

FIGURE 10.14 Variation of exergy and specific exergy in comparison with heterogeneity (A) and species richness (B) along the gradient of eutrophication gradient. For each situation, respectively, noneutrophicated (ZC), intermediate eutrophicated (INT), and eutrophicated (EUT), we indicate the average values and the standard deviation, taking into account the entire yearly data set. The spatial variation of exergy and specific exergy was significantly correlated ($r = 0.59$; $P \leq .05$). The spatial variation of heterogeneity was not significantly correlated neither with exergy or specific exergy ($r = -0.48$ and $r = 0.38$, respectively; $P \leq .05$).

It was possible to observe (Table 10.15) that the *Zostera* dominated community had the highest TST, followed (unexpectedly) by the strongly eutrophic system, and finally by the intermediate eutrophic area. The development capacity was highest in the *Zostera* beds and lowest in the intermediately eutrophic area.

The index differed significantly among the three areas. Due to the logarithmic nature of this index, small differences can represent appreciable disparities in structure. The average mutual information (AMI) was slightly higher in the noneutrophic area, followed closely by the eutrophic area, and was lowest in the intermediate eutrophic area.

TABLE 10.15 Network analysis Ecosystems Indices for the Three Areas.

Information Indices	Noneutrophic Area	Intermediate Eutrophic Area	Strongly Eutrophic Area
Total system throughput (g AFDW m^{-2} y^{-1})	10,852	1155	2612
Development capacity (g AFDW m^{-2} y^{-1}; bits)	39,126	5695	10,831
Ascendency (%)	42.3	30.4	36.7
Overhead on imports (%)	12.3	8.2	6.2
Overhead on exports (%)	1.3	1.5	2.5
Dissipative overhead (%)	17.7	22.1	19.9
Redundancy (%)	26.4	37.8	34.6
Average mutual information (bits)	1.52	1.50	1.52
Φ/TST	2.08	3.43	2.62
CONNECTANCE INDICES			
Overall connectance	1.67	2.43	2.1
Intercompartmental connectance	2.41	3.57	2.63
Finn cycling index	5.75E−02	0.2045	0.1946
Total number of cycles	74,517	15,009	9164

Concerning ascendency, it increased in order from the intermediate eutrophic to the heavily eutrophic zone to the *Zostera* meadows, while redundancy increases in the opposite direction. The long-term study in the Mondego estuary indicated that years of low precipitation tended to be associated with reductions in turnover rates and increases in water column stability, temperature, salinity, and light penetration (Martins et al., 2001). These changes in habitat conditions encouraged blooms of macroalgae that gradually replaced the resident macrophytes (Marques et al., 1997; Martins et al., 2001). In the intermediate and strongly eutrophic areas, primary production is largely the result of these macroalgal blooms. Production appears as a strong pulse during this specific time, but remains at very low levels during the rest of the year. This limited temporal interval of primary production results in a significantly lower figure for the cumulative annual primary production and TST in these areas as compared with the corresponding measures in the *Zostera* beds. Comparing the AMI values of the flow structure for the three areas, it is possible to discern a very small decrease in the measure among the three zones, suggesting that, as regards trophic structure, these areas are indeed different. The three zones appear nevertheless much more distinct by eye than is illustrated by the AMI values. In light of these results, the network definition of eutrophication appears to be inappropriate for the Mondego estuarine ecosystem. It would be more accurate to describe the enrichment processes occurring in this ecosystem as “pulse eutrophication.” This process could be characterized as a disturbance to system ascendency in the form of an intermittent supply of excess nutrients that, when coupled with a combination of physical factors (e.g., salinity, precipitation, temperature, etc.), causes both a decrease in system activity and a drop in the mutual information of the flow structure. Even though a significant rise in the TST occurs during the period of the algal bloom and at that time there is a strong increase of the system ascendency, the annual picture nevertheless suggests that the other components of the intermediate and strongly eutrophic communities were unable to accommodate the pulse in production. The overall result was a decrease in the annual value of the TST and, as a consequence, of the annual ascendency as well. Regarding the results of the trophic analysis, the *Zostera* community has one more trophic level than those counted in the strongly eutrophic chain, implying that this community possesses a more complex web with additional top consumers. At the same time, the *Zostera* community exhibits lower transfer efficiency at the first trophic level, probably because the production of *Z. noltii* meadows usually cannot be eaten directly, but needs to be decomposed first (Lillebø et al., 1999). Concerning the analysis of cycled materials, the overall percentage of cycled matter increases as the degree of eutrophication rises. This is indicated by the Finn cycling index (FCI) that reveals the proportion of TST that is devoted to the recycling of carbon (Finn, 1976).

Odum (1969) suggested that mature ecosystems recycle a greater percentage of their constituent material and energy than do pioneer or disturbed communities. Hence, according to Odum, the progressive increase in the FCI would suggest the maturation of the ecosystem. It has been observed, however, that disturbed systems also often exhibit greater degrees of recycling. The speculation is that such an increase in cycling in disturbed systems is the homeostatic response that maintains in circulation resources, which before the perturbation had been stored as biomass in the higher organisms (Ulanowicz and Wulff, 1991). This latter scenario seems consistent with the present results. When the whole-system properties of the three areas were compared, the measures associated with the system considered to lie between the two extremes in nutrient loading did not plot intermediate to the other two. From this viewpoint, the intermediate eutrophic area appears to be the most disturbed of the three areas, since it has the lowest ascendency, AMI, TST, and development capacity values and the highest figures for redundancy and FCI.

10.9 CONCLUSIONS

Chapters 2–9 have shown several ecosystem properties that need indicators to be measured. This chapter has presented the application of these indicators. All these indicators are used to compare characteristics and performance of different ecosystems or of an ecosystem in time, more than to give absolute measures. These indicators cover a wide range of important properties of ecosystems, more than those shown in this chapter, for the evaluation of ecosystem health. Here just few examples have been picked among the many to let the reader have at least an idea of what can be done with these indicators, but nowadays a whole literature of papers and books can provide further examples and types of applications. The use of these indicators span from agricultural to industrial systems; from ecosystem management to ecological economics.

Especially for management purposes it is necessary to use these indicators with others, more focused on particular aspects than on the global ecosystem. Nonetheless the approaches used in this chapter are fundamental to describe ecosystems as “systems” and not just as the sum of singular components and therefore should always be used. They provide information that is sometimes complementary and sometimes overlaps: in this direction more research is needed to clarify the level of overlapping and to fully explore the essence of the *indicandum* provided by every indicator, but their relevance is undoubted.

C H A P T E R

11

Ecosystems Carry Important Messages to Managers and Policy Makers

> “Act so that the effects of your action are compatible with the permanence of genuine human life”; or expressed negatively: “Act so that the effects of your action are not destructive of the future possibility of such life”; … ***Jonas (1984)***

The above quotation stems from the philosopher Hans Jonas book, “*The Imperative of Responsibility*,” that puts an ethical perspective to our ever-continuing applications of technology to improve our well-being and living conditions. To formulate his perspective in a simple manner, and taking his argument seriously, it means that every time we implement a new technology, we also need to ensure that we do so in a responsible manner. This in turn raises the question of what responsibility means in general, and what does it mean when dealing with the consequences of our use of technology to our environment in particular. That problems arise from the human use of technology is not entirely new, but the number of problems emerging from this use has been accelerating since the rise of fossil fuel based industrialization that began around the 19th century and has been enforced with the so-called chemical revolution throughout the 20th century.

In addition, in our attempt to achieve a sustainable society, it is no longer sufficient to consider only the present, i.e., conditions that are proximate in time and space. It is much easier to establish a responsible behavior toward our immediate environment, which historically had been our primary focus. Jonas remarks such proximate considerations to be characteristic for our traditional ethics, but for the rapid development of technology we need a new and ethical planning that is more complex, a new ethics able to consider also conditions more distal in time/space and that will include both considerations on humans, society, and nature: exactly as it is presented in the Rio declaration; exactly as argued in the Millennium Goals and 17 Sustainable Development Goals; and exactly as it is included in the Seventh Generation Principle of the North American Indigenous people.

Not only we as individual humans and representatives of humanity need to consider this in our private life. In most countries, we have transferred the responsibility to formulate an organized responsible behavior to the state government and its related authorities. This means that considerations such as the one presented above should be at the core of any management and policy making in the environmental area, of any government or state, regardless if it has a Marxist, conservative, or neoliberal point of view as entrance point, which does not really matter when it deals with responsible politics and acts toward the environment. Any policy not obeying ecological principles or rules, simply ignoring warnings or neglecting considerations, will fail and most likely will, which historically had been our primary focus eventually lead to collapse. Examples of cases for even complex societies are legion (Diamond, 2011; Tainter, 1990, etc.).

Recent research has pointed out the importance of proper policy government to successful and sufficient environmental management (Scavenius and Rayner, 2017). The realization of a true successful development toward society is probably likely to lie somewhere in between two radical points—that of governmentality (Foucault, 2016) at one end and true bottom up, participatory, and action research approaches. Which balance is the more beneficial is likely to differ from case to case. Meanwhile, although the number of studies is limited and knowledge in the area is rather fragmented, some “rules of thumb” and proper indicators may be found and will be sketched in the following.

11.1 ECOSYSTEMS IN A SUSTAINABILITY PERSPECTIVE

Very often today ecosystem management can be observed to have moved away from its (natural) materialist and scientific background—or at least it seems to have been split up and is now shared with other disciplines such as the

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social and economic sciences. This is perfectly illustrated with the normal view of sustainability to consist of a triadic relation between economic, societal, and environmental perspectives. As a simple example, we notice that very early on the introduction of the concept of sustainability, we came to talk about the economic, social, and environmental aspects. The sequence alone serves to illustrate how quickly environmental concerns were having a secondary position in priorities. Later, both a human and spiritual dimension has been added. But the sustainability aspect is entering in many more disciplines, e.g., law and policy, micro- and macroeconomics, anthropology, proposals of design and innovation in technological development, architecture, etc.

One first point to be made here is that the whole field of sustainability has been developed—exactly not as a whole—but in a rather separate (one may say atomistic) manner, each field taken its own stance on what exactly sustainability is or should be about, and almost always ignoring that none of the forms will exist if the physico-material and geochemical basis is not there. Therefore, this needs to be ensured. Meanwhile, together with this, each subdiscipline spawns a new set of terms—a new vocabulary has been developed that tends to be so specialized within the separate fields that makes it difficult, not to say impossible, to communicate around such a critical topic, that is, how to behave properly and hopefully improve conditions and ensure our existence on Earth, our common place in time and space?

Second, among the terms it also has been very common to invent the new concepts around the use of metaphors. Indeed, metaphors might have their own right, serving as summarizing and popularizing terms believed to have a high explanatory power or value. The problem is that when often they seem to have the necessary explanatory power, rather they serve to blur the picture of what was otherwise thought to be clear. The problem of aggregating concepts alone may also well be illustrated by this book. For taking real action on the environment, doing proper management, i.e., take the right decisions in a case of, for example, mitigation, restoration, remediation, it is necessary to understand ecosystems, their properties, their behavior, and to take the right measures one need to choose the right tools among the ones presented in the above.

11.2 MANAGEMENT WITH NATURE

The coexistence of humans and nature, as we may see from the many emergent environmental problems observed through the last decades, is intricate and complicated in character. The construction of scenarios around the possible impact of an increased greenhouse effect, due to emissions from human activities, and the disturbance of chemicals on our own health and reproduction demonstrates clearly that our technological evolution and development most often strikes back on us with unpleasant secondary effects. Our impacts are now of such a character that we have been forced to realize that our geochemical impact in time and space is of such an order of magnitude that it exceeds that of other organisms. Hence, we have dedicated the name Anthropocene to describe the present time on Earth.

Truly, we have an excessive and negative impact on Earth. We take up more and more space, exploit more and more of the finite resources, and use “sophisticated” chemicals, much of it having an impact on remote places, in what was a few decades ago believed to represent pristine nature, all with the result that we do not have any real nature “sensu stricto” any more.

This does not mean that the anthropogenic nature we observe today does not possess any similarities with what we would consider as proper nature. In fact, the functional principles appear to be more or less the same, although the functionality is heavily constrained by our existence and our societies. Learning from this functionality, for instance, through ecosystem theory and ecological engineering (EE), and obeying functionality through mimicking (Nielsen, 2007b; Nielsen and Müller, 2009), it has often been shown to be beneficial also in economic terms and in fact examples are compiling that we should act more along this direction in the future, as suggested, for instance, in nature-based solutions such as biomimcry, ecomimcry, green chemistry, and circular economy.

Using Ecosystem Knowledge to Improve Management

In aquatic environmental management, we have observed both improvements and critical situations over the years. With the technological development over the latest century in general and after the Second World War in particular, we have come to dominate, rule, and exploit nature to an extreme extent. This has—beyond any doubts—been a success in that the standard of living for most people has improved and is still improving in terms of daily food calories available, medical care, energy use, resource consumption, and access to transportation.

Meanwhile, this development has also had its costs. Overfishing has been found to occur in many areas, fights over quotas among nations at regional level and even within nations tell their own sad story. Considering that we have even placed ourselves in a situation where we are—on one hand—not able to determine what will happen to the oceanic ecosystems as a result of increasing greenhouse gas emissions and—on the other—not able to find an agreement on what the exact cause(s) to the conditions are, it is clear that we still have a long way to go. Scientific evidence has not been successful in passing on the message that it is indeed possible to catch fish populations to extinction, even if examples can be found in most ecological textbooks. And, what about the amount of plastics floating around not only on the coast line but also concentrating in the centers of various oceanic gyres in the greater oceans? In fact, a recent exploration to the deepest part of the planet–the Marina Trench–discovered a plastic bag on the sea floor 11km below the surface. Have we learned to prevent and are we able to restore near coastal ecosystems, estuaries, and lagoons that are important as breeding and nursery ground that should in turn literally feed back to our fisheries in open waters? Only little improvement if any has been made, and at the end we may have to put our confidence to the ethical and religious arguments, like the responsible behavior proposed by the philosopher Hans Jonas or as argued by the Pope Francis in his second encyclical.

Management has been improved for many freshwater systems, and at least at regional levels, although mainly in the industrialized countries where directives or similar instructions are found in the form of, for instance, the European Water Framework Directive, into which many ecosystem principles have been incorporated. It is remarkable to note that the environmental systems that are closest to our everyday life are the first ones to receive attention. Many lakes, rivers, and streams were polluted during the green revolution if they were allowed to exist at all and put in to large drainage systems. It is tempting that the visual impact of green and sometimes smelling lakes, dead fish, etc., indirectly has led to the fact that these were the first areas to be taken care of. In referring to the above situation of oceans, the Convention on Fishing and Conservation of the Living Resources of the High Seas entered into force in 1966, but problems persist. We may hope that the European Marine Strategy Framework Directive and other approaches will ratchet up efforts to be taken here.

Engineering the Natural Way—Aquatics

Within the area of Ecological Engineering (EE), it has been realized that we should learn to view "humans as part of nature and not apart from nature" (Mitsch and Jørgensen, 2003), and many of the first efforts within EE were concentrated on mitigation and remediating human activities by the use of constructed wetlands that might rely on the restoration of previous conditions of the landscape or the construction of totally new wetlands in a true mix of ecology and engineering (Mitsch and Jørgensen, 2003; Kangas, 2003; Kadlec and Wallace, 2009).

Meanwhile, less elegant solutions were chosen that are not considered to be consistent with management in accordance to ecosystem principles. For instance, it was found that the early reliance on "the solution to pollution is dilution" was not sufficient as an operational paradigm. This approach promoted diverting pollution from small lakes to just dilute it in larger water bodies, typically nearby coastal waters. Later, it was found that this approach just led to the emergence of problems elsewhere. In brief, it was found that the easiest and most sensible thing to do was to go back to the actual causes of problems by "treating pollution at its source." This approach deals with the root cause of the pollution and the symptoms it delivers. Other scientific disciplines were born related to these problems such as cleaner production and industrial ecology. Those disciplines are outside the topics of this book but definitely go hand in hand with the ecosystem principles, for instance, in their search for energy efficiency and resource optimality.

As an example, traditional Danish aquaculture used to be carried out in a manner that was harmful to the environment using natural wetlands and based on water from rivers and streams. It was practiced as a throughflow system of production of fish from feeds, with excess feeds and fecalia in outlets causing pollution in downstream areas, where sometimes waters ended being of very poor quality, resulting in the absence of benthic organisms or natural fish in the output environment. Today, model systems have been developed together with the aquacultural farmers (Svendsen et al., 2008) that are based on almost totally recirculated water (recirculating aquaculture systems) described in Bregnballe (2015), and using established wastewater technology such as biofilters and activation of sludge to keep water clean in the plant. At the same time, excessive sludge is often treated through constructed wetlands. Often it is simply the dams from the former low technology aquaculture plant that have be converted into constructed treatments wetlands, serving to the final polishing of the wastewater to bring it back to good river water quality. The ponds act as natural ecosystems and support natural environment by a variety of ecotones, bringing back functionality and biodiversity.

Engineering the Natural Way—Terrestrial

For terrestrial systems to be managed in accordance with ecosystem principles, we face more obstacles as we also want that the ever-increasing global population should be fed sufficiently both in quantity and quality. No one seems to disagree with this goal, but the means and prejudices connected to it are abundant and often prevent adequate communication and action. We observe mainly two fronts. On one side, we may place those who believe that the situation needs to be handled by a new green revolution and implementation of ever-increasing monoculture agriculture based on gene-modified organisms and basically relying on a diverse set of technological fixes. On the other, we find people basically believing that shifting diets and diversity can solve the problems with both food quantity and quality, lower the demand for chemicals, and thus eliminating health and environmental problems caused by its use of which our conventional farming systems are so heavily depending on.

Several new ways of doing agricultural farming making use of ecosystem principles can be found in literature under a variety of names such as integrated farming, agroforestry (AF), permaculture (PC), organic, or biodynamic farming.

Integrated farms have been found to be just as competitive as conventional farming. In a study of four Filipino farms (Dalsgaard et al., 1995; Dalsgaard and Oficial, 1997), it was found that farmers still practicing in a traditional Filipino manner and having around 30 various crops of a high number of various vegetables and even a few animals produce at the same level or even above a farmer who has decided on modern almost monocultural farming. Furthermore, the traditional farmers experience a stability with production of various crops dispersed over the whole year; and thus, have a higher guarantee for food for the family both in terms of quantity and quality. This also involves economic stability as the traditional farmer always will have something to sell even if a few crops fail and as he has no or little need for investments other than work. Usually, such a farm can be handled by the family alone. As opposed to this, the conventional modern farmer needs to invest in fertilizers and pesticides and takes the risk of one successful crop: if something fails, it is crucial. If everything is sold at the same time, then tender is high and prices are therefore low—demands for other food sources become high and prices high. Such a farm cannot be handled by the family alone and it is necessary to hire workers around the time of harvest. All in all, the farmer is only marginally more productive with a much higher risk and lower income. It is hardly necessary to say that the multidiverse system is much more in accordance with ecosystem principles which were also accounted for in terms of diversity, cycling indices, and exergy calculations. Environmental, social, and economic sustainability thus goes hand in hand. Similar observations were made among a set of around 37 Brazilian smallhold farmers carrying out various farming practices in the Amazonian area around Belèm (Siegmund-Schultze et al., 2007, 2010). Here a mix of agricultural crops combined with extensive cattle farming seemed to offer both lower environmental impacts and economic stability.

The two types of agriculture mentioned above—PC and AF—with the inclusion of diversity make use of additional principles. First of all, conventional farming in general produces more than one crop but rarely on the same piece of land, one crop for one year. Meanwhile, rotation is needed to avoid too many problems with diseases and the following necessity to use pesticides. The crops in PC and AF are perennial plants as well as adding bushes and trees to the system, reducing erosion, and thereby increasing ecotones, exploiting the space in not only two but three dimensions (as a rain forest). One recent development (better to say rediscovery) even integrates with animal husbandry such as growing pigs in woods (which is believed to correspond to the original and normal life of pigs) or having geese and ducks as weeders and fertilizers at the same time with wine production.

AF can be considered as the union of two independent systems that are joined to implement an optimal use of resources and produce the same coproducts as the originating ones. As previously seen, emergy methodology is particularly suitable to account for coproducts. With respect to other metrics, e.g., life cycle assessment or energy analysis, in emergy, allocation of input and output flows is not allowed. By definition, the environmental cost of two or more products obtained by the same system is the total emergy flow supporting their production.

An example of the emergy evaluation of an AF system has been presented by Patrizi et al. (2017), demonstrating that the integrated system enables, in emergy terms, a 33% of saving with respect to two separate systems producing the same products.

The AF system assessed (Fig. 11.1C) was obtained by integrating a geese rearing system (Fig. 11.1A) in an already productive vineyard (Fig. 11.1B). Geese have been chosen as they graze grassland without eating grapes acting in this way as natural weeders and at the same time ensure natural fertilization through their droppings.

Emergy evaluation has been used to appraise the benefits of such an agro-livestock integrated system, although other benefits have not been included such as improvement of the soil quality due to the geese integration (Clark and Gage, 2009). Moreover, other studies have demonstrated that the meat quality of goose produced in the integrated system has higher nutritional quality (Sossidou et al., 2015).

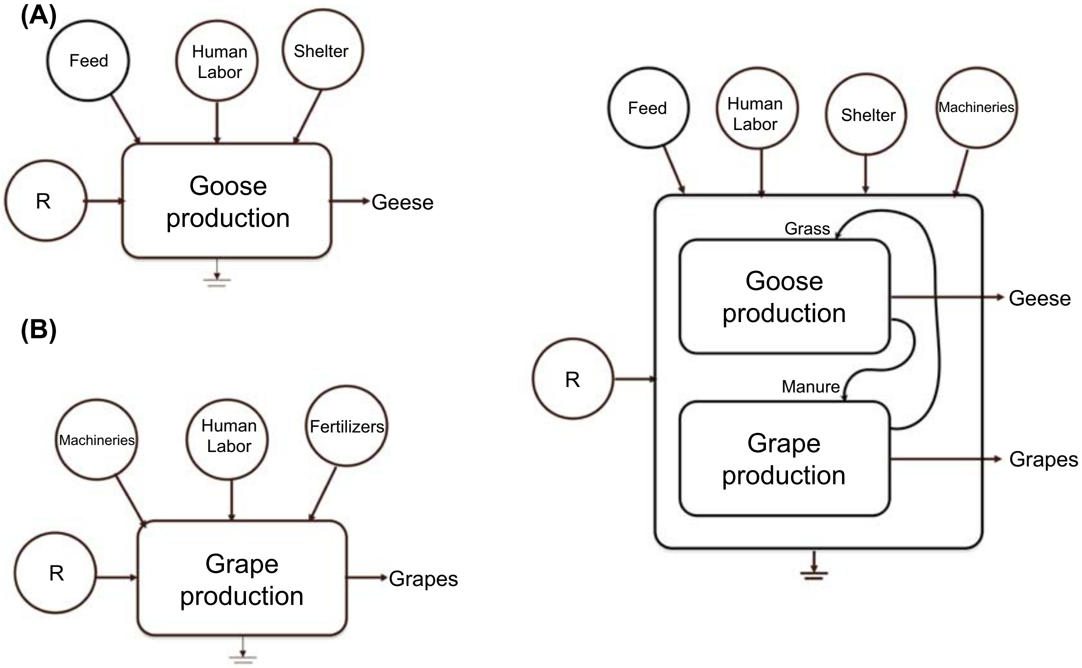

FIGURE 11.1 Energy diagram of geese production system (A), grapes production (B), and the agroforestry system (C) Renewable and nonrenewable input flows are represented by *circles*. *Arrows* represent the flows (external or internal) entering in the production systems.

In fact, all the abovementioned types make use of biodiversity to make productive ecosystems with plants that may support each other by physical or natural chemical protection against pests such as allelopathic effects or making use of each other's effects on the biogeochemical cycling in soils, for instance, by use of double- or even multicropping with legumes able to amend the soils with nitrogen.

11.3 INDICATING MANAGEMENT SUCCESS

One big question arises almost immediately from the above principles and that is how to express the eventual success of management and thereby be able to evaluate how successful initiatives and measures may be to improve overall well-being of those affected by the decisions (including the environment).

Three indicators have been identified that may be applied at different hierarchical levels but also for a holistic evaluation—that is dealing with sustainability at macroscopic level. Until now, three different approaches may be identified and discussed in detail here: the cubes approach, the sustainability trigon, and establishing exergy budgets and balances. Several other ways of viewing our impact on planet Earth may be developed into real indicators. Of these ecological footprint (Rees, 1992; Rees and Wackernagel 1994), emergy (Odum, 1988, 1996), and the numerous SDG targets have gained some popularity.

Meanwhile, using many of the indicators represents a problem in itself by being more than a dual sword. Simple indicators often do not tell enough other than that conditions for a particular organism are poor, but do not indicate any causality of a problem. To do this, more holistic approaches are needed. However, the calculation of such indicators demands a high degree of expertise to be involved in both system definition and calculation of the relevant stocks and processes. The danger is now that the more aggregate a holist indicator is, the more of its explanatory power is also lost, i.e., again it may indicate that something is wrong but not where and certainly it is not going to tell us exactly what to do.

The big issue is how can ecosystem principles be applied to create, understand, and test environmental management scenarios. All in all, this should tribute not only to improved management but also lead to the introduction of changes in policy solutions that should increase movement toward increased sustainability of our societies. Below, we present three recent approaches which may be applied as measures in monitoring with the purpose to follow the relative success of management initiatives.

A Framework for Sustainability Assessment—Cubes

The typical representation of sustainability focuses on the three aspects from the original Agenda 21: environment, society, and economy. These can and should not be treated as equivalent components (as it is possibly understood from Fig. 11.2), because they have very different space and time-scale characteristics: while the economic system changes rapidly and something economically unfavorable can become feasible changing taxes or incentives, the social system is much slower in changes and for the environment there is nothing we can do to make favorable something that is harmful. A more realistic representation shows nested circles with environment at the base, with society wholly in that circle and economy wholly in the society circle. Another version that does not use overlapping circles is given below.

A representation has been introduced that extrapolates an input-state-output (I-S-O) framework developed for ecosystems: an ecosystem is an open system, continuously fed by energy and matter inputs. These inputs are captured and transformed/metabolized and synthetized by the system, whose combined efforts generate goods and services, as outputs. Part of the outputs can be exploited for human purposes. The I-S-O framework enables the investigation of the ability of ecosystems to attract primary energy, transform it into a structure, and generate services.

This approach gives the idea of a relational order that links the three dimensions: the input, the state, and the output (see Fig. 11.3). Human systems behave according to the previous scheme: the environment provides the goods and services that are used by societies for their well-being; an organized society has a useful economic production that contributes to the well-being as well. We can therefore adopt a pyramidal representation of sustainability (Fig. 11.3A), which highlights the succession of stages in accordance with the I-S-O scheme. The main link between environment and the socioeconomic system is constituted by ecosystem services, which are used in their many forms. It is also important to stress the crucial role of feedbacks (Fig. 11.3B): the economy influences both environment and society; and society feeds back to the environment in different ways (that can be, generally speaking, positive or negative).

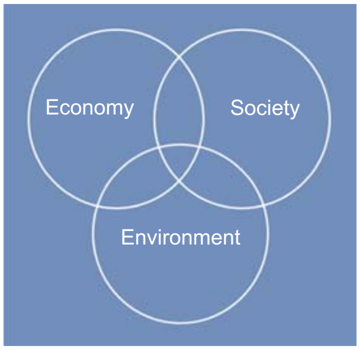

FIGURE 11.2 The "usual" representation of sustainability (Barbier, 1987).

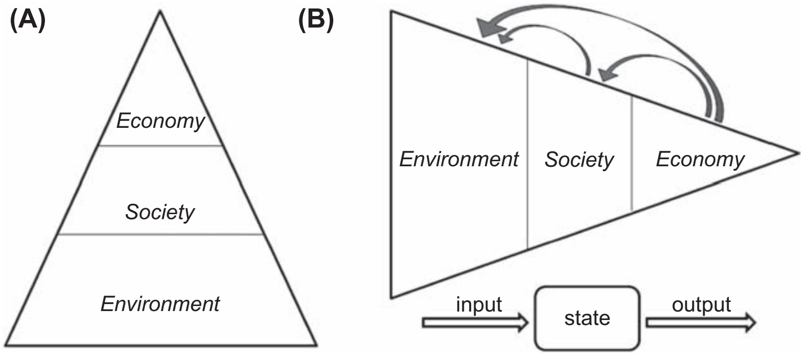

FIGURE 11.3 A pyramid represents better sustainability showing that a society is based on resources and produces an economy. There are feedbacks from economy to society and environment.

Using such a “minimal” representation of sustainability, the status of a national system can be represented by a three-axis diagram where three different (system) indicators are used to account for resource use, societal organization, and goods and services produced, respectively (Pulselli et al., 2015). This approach represents a trade-off that aims at maximizing information with the minimum number of indicators to illustrate the sustainability level of a system. The three indicators should be representative of the system as a whole. Each of the three indicators chosen should represent one of the sustainability aspects, environmental, societal, or economic aspects, respectively. The aim is to depict the three different dimensions of system sustainability independently, ensuring that every indicator maintains its identity and complementary informative capacity. This representation also avoids the use of hundreds of indicators that are very difficult to interpret.

Several choices are possible for indicators at the national/regional level. For example, in the case of environment, ecological footprint, emergy, or indicators derived from material flow analysis on the environmental axis; indicators of social capital include equity within a society (e.g., Gini index or Palma ratio), of labor or of education for the social axis; and indicators such as gross domestic product (GDP), the Index of Sustainable Economic Welfare or genuine progress indicator on the economic one. A first analysis was conducted by Pulselli et al. (2015) using the emergy flow per capita (Odum, 1988, 1996); the Gini index of income distribution, and the GDP per capita on the environmental, social, and economic axes, respectively (Fig. 11.4).

We have seen what emergy represents; in the case of a national economy it accounts for the resource use, measured in term of direct and indirect solar energy, which is necessary to support the country’s population, with all its consumption. The Gini coefficient is a measure of inequality ranging from 0 (in the situation of perfect equality, where every unit has the same income) to 1 (in the situation of greatest inequality, where only one unit receives the whole income). Even if, strictly speaking, the Gini index is an economic indicator, it has been shown that inequality is strongly correlated with health and social problems (Wilkinson and Pickett, 2009). GDP is the sum of the market value of the overall set of goods and services produced by an economic system in a given period of time (generally 1 year). It can thus be intended as an indicator of the economic output.

Pulselli et al. (2015) examined 99 national economies, grouping them into eight subcubes separated by the median value of the three axes. Data are referred to the year 2008 because it was the last one available for emergy (Fig. 11.5). Most of the economies (85) fall in four of the eight possible subcubes, while the other 14 points fall in less populated subcubes, but in zones that are very close to median values of at least one of the indicators. From the results, a strong relationship between resource use per capita and GDP per capita emerges, pointing out how economic growth drives, and depends on, an increasing requirement of energy and matter to be transformed by the economic system, while the level of inequality on societies is quite independent of the other two metrics (Pulselli et al., 2015). The area of the cube where there should be nations with low level of resource use and high GDP is practically empty indicating that dematerialization is a goal hard to be reached.

The temporal dimension is a key factor of this representation: further than the ranking of the nations in 1 year, also the evolution of a single point in the diagram is meaningful to follow the behavior of a nation in time (see Fig. 11.6). This can be useful to evaluate the effects of national policies not only in economic but also in social and environmental terms (Pulselli et al., 2015).

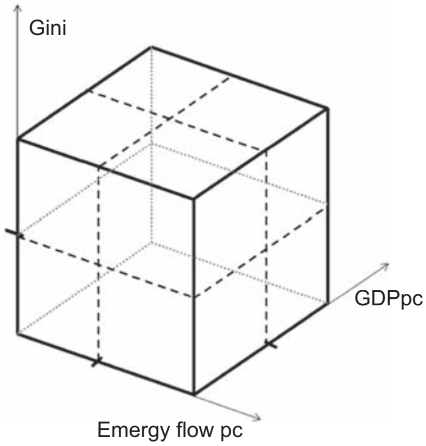

FIGURE 11.4 The cube and subcubes within which we represent the national economies.

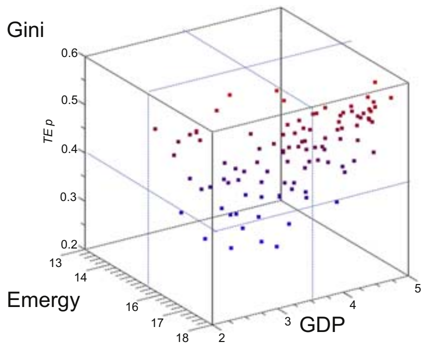

FIGURE 11.5 The 99 economies in the cube. Each segment is divided using the median value **(mettere figura giusta)**.

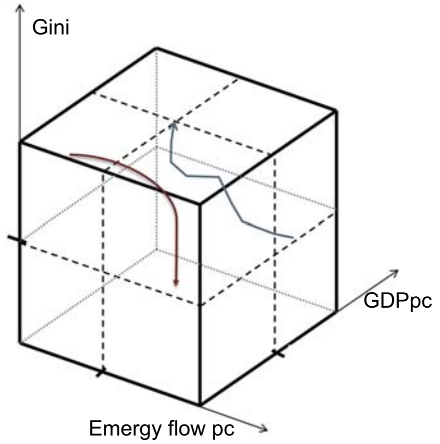

FIGURE 11.6 Evolution of a nation within the cube framework.

In fact, after the EU "beyond GDP" initiative in 2009 was taken, a number of initiatives have been implemented to complement GDP and its prominent role in policy decisions. In Italy, the BES framework (acronym for Benessere Equo e Sostenibile, that is equitable and sustainable well-being) was developed (see ISTAT and CNEL, 2013; 2014, ISTAT, 2016), "a measurement tool for progress in Italy" (Riccardini and De Rosa, 2016). As a consequence, a subset of indicators belonging to the BES framework has been selected by a Commission of experts for the Ministry of Economy and Finance (Ministero dell'Economia e delle Finanze, 2017) to guide political economic measures; this subset is constituted by greenhouse gases emissions (that is also a proxy for the environmental support required for economic production), a measure of equity and the number of jobs as well as GDP. The result of the Italian parliament and government is very much in line with the outcomes of Pulselli et al. in the choice of relevant indicators. It remains to see if they will be used and interpreted as separate issues, as in a Barbier-like scheme, or in a relational order as suggested by Pulselli et al.

A Framework for Sustainability Assessment—Trigon

Integrated environmental management characterizes and follows the development of environmental problems including, eventually, recovery processes, requires a sound diagnosis and a combination of solution methods. This implies integrating the knowledge about such problems and their causes, as well as about the ecosystems involved, which draws very much from systems ecology and ecosystem principles (Jorgensen et al., 2016).

Indeed, all types of environments worldwide are threatened as a consequence of pollution, over exploitation, and impacts of climate change, and, consequently, there is a well-identified need for approaches to sustain and, where necessary, restore ecosystems (Hughes et al., 2005). Although quite spread, the concept of *sustainable development*—seen, for instance, as "development that satisfies present needs without compromising the possibility of future generations satisfying theirs" (Brundtland, 1987)—still remains relatively nonoperational, and its application requires additional quantification from the scientific, cultural, and socioeconomic points of view, besides being necessary to take into account time, relationships, and biophysical limits (Pulselli et al., 2008).

The way human society interacts with the various needed living and nonliving natural resources, which constitute what is called natural capital, is still controversial, involving at least two main contrary perspectives regarding the conceivable practical mean of sustainability: weak and strong sustainability. Weak sustainability admits that human well-being must continue through intergenerational time scales, considering that natural capital and man-made capital can be interconverted in the scope of specific production processes (Brand, 2009). Consequently, weak sustainability also accepts the option of depleting natural capital, unless its requirement tends to decline over time (Brand, 2009). Inversely, strong sustainability takes up a complementarity between natural capital and man-made capital, assuming that the whole stock of natural capital has to be preserved for present and future generations in the long run, and therefore that human society must keep each type of capital intact over time (Brand, 2009). In any case, environmental concerns related to resource use forced the entrance of ecological sustainability into international agendas.

Ecosystem principles provide a set of useful ecological-oriented definitions to define as clearly as possible the concepts involved in creating environmental management scenarios, whose environmental ideologies and sustainability perspectives are summarized, for instance, by Jørgensen et al (2016) (see Table 11.1), although such concepts are not always used with the very same meaning, obviously depending on the field where they are applied (e.g., ecology, economics, policy, etc.).

Sustainable environmental management can only be attained if options and actions undertaken are environmentally and ecologically sustainable, economically realistic, technologically feasible, socially desirable, or at least socially tolerable, administratively manageable, legally admissible, and politically opportune (e.g., Elliott et al., 2006; Bunce et al., 2008; Mee et al., 2008; Ojeda-Martínez et al., 2009). All these aspects of ecosystems are intimately linked and are essential conditions to achieve the maintenance or even the increase of economic goods and services demanded by a developing society and simultaneously maintaining and protecting ecological goods and services; these together represent environmental goods and services (Kay et al., 1999).

Environmental restoration, for instance, is crucial nowadays and involves dealing with complex problems such as (a) losses of species diversity, habitats, and a reduction in habitats' heterogeneity and size, (b) changes in dynamics and spatial distribution of many species, as well as diminution of their population size, (c) fragmentation of habitats and associated increase in the vulnerability of the remaining isolated pouches, and (d) reduction of economically significant services and goods naturally offered by ecosystems (e.g., Elliott et al., 2007). This implies dealing with ecological theories and concepts, of which some are well understood or at least appropriately defined, like, for instance, the nature of ecosystem structure and functioning, whereas others, like resilience, carrying capacity, or ecosystem goods and services are not yet adequately quantified.

From the ecological point of view, health of ecosystems is most often assessed based on the abundances of few conspicuous (or even charismatic) species, namely birds, fishes, and marine mammals. Nevertheless, the mechanisms underlying temporal or spatial variations in abundance are frequently poorly understood, and the way changes in these species influence ecosystems as a whole is rarely addressed (Hughes et al., 2005). Ecosystem principles and its understanding are here of crucial importance. In this sense, resilience-based management constitutes an innovative and appropriate approach, providing a shift in focus from the conservation of targeted species to the active management of functional groups supporting critical processes, and the maintenance of ecosystem's services (Hughes et al., 2005). Such focus on functional groups assumes the importance of species interactions and ecological roles (including that of humans) in sustaining ecosystem's resilience through spatial and temporal scales, representing a clear change in perspective (Folke, 2006).

The resilience concept, despite its central position in sustainability science, has been suffering significant changes through the last three decades (Walker et al., 2004). In fact, there are confusions around the term. For instance, the perspective that it refers to the intrinsic capacity of a system of coming back to a prior or similar state after a disturbance, or its capacity to tolerate stressors, is often assumed (Elliott et al., 2007). Yet, there are at least three other meanings which can be found in the literature. One refers to the dynamics of close to equilibrium systems, being defined as the time necessary to their return to an equilibrium point after a disturbance, addressing therefore system's recovery. This is commonly called "engineering resilience" (Holling, 1996; Folke, 2006), being in a large extent equivalent to the stability property "elasticity" (Grimm and Wissel, 1997) or "resistance to change" (Levin and Lubchenco, 2008). A second one is defined as the capacity to absorb stress and still maintain "function," referring to the dynamics of far from any equilibrium steady-state systems, and has been called "ecological resilience" (Gunderson and Holling, 2002; Folke, 2006). It essentially corresponds to the capacity to maintain functioning in spite of the multiple stressors which may affect an evolving system (Levin and Lubchenco, 2008). This second meaning addresses

TABLE 11.1 Environmental Ideologies and Sustainability Perspectives (Nunneri et al., 2005; Turner et al., 2003; Turner, 2008; Marques et al., 2009).

Very Weak Sustainability	Weak Sustainability	Strong Sustainability	Very Strong Sustainability	
Resource exploitative, growth maximization position.	Resource conservationist and managerial position.	Resource preservationist position.	Extreme preservationist position.	
Antigreen economy; unfettered free markets; widening income inequality not problematic; free trade in international markets.	Green economy natural capitalism and new industrial systems green markets guided by economic incentive instruments (EIs) (e.g., pollution charges, etc.) in combination with voluntary agreements.	Deep green economy, steady-state economy regulated by macroenvironmental standards and supplemented by EIs and international agreements.	Very deep green economy, heavily regulated to minimize resource-take; national environmental duty of care formally regulated; extensive and binding international agreements.	Green labels
Primary economic policy objective, maximize economic growth (max gross national product) (GNP); no formal policy integration processes.	Modified economic growth (adjusted green accounting to measure GNP); formal policy integration and review on institutional structures of growth and environmental quality.	Zero economic growth; zero population growth; binding policy integration.	Reduced scale of economy and population; sustainability accounting the primary approach.	Type of economy
Taken as axiomatic that unfettered free markets in conjunction with technical progress will ensure infinite substitution possibilities capable of mitigating all local scarcity limit constraints (environmental sources and sinks); voluntary approach to environmental regulation and intervention.	Decoupling of growth and environmental quality important but infinite substitution rejected. Sustainability rules, e.g., constant natural capital rule; use efficiency and productivity; sustainability indicators; and monitoring.	Decoupling plus no increase in scale; systems perspective—health of whole ecosystems very important; overcompliance with international environmental agreements; and sustainability assessments and audits.	Scale reduction imperative; at the extreme for some there is a literal interpretation of the Gaia hypothesis with moral obligations.	Policies and management strategies
Support for traditional ethical reasoning; rights and interests of contemporary individual humans; instrumental value (e.g., recognized value to humans) in nature.	Extension of ethical reasoning: caring for others motive intergenerational and intergenerational equity (i.e., contemporary poor and future people); instrumental value in nature.	Further extension of ethical reasoning: interests of the collective take precedence over those of individual primary value of ecosystems and secondary value of component functions and services.	Acceptance of bioethics, i.e., moral rights/interests conferred on all nonhuman species and even the abiotic parts of the environment: intrinsic value in nature (i.e., valuable in its own rights regardless of human experience).	Ethics
Low level of environmental awareness in the public.	Wider public education, establishment of stakeholder groups and of, e.g., roundtables to increase inclusion.	Strong local/community awareness and action campaigns.	Cultural shifts to the maintenance of local livelihoods and environmental stewardship.	Degree of public inclusion

more the system's renewal, regeneration, or reorganization after a disturbance than its recovery (Folke, 2006), which implies the assumption that disturbances and spatial heterogeneity determine the behavior of each system to be unique. As a consequence, recovery trajectories might be difficult or impossible to predict, due to the complexity of the system combined with unexpected compounded effects of disturbance, and a recovered system may eventually look identical to the previous one but is not the same system. As any other living system, it will be continuously developing (Folke, 2006). Differences in degradation and recovery trajectories can be called system hysteresis (Elliott et al., 2007), and, in practical terms, ecological resilience can only be estimated by means of resilience proxies (Carpenter et al., 2006), which must be based on a broad resilience analysis, together with the identification of specific disturbance regimes and societal choices regarding desired ecosystem services (Brand, 2009). A third, recent definition is an extension of the ecological resilience, which puts the context of resilience into the entire adaptive cycle and a system's ability to successfully navigate this over and over through growth, conservation, collapse, and reorganization (Fath et al., 2015).

In simple terms, an ecosystem's degree of ecological resilience tends to be assumed as inversely related to its degree of threat (Brand, 2009), and therefore holding information on ecological resilience and system efficiency constitutes a prerequisite to assess whether an ecosystem will reach a critical state as a response to environmental stressors (Ulanowicz et al., 2009). Thus, a critical state regarding natural capital matches an extent in environmental degradation that exceeds a threshold beyond which the current level of social welfare cannot be supported. Such an ecological criticality appears therefore to be most important for the maintenance of ecosystems services and goods (Jax, 2005) and the sustainable use of their natural capital (Brand, 2009).

On the other hand, ecosystems and their modification as a function of human stressors must be examined accounting to their carrying capacity and its loss next to stress. Carrying capacity was originally defined as the number of individuals of a population that can be supported by a given environment without significant negative impacts to that population and that environment. This merely ecological definition does not entirely capture the multilayered processes of human–environment relationships, which have a fluid and nonequilibrium nature, perhaps neglecting the influence of external forces on environmental change (Moore et al., 2009). Indeed, carrying capacity must also be related to the social and economic aspects of ecosystems (Elliott et al., 2007), looking on which level of human activities and anthropogenic pressure can an ecosystem tolerate before undesirable changes occur, because humans' relationships with their environment are in principle more complex than those of other species with theirs (Pulselli et al., 2008). Actually, humans have the capacity to modify the type and degree of their impact on their environments and can—at the limit—decrease irreversibly environment productivity and/or radically occupy or transform space. Many species can modify the carrying capacity of their systems, but because only humans can manipulate ecosystems to such a drastic extent, the concept of carrying capacity must be expanded to include socioeconomic aspects (MacLeod and Cooper, 2005; Elliott et al., 2007).

A holistic approach to understand, manipulate, and manage the environment may be provided by linking and integrating ecosystem principles and the management framework. It is crucial to relate environmental management to the dynamics of ecosystems, namely the relations between biodiversity and ecosystem function, because ecosystems are complex adaptive systems, characterized by their historical dependency, as well as by nonlinear dynamics, threshold effects, various basins of attraction, and limited predictability (Folke et al., 2004; Duit and Galaz, 2008; Moore et al., 2009). For instance, it has been shown that estuarine ecosystem's temporal stability and biodiversity might follow different trends in relation to the systems' ecological quality status, exhibiting therefore a nonlinear relationship (Pinto et al., 2013b, 2014a), with the optimal condition (higher values) occurring for average values of species richness, which may in turn influence ecosystem services' provision. In the same estuarine system, these findings were confirmed through the analysis of food webs under distinct levels of eutrophication pressure, using mass-balanced models: a tendency for a decrease in food web connectivity was observed during a recovery process, from more eutrophic to less eutrophic conditions (Baeta et al., 2011), while the ecosystem's temporal stability tended to increase in the same period.

How can this panoply of theoretical concepts be applied in environmental management, which often involves so many uses and users, sectorial interests, and governance regimes (Costanza et al., 1998, 1999)? Aiming at the restoration or the sustainable use of a specific ecosystem, how to decide which will be the best possible course of management in a multitude of driving forces which may be conflicting? Marques et al. (2009) proposed the use a conceptual guidance tool—the ecological sustainability trigon (EST)—which may possibly be useful as a sort of compass to provide orientation in the process of building and testing management scenarios to approach environmental problems. This proposal was mostly based on ideas upcoming from the marine coastal and estuarine research but seems to be also applicable to other domains.

Using EST in Building Management Scenarios toward Ecological Sustainability

It is generally accepted that there is an intrinsic complexity in environmental problems, and also that these are closely related to the development of human society. As a consequence, possible solutions to environmental problems always require taking into account different points of view, often expressing the conflicting perceptions of multiple sectors, uses, and users (Costanza et al., 1998, 1999). Different economic scenarios (Fig. 11.7) (Turner et al., 1994, 2003; Turner, 2008) have been to a certain extent trying to address the uncertainty involved in dealing with environmental problems, and it is clear that in what way the natural or the social systems become favored will greatly depend on the different options and systems of decision (see Table 11.1). With regard to sustainability, environmental scenario analysis is therefore required as a tool to recognize and characterize central questions (Table 11.2), as well as to take decisions about priorities and solutions (Kontogianni et al., 2001, 2004; Swart et al., 2004).

Although sustainability science is complex and uncertain, it is possible to encompass all the different viewpoints and concerns in the frame of three major driving forces (Marques et al., 2009; Jorgensen et al., 2016):

a) The search for human well-being and the maintenance of human health and safety;
b) The attempt of ecological sustainability and maintenance of natural environmental well-being;
c) Systems' resilience in face of an increasing human pressure, resulting from population size and demand for wealth creation.

Certainly, it is needed to assume that research should complementarily cover these three views and simultaneously fulfill the goals of creating knowledge and wealth and improve life quality. The search for human well-being, from the governance point of view, is often endorsed as corresponding to GDP or to stakeholder benefits, which could ultimately be expressed by some sorts of metrics such as well-being indices (Diener et al., 1999; Diener, 2000) (Fig. 11.8). The straightforward societal objective has been maximizing economic goods and services, which is usually reflected in governmental approaches, and at the same time, into a certain extent, protect ecological goods and services, at least to avoid business of being accused to harm the later ones or to prevent countries from being subject to legal violation proceedings for not fulfilling rules settled in common legislation, as it is the case of the European Union Directives (Marques et al., 2009).

Sustainability indicators and composite indices have been progressively accepted as valued tools in terms of policy making and public communication with regard to environment, economy, society, or technological improvement (Singh et al., 2009), as well as to human quality of life (Diener and Tov, 2012). Nonetheless, in many cases,

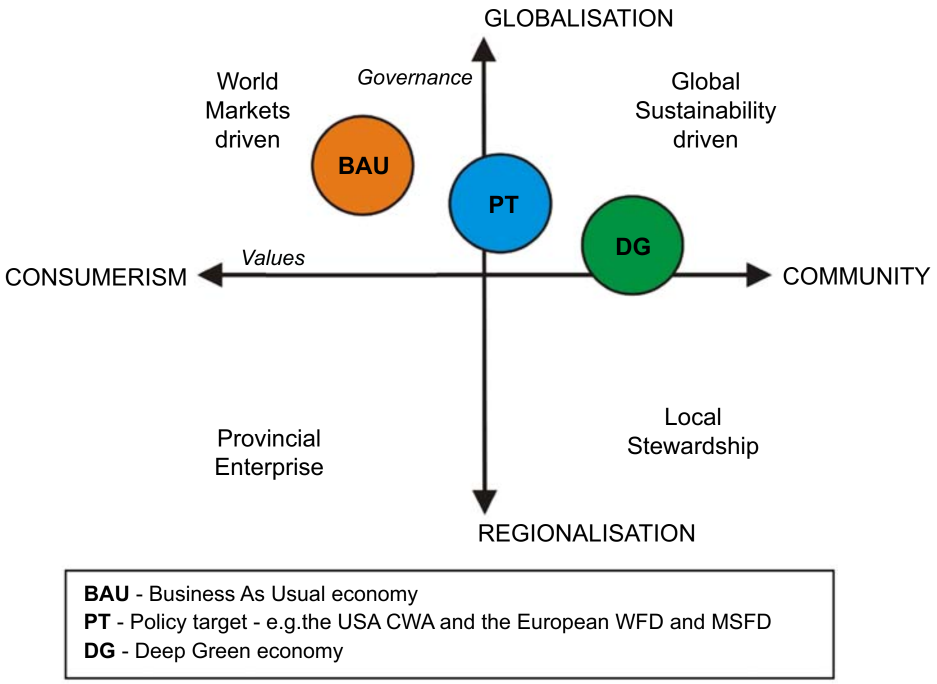

FIGURE 11.7 Different economic scenarios resulting from supporting the natural or to the social system, as a function of political decision systems. *Based on Turner, R.K., Pearce, D., Bateman, I., 1994. Environmental Economics: An Elementary Introduction. Harvester Wheatsheaf, London, 328 pp.*

TABLE 11.2 Core Questions for Sustainability Science.

1. How can the dynamic interactions between nature and human society—including time lags due to inertia—be better incorporated into emerging models and conceptualizations that integrate the global systems, human development, and sustainability?
2. How are long-term trends and widely varying spatial scales in environment and development, including consumption and population change, reshaping nature–society interactions in ways relevant to sustainability?
3. What determines the vulnerability and resilience of the nature–society system in particular kinds of places and for particular types of ecosystem and human livelihoods?
4. Can scientifically meaningful limits or boundaries be defined that would provide effective warning thresholds beyond which the nature–society systems are at a significantly increased risk of serious degradation?
5. What systems of incentive structures—including markets, rules, norms, and scientific information—can most effectively improve social capacity to guide interactions between nature and society toward more sustainable trajectories?
6. How can today's operational systems for monitoring and reporting on environmental and social conditions be integrated or extended to provide more useful guidance for efforts to achieve sustainability?
7. How can today's relatively independent activities of research, planning, observation, assessment, and decision support be better integrated into systems for adaptive engagement and societal learning?
8. How can future changes be determined and predicted in a creative, objective, rigorous, and policy-relevant manner that reflects sustainability and incorporates different perspectives?

Modified from Kates et al., 2001; Swart, R., Raskin, P., Robinson, J., 2004. The problem of the future: sustainability science and scenario analysis. Glob. Environ. Chang. 14, 137–146. https://doi.org/10.1016/j.gloenvcha.2003.10.002; Marques, J.C., Basset, A., Brey, T., Elliott, M., 2009. The ecological sustainability trigon – a proposed conceptual framework for creating and testing management scenarios. Mar. Pollut. Bull. 58, 1773–1779. https://doi.org/10.1016/j.marpolbul.2009.08.020.

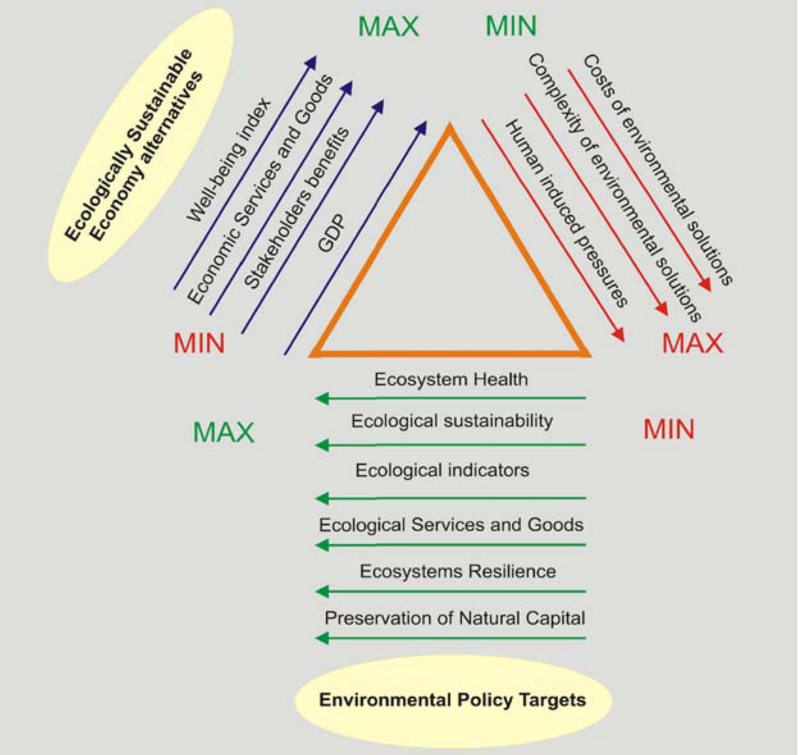

FIGURE 11.8 The ecological sustainability trigon (EST) (Marques et al., 2009) illustrating the expected trends and relationships between variables assumed to be correlated with ecological sustainability, human well-being, and human-induced pressures. The bottom and left-hand axes of the EST indicate how governance and societal systems must be linked to environmental management, namely through the definition of policy targets and the choice of ecologically sustainable economy alternatives, while the right-hand axis illustrates how increasing human pressures imply consequences on the other two axes. Green—good; red—bad.

when applied in policy, sustainability indices appear to fail in fulfilling fundamental scientific requirements, turning them somewhat useless or even confusing for policy advice (Brunner and Starkl, 2004; Böhringer and Jochem, 2007; Marques et al., 2009). However, despite difficulties in establishing unquestionable quantitative relations, the concept of environmental integrity is normally associated to the aim of ecological sustainability. Environmental integrity can be perceived from different theoretical orientations, all involving inherent uncertainties (Fig. 11.8). The panoply of tools available to evaluate environmental integrity (e.g., environmental quality indices) is vast, although probably none of those tools is entirely appropriate (Pinto et al., 2009). On the other hand, the value of integrated approaches has been illustrated (Pinto et al., 2014a), particularly through examples where the DPSIR (drivers, pressures, state change, impacts, response) approach can be related to the selected indicators (McLusky and Elliott, 2004; Aubry and Elliott, 2006; Borja et al., 2008; Gray and Elliott, 2009; Pinto et al., 2013b). Furthermore, a new interest in defining, measuring, and protecting ecosystem goods and services developed from the acknowledgment that economic prosperity depends on ecosystem functioning and that many natural ecosystems are threatened (Pinto et al., 2010).

Independently from such recognition regarding the importance of ecosystem services and goods, there are two main problems in assessing them, which are (Heal and Kristrom, 2005): (1) certain functions do not become important always at the same scale, and (2) the integration and aggregation of all temporal and spatial scales information may originate problems due to the fact that interrelations and feedback loops may operate at scales above the level being assessed (Pinto et al., 2010). A good illustration of this is the dependency of economic goods and services at one area from the successful functioning somewhere else. For instance, estuarine fish nursery grounds in one area create the conditions for the existence of marine commercial stocks in another area (McLusky and Elliott, 2004; Pinto et al., 2010). As a consequence, scaling rules attempting to describe ecosystem service's provision and delivery, especially for open and dynamic systems, still require to be quantified and defined (Limburg et al., 2002; Pinto et al., 2013a, 2014a).

The human population pressure is increasing as a consequence of population growth and the associated higher resource consumption and pollution related to the pursuit of satiating cumulative human needs. The complexity, difficulty, and intrinsic costs of solutions necessary to deal with environmental problems created by such pressure have been increasing gradually (Fig. 11.8). There is no reason to think that the needs of future generations will be different from ours in terms of quantity and quality, and therefore we may anticipate that two changes might happen as compared with today: (1) decrease in global carrying capacity and (2) decrease in the number of choices available, meaning by this both the number of different resources and our capacity to exploit them. Possibly, both in terrestrial and aquatic ecosystems, shifts in regimes in relation to resilience and the functional roles of biological diversity will occur (Folke et al., 2004; Pinto et al., 2014a), and eventually future generations may have to adapt rapidly their ways in accordance to ecosystem's sustainable management (Pinto et al., 2014b).

Another aspect includes the transformation to a society that is able to understand and implement long-term thinking into its policy and decision-making. This will require rewards to be given for different outcomes than simply short-term gain and can be promoted through collective incentives and through a new holistic paradigm. The ultimate goal is to find a situation that encourages win-win situations for humans and the environment, similar to what other organisms in the environment currently experience in their surroundings: a tree growing in the forest improves the health and quality of the forest. One recent attempt to explain this new paradigm can be found in Fiscus and Fath (2019). A key feature of this win-win approach is identifying and enhancing positive feedback loops that work in the direction of gradient formation. These positive, autocatalytic cycles are critical for the continued performance of any complex adaptive system and promote extended diversity (Ulanowicz, 2003; Hordijk and Steel, 2017; Cazolla Gatti et al., 2018).

We assume here that ecological sustainability constitutes a major goal for human society, which reflects in international agreements adopted by most countries (e.g., the Convention on Biological Diversity, Sustainable Development Goals, United Nations Framework Convention on Climate Change, etc.) and national laws approved. Nevertheless, at the present levels of human population size and associated environmental pressure, it is not conceptually possible to maximize at the same time ecological sustainability and stakeholder benefits. Still conceptually, it would eventually be possible to maximize ecological sustainability in a situation of extremely large human population size, but this would entail considerably low standards of human well-being. Of course, in the short term, we may consider maximizing stakeholders' benefits and environmental anthropogenic pressures, but only if we renounce to the goal of ecological sustainability, compromising the future in the longer run. It is clear that in this "game of possibilities," there is no conceivable scenario that allows maximizing the simultaneously ecologically sustainable solutions for human development, the search for human well-being, and environmental human-driven pressures, although a trade-off between the three might be conceptually possible. Marques et al. (2009) called

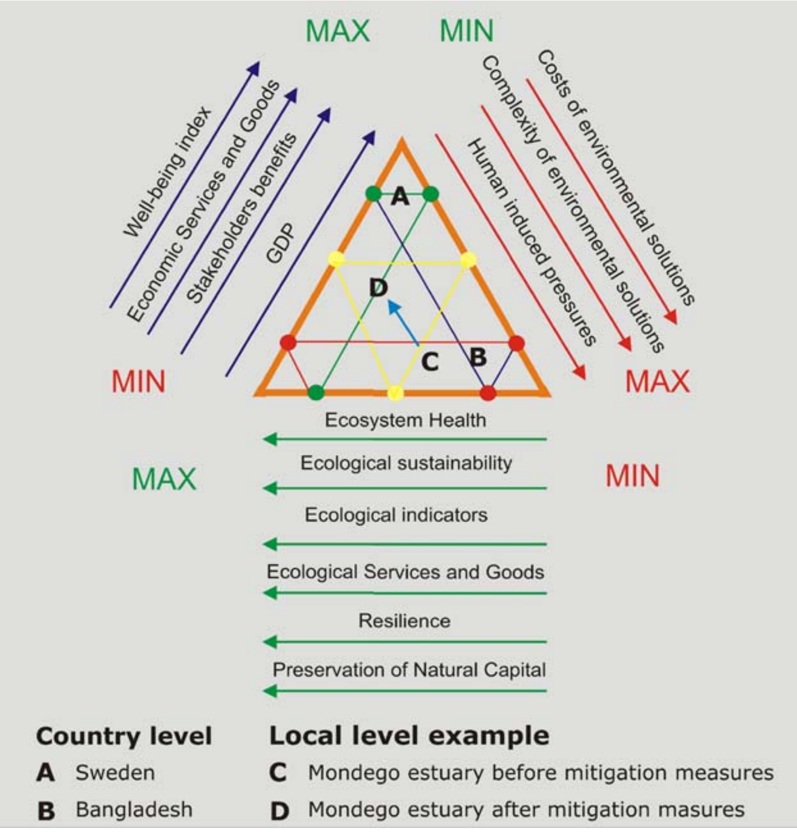

FIGURE 11.9 Proposed use of the ecological sustainability trigon in building and analyzing management scenarios: analysis of the expected variations and relationships of different indicators and variables correlated with ecological sustainability, human well-being, and human-induced pressures (see legend of Fig. 2 for details). Green—best scenario; red—worse scenario; yellow—acceptable scenario.

such trade-off the "ecological sustainability trigon" (EST) (Fig. 11.9), in which the bottom and left-hand axes indicate how governance and societal systems must be linked to environmental management to increase the chances of moving both from MIN in the direction of MAX, which constitutes the goal. The right-hand axis illustrates how increasing human pressures from MIN (best scenario) toward MAX (worth scenario) inevitably conditions the other two axes determining adverse consequences.

Different issues under discussion (indicators, objectives, pressures, etc.) can be arranged along the EST corresponding axis, which allows an immediate and intuitive rough integrated view of conceivable implications of policy or management decisions, even when processes behind relationships are not completely understood, as it is often the case in estuarine and coastal ecosystems. Furthermore, while relationships are assumed to be nonlinear, all imaginable case studies roughly correspond to a position on the EST frame. At the country scale, Sweden, for instance—a small, rich population, with good coastal ecosystem governance, few environmental problems, and a high capability to tackle those problems—would be placed approximately in position A (Fig. 11.9). On the other hand, Bangladesh, including the Sundarbans mangrove area, which have a large population and high human stress, poor funding, and badly structured governance systems to implement resolutions, large pressures on ecosystems, and solutions almost ecologically insensible, which distresses its population well-being, could come approximately to position B. At the local scale, as a result of the application of some mitigation and recovery measures aiming at dealing with eutrophication problems, the Mondego estuary, on the western coast of Portugal, which has been long last studied, showed an improvement in its ecological quality condition during the last decade, and a positive evolution of regulation and cultural ecosystem services, concomitant into a certain extent to an increase in stakeholders' benefits (Pinto et al., 2013b; 2014a). This corresponded roughly to a gradual evolution from position C to position D since the mid-1990s up to present (Fig. 11.9).

The two classic examples at the country scale plus the third one at the local scale illustrate how the EST may help decision makers (a) in identifying the links between drivers and (b) in clarifying/deciding about the best management options to convey any system closer to an optimal condition in the trigon. Independently, from the scale of the management scenario we may want to build, the EST may in principle be used as a conceptual guidance tool, which constitutes one of its most interesting features.

Obviously, we must accept that certain things can be managed and other things cannot, and consequently choices have to be made. It is regarding such choices that the EST may constitute a useful intuitive tool. Bangladesh, for instance, at least in the short term, cannot alter its population size and concomitant human pressure, but governance and environmental management could eventually be improved. Similarly, at a local-scale environmental management, some pressures can be handled, such as, for instance, in the Mondego estuary, where mitigation measures included altering the discharge of point-source polluting materials, allowing decrease in eutrophication symptoms in estuarine areas, although the general eutrophic situation in the river basin could not be yet solved (Veríssimo et at., 2013). On the other hand, climate change, as an "exogenic unmanaged pressure," is an example of something which cannot be managed. In fact, far from managing it, local managers can only respond to its consequences.

In general, it must be accepted that solving the increasing complexity of environmental problems cannot be the only condition to reconcile the difficulties in accounting for the three driving forces simultaneously (achieve and keep ecological sustainability human well-being goal, and dealing with human population/size pressure). Indeed, the benefits from pursuing a possible harmonization by implementing complex solutions will not increase linearly as a function of that complexity, as the intrinsic costs (energy and money) will plausibly become unsustainable in the long run (Fig. 11.10).

What Might Be the Advantages of Using the Ecological Sustainability Trigon?

The EST proposal (Marques et al., 2009) represented a tentative and intuitive view which has been requiring further testing and debate (Pinto et al., 2013a; 2014a; 2014b). In fact, the number of variables that must be taken into account when building management scenarios is often very high, as well as the uncertainties regarding their relationships and trends. The core problem resides in understanding into what extent interactions between given economic and ecological systems are sustainable, which involves cross-scale, transcultural, and transdisciplinary fundamental questions, calling for innovative approaches in research, in policy, and to build social institutions (Costanza et al., 1998, 1999). EST as a conceptual framework has been tested with interesting results at local level case studies (Pinto et al., 2013a; 2014a), as a kind of compass to provide orientation in building management scenarios ("In which direction do we want to go?" "How do we get there?"), alternatively to more conservative forecast scenarios ("Where are we going to?"). In fact, besides addressing adaptations to current conditions and actions to be

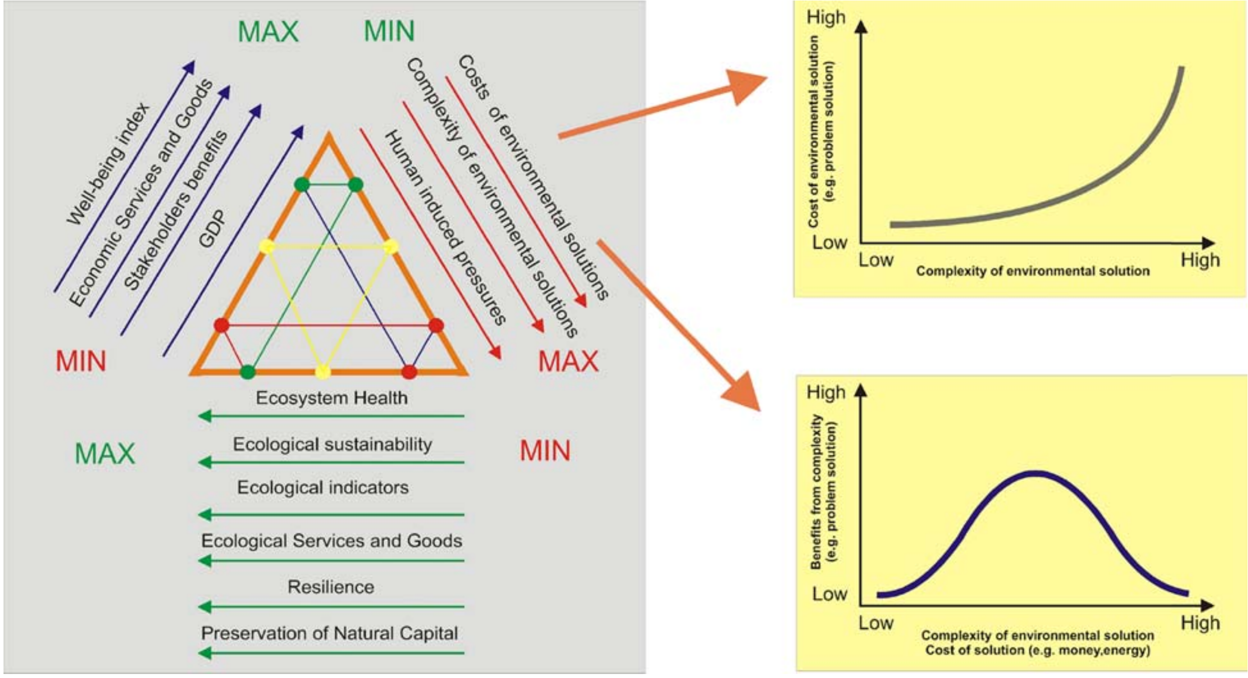

FIGURE 11.10 Proposed use of the ecological sustainability trigon in building management scenarios: expected trend in costs and benefits as a function of an increasing complexity of environmental problems solutions, namely to meet policy targets, forces the adoption of environmentally viable economic activities.

undertaken in the short term, management scenarios should also be built to accomplish transformations toward more sustainable development pathways (Folke, 2006).

As shown in Figs. 11.8—11.10, different variables whose tendencies of variation are in principle correlated can be arranged along the corresponding sides of the triangle, with their expected trends varying from maximum (MAX) to minimum (MIN). Examples of variables are provided, but many other could of course be included, which may prove particularly useful namely when policy-targeted approaches are pursued in exploring ecosystems' resources (e.g., implementing the European Water Framework Directive or the European Marine Strategy Framework Directive) (Pinto et al., 2014b).

For instance, applying governance theory, which accounts for the legal and administrative aspects of policy implementation, implies establishing hypothesis on how different governance forms can be expected to handle processes of change, which are characterized by nonlinear dynamics, threshold effects, and cascades, being therefore poorly predictable (Duit and Galaz, 2008). In addition, perhaps due to scientific uncertainty and to lack of consensus among scientists, linkages between ecological science and environmental policy are poor, which jeopardizes the transfer of science into management (Moore, 2009; Pinto et al., 2010; Borja et al., 2011). The usefulness of the EST as an orientation tool may possibly be more explored in testing governance hypotheses. Moreover, EST can also be tested in analyzing and integrating, at least approximately (especially as correlations are far from being linear), the expected variations and interactions between different variables assumed to be correlated with ecological sustainability, human well-being, and anthropogenic pressures. Namely for decision makers, these possibilities represent a great potential with regard to an intuitive clarification of what might be compliant and what is probably not compliant with the goal of sustainability, as well as in establishing possible safety margins in the "game of possibilities."

One of the advantages of the EST approach is being able to address and measure the different environmental components with a same species-specific currency, i.e., the human society view and, at the same time, of describing at the light of ecological theory our behavior, energetics (economy), and dynamics. More than ever, the incorporation of our behavior, energetics, and dynamics into an ecosystem integrity framework represents a crucial challenge for the science of ecology, which requires measures of ecological status from the ecosystem organization and functioning points of view, rather than from pressures and vulnerability. Nevertheless, the EST approach allows making the evaluation criteria for environmental management scenarios more explicit, meaning that scales should match (time and space), interactions should match (relationships), and rates should match (biophysical limits), constituting therefore a promising tool for gap analysis (information concerning knowledge lacunae), as well as to address new research questions.

Exergy and Carbon Budgets to Evaluate Sustainability

During the initiation and implementation of projects that are believed to bring our societies toward a more sustainable condition, several questions often arise. Most commonly, the questions are concerned with issues such as what is our present state? where are we at all with respects to our wishes and ambitions? and what directions should we take? After decisions have been made on carrying out a specific project and implementing certain measures, it is logical that one would ask even more questions like how are we proceeding? what was the actual effect? how far have we gone along the path toward sustainability?

These questions are not specific to any stakeholders or actors in such a process but are rather common in character and following them would be a good idea to implement a method that could lead the transition in a more generic manner. With this, we mean a common approach that would cover all situations and have the ability to translate the results of a given analysis into a "best practice."

We may in this situation introduce an understanding of our societal systems in a manner that includes three major subsystems that each need to be preserved and ensured for our sustainability in the future, namely adequate, sufficient supplies of food, energy, and water. It is important to notice that these subsystems are highly interlinked, and the coupled system is often referred to as a NEXUS. The problems related to preserving them all and at best in an optimal manner is known as NEXUS problems (Beck and Villarroel Walker, 2013; Vora et al., 2017).

Furthermore, the subsystems are somehow strongly dependent on physico-geographical conditions and therefore it is impossible to point out specific, optimal solutions to all areas of the globe. The conditions vary so much that there is no chance that "one size will fit all," so we will face a problem of finding a variety of solutions that all may be applicable but with various degrees of importance, ways, and degrees of coupling. Solutions are specific and nongeneric, only methods may be generic in this case.

The overall aims of the method will be at least three:

1) The method should allow us to tell about the state of the system and allow us to monitor our system with respect to eventual progress or degression as consequence of initiatives
2) It should allow us to transgress the problems of the various elements of the NEXUS, i.e., to bring all elements in the same currency
3) It should allow to give sensible and pragmatic indications on where, when, and how to take action—in particular when combined with economic considerations to reach the maximum impact on improving sustainability

The combined considerations on technological feasibility and impact on efficiency on one hand and the economic gains and socioecological impact on the other are important in identifying what is often political language referred to as "the lowest hanging fruits."

In many cases, having such knowledge will provide us with a deeper insight—a secondary and positive side effect.

Unifying Matter and Energy

Following the previous, we need a method that allows us to combine both matter and energy to evaluate where and it makes most sense to implement changes to our systems, or if it makes sense to make the changes at all.

The physical concept of exergy is believed to provide us with much information in the above directions. It gives us an idea not only of energy used but also tells us about the energy's capacity to do work. By indicating the quality of energy, we get the information whether a given amount of energy could or should have been used for something else. A primary strength is that it also applies directly to matter because raw materials and other chemical compounds used in our society also possess an exergy value corresponding to the content of free chemical energy.

What happens during the consumption of both energy and matter in our society is that exergy is broken down, destroyed, or dissipated—what term one prefers to use to describe the imperative of the second law of thermodynamics, that all energy conversions have the price in terms of part of the energy being lost and converted into entropy. Meanwhile, for optimization, it is exactly the amounts used and lost that are interesting. Are the high amounts of inputs really necessary? Are the high dissipative losses really necessary? Or do we already know ways to do the things with higher efficiency? Is better technology available?

Deconstruction of Society for Analysis

Implicit in the above questions is that all parts of human life are not equally important: some are more fundamental, others are luxuries; some are more short term, and others have lasting shadows across space and time. The NEXUS perspective takes an entrance point in shaping the basic material-energetic part of our everyday life in society. Water is vital for drinking, irrigation, and many production processes. Energy may be provided by using various chemical compounds of high exergy density and is needed for heating, cooking, transportation, and for industry to provide us all with various goods and services. Food production needs both energy and water. Historically, these two factors have been delivered to agriculture mostly by renewable resources (as ecosystem services from the soil formation, hydrological cycle, solar radiation, and biological pollination, to name a few), but modern conventional agriculture subsidizes these renewable flows with impressive amounts of fossil fuels and fossil water.

All together, it is difficult to tell exactly where one should put the greatest efforts in increasing the efficiencies. Is it through optimization in industry through greener technology, cleaner production, or industrial ecology, or is it merely by changing and decreasing existing consumption patterns? How do we decrease the need for destroying the landscape due to increasing demands from population and consumption pressures?

Actually, we need to have better information about all sectors that are involved in shaping our living conditions. To achieve this, we propose to acquire knowledge regarding the exergy flows through a set of basic sectors to which our activities belong, including the following (Fig. 11.11):

1) The energy sector—electricity, heating, and transportation
2) A public sector that represents all buildings and consumption in our societal infrastructure
3) A private sector that represents our residences and domestic consumption herein
4) An industrial sector that provides us with all goods and services (other than the ones related directly to energy or agriculture)
5) A "natural resources" sector that builds on our exploitation of terrestrial and aquatic systems, such as agriculture, forestry, and fisheries
6) A waste sector that really is a measure of wealth and all the above sectors contribute to it

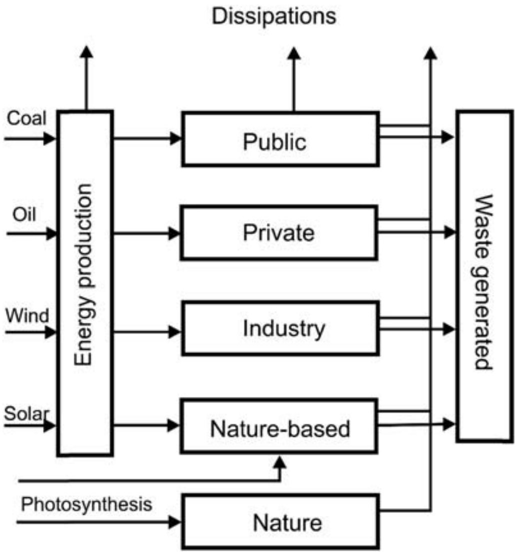

FIGURE 11.11 How exergies are driving and converted in our society. Fossil fuels and renewable energy sources are converted mainly into electricity and heat passed on to all anthropogenic sectors. Industries include all activities from production proper to commercial trade. Natural resources (termed nature—based in the figure) sector represents all activities that are based on a seminatural function of ecosystem.

7) A natural sector or Nature "per se"—a set of our environment that exists and functions with a relatively low human impact

Nielsen and Jørgensen (2015) use this conceptual framing as well as a recent study by Skytt et al. (in print). In the latter, they point out that transport makes up a large part of our energy consumption and that splitting up this activity on particular sectors makes it difficult to decide exactly where action should be taken in future.

To simplify the case of either the society or the individual sectors—and analyze the "sustainability state"—it is useful to provide data on inflows and outflows but also the stored exergies of the sector (Fig. 11.12). At the same time, inflows and outflows are split in

1) Energy flows from renewable resources
2) Energy flows from nonrenewable resources
3) Material flows from renewable resources
4) Material flows from nonrenewable resources

In the same manner, outflows may be distinguished. For energy, it might be useful to know if the energy leaving is still of high exergy value or if it is no value any longer. For matter, the potential for recycling and reusing is interesting, but one should consider that the required additional energy is needed for upgrading that is inherent in principles like "cradle-to-cradle" or "circular economy." The best solution is coupling processes efficiently together such that the wheels spinning on one help drive the other, thereby reducing or eliminating wasteful expenditures. For example, driving in one's car several kilometers to recycle one aluminum can is energetically a loser (regardless

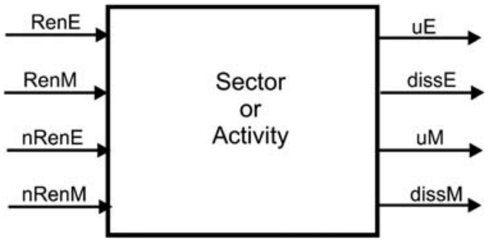

FIGURE 11.12 The conversion of energy and matter within a sector, where it is either accumulated in the sector or exported as either useful or dissipated (nonuseful) amounts of energy and matter. Matter is considered to be dissipated when exergy expenditures exceed exergy used in the recycling process.

of what the price of gasoline or aluminum is), but if recycling is done in an integrated fashion, then possible win-win scenarios may emerge.

Indicating a Sustainability State

Having established balances of energy and matter flow in accordance to the description above, several obvious ways to establish indicators of sustainability emerge, such as

1) Exergy balance
2) Ratio or fraction of renewables expressed as exergies
3) Structural costs in terms of exergy

Exergy balance: In principle, the change in structure of the system should be higher than zero meaning that society builds up its infrastructure. But again, the system should, in principle, maximize its output. At the same time, the difference between input of exergy and output of dissipated/destroyed exergy should decrease pointing at increased efficiency.

Infrastructure efficiency: The same structure or increasing structure should be maintained for a decreasing input, i.e., more structure, goods, and services have been provided for less expenses, again pointing at increases in efficiency and related to the previous. For more details, see Nielsen and Jørgensen, 2015.

Society should increasingly be based on renewable resources. This could be expressed as a share of either (1) the ratio of renewable exergy to nonrenewable exergy or the fraction of renewable exergy out of the total exergy intake.

Concerning the carbon budget—it is easy to establish a positive balance due to ecosystem services through photosynthesis—at least for a rural society. When population density becomes higher, with more and more people such as in urban areas and with the corresponding decreasing importance of a “natural” component, it seems almost impossible to establish a positive carbon balance (higher uptake that emission). Meanwhile, both types of systems should share the same goal namely a decreasing per capita emission in terms of CO_2 equivalents. For more details, see Jørgensen and Nielsen, 2014.

11.4 CONCLUSIONS

A new way of thinking is needed in environmental management. First of all, we need a management approach which presumes an intrinsic value for nature and that nature also provides unsubstitutable services, being it (1) renewable energies in the form of solar radiation, (2) diverse and productive ecological systems, (3) geophysical resources such as fossil fuels, metals, or other material, (4) life-giving water and climate, and (5) recreational, psychological, and spiritual experiences.

All of these perspectives are included in the visions of sustainability. Meanwhile, it is necessary to base management on the biophysical components otherwise neither societal nor economic sustainability will be achieved. In other words, socioecological management needs to be based on the concept of strong sustainability as none of the other forms will be fully exchangeable to environmental sustainability, i.e., no money can replace biodiversity and adjacent losses in functionality, no government can replace hierarchical structures and cybernetics of nature.

Hence, we need to redefine management taking into consideration all the above features of natural functions identified above and incorporate the considerations in elaborations of policy formulations and planning of measure. Then, and only then, we may be able to achieve sustainable development. The ecological principles advanced throughout this book are the starting point for that effort.

CHAPTER

12

Conclusions and Final Remarks

12.1 ARE FUNDAMENTAL ECOLOGICAL PROPERTIES NEEDED TO EXPLAIN OUR OBSERVATIONS?

Take a walk on a pleasant May day in a Chinese temperate deciduous forest, visit the Serengeti National Park in Tanzania when the wildebeests are migrating North, paddle a canoe through a North American wetland, or hike the alpine tundra of Austria, whatever your preference, you will be impressed by the diversity and beauty that nature offers to you. We know that the diversity of nature is enormous, in terms of ecosystems, species, genetics, and biochemistry. For example, focusing just on species richness, we can find on the order of 10^7 different species on earth. We also have a fairly good image of evolution from 3.8 billion years ago when the first primitive life-environment processes emerged and evolved to the level of our own species, *Homo sapiens*, in possession of modern, advanced technologies: medicines, airplanes, industrial nitrogen fixation, Internet, and so on. From one perspective, we know that all the resources we have and utilize originate from nature and end up back in nature as a throughflow supporting modern civilization (as is being measured in new fields such as urban metabolism, industrial ecology, life cycle analysis, etc.). But in addition to this ultimate dependency, we could also turn the question around and ask: which properties do ecosystems have that explain the diversity, adaptability, and beauty of nature and evolution? How can we explain that the interactions between matter, energy, and information lead to the complex web of life-environment processes on earth, as we observe? We definitely do not need an intelligent designer to come up with a clear and fully acceptable explanation. This book presents an overview of what systems-based, thermodynamic properties are known to underpin this natural growth and development, and by extension the emergence of human agency and actions.

12.2 PREVIOUS ATTEMPTS TO PRESENT AN ECOSYSTEM THEORY

Previously, various attempts have been made to present an ecosystem theory that could be applied to explain quantitatively ecosystem constituting elements, processes, and regulation as well as their respective responses to disturbance and changing impacts. While we cannot cover all the attempts here, we focus on a few based-on systems perspectives and thermodynamics.

One of the early pioneers in Systems Ecology, Kenneth E.F. Watt, proposed his theory in the important work *Ecology and Resource Management* in 1968, which opened the way for greater systems thinking in ecology. In the 1970s, B.C. Patten edited four volumes with the title *Systems Analysis and Simulation in Ecology.* These volumes gave the state of the art of and were a useful reference in systems ecology. Taken together, these volumes comprised an early attempt to develop an ecosystem theory. During the 1980s, a number of scientists contributed to further developing ecosystem theory: H.T. Odum, R.E. Ulanowicz, B.C. Patten, R. Margalef, C.S. Holling, and S.E. Jørgensen, to mention a few. H.T. Odum's book from this period, *Systems Ecology: An Introduction*, is probably one of the best attempts to make a comprehensive ecosystem theory. The discussion of hierarchy theory, allometry, and scaling problems in the 1980s should also be mentioned. T.F.H. Allen and T.B. Starr in their book *Hierarchy, Perspectives for Ecological Complexity* (1982) and R.V. O'Neill, D.L. De Angelis, J.B. Waide, and T.F.H. Allen in the book *A Hierarchical Concept of Ecosystems* (1986) presented hierarchy theory and made it an almost fully accepted part of ecosystem theory. Peters'(1983) publication of many allometric principles should also be mentioned in this context. Polunin (1986) edited a book titled *Ecosystem theory and application,* which was an early attempt to apply ecological theory to address some of the global environmental issues of the day. The 1980s and early 1990s saw a lot of interest in the Stream

https://doi.org/10.1016/B978-0-444-63757-4.00012-7

Ecosystem Theory (e.g., Cummins et al., 1984; Minshall et al., 1985; Minshall, 1988; Wiley et al., 1990) which focused on streams as open systems, controlled primarily by their allochthonous riparian input.

In 1992, S.E. Jørgensen gave an overview of these contributions in his book *Integration of Ecosystem Theories: A Pattern*. The various contributions to an ecosystem theory were very different, but a closer study of the proposed theories revealed that they actually were different angles and covering different aspects, but largely were consistent, complementary, and formed as the title of the book indicates a pattern. H.T. Odum's theoretical contributions to systems ecology were summarized by C.A.S. Hall (1995) in the book *Maximum Power: the Ideas and Applications of H.T. Odum*. R. Margalef's (1997) book *Our Biosphere* summarized his contributions to systems ecology. It was based on a well-balanced mix of thermodynamics and ecology. *Macroecology* by J.H. Brown (1995) presented from this period a quantitative ecological attempt to explain biogeophysical observations, and Reynolds (1997) expanded his ideas on theory describing aquatic habitats.

Patten and Jørgensen (1995) edited the book *Complex Ecology: The Part-Whole Relation in Ecosystems* in which 31 systems ecologists contributed, presenting a wide overview of many different approaches and viewpoints, from quantum considerations, to modeling theory, to network theory, to cybernetics and thermodynamics. Furthermore, Jørgensen, Patten, and Straškraba published a series of papers in the journal *Ecological Modeling* under the title "Ecosystems Emerging." The paper subtitles to date are (1) Introduction, (2) Conservation, (3) Dissipation, (4) Openness, (5) Growth, and (6) Differentiation. The remaining papers originally planned included (7) Constraints, (8) Adaptation, (9) Coherence, and (10) Applications. Similar to this book, these papers are rooted in thermodynamic laws and basic properties of ecosystems.

Coming from a more biogeochemical perspective, Ågren and Bosatta (1996) published *Theoretical Ecosystem Ecology: Understanding Element Cycles*, which put emphasis on the importance of carbon and nitrogen cycling in ecosystems and is a commonly used textbook in this field.

In 2001, Jørgensen and Marques published "Thermodynamics and systems theory, case studies from hydrobiology" (Hydrobiologia 445, 1—10). The paper claimed that ecosystem laws could be developed and applied similarly to the application of physical laws in physics. Similarly, the December 2002 issue of the journal *Ecological Modelling* (volume 158: 3) was based on nine papers by different authors invited to show that we could explain theoretically many papers published in ecology, which themselves were presented as observations or rules without any theoretical basis. The nine papers were a successful attempt to explain theoretically the phenomenological behavior observed in ecology.

In 2004, Jørgensen and Svirezhev published *Towards a Thermodynamic Theory for Ecosystems*. The book covered a major part of the ecosystem theory because thermodynamics is the foundation for understanding many ecosystem processes. Thermodynamics is, however, a difficult scientific discipline to understand, which unfortunately prevents wider application. The presented theory is, however, coherent and is able to explain many ecological observations. The book is important as it links the traditional thermodynamics normally dealing with ideal gases to this new domain of a more macroscopic understanding of the energetic relations between elements quite different from molecules (Nielsen, in print).

To claim that we have laws providing precise predictive capacity is a simplification in the sense that ecosystem laws inevitably will be different from physical laws due to the complexity of ecosystems compared with physical systems. Expressed differently, it will be much harder to formulate causality in ecology than in physics, the heterogeneity of ecosystems simply opens up to a world of multiple causalities to be possible and realized, but there seems no doubt that ecosystems also have some general *properties* that can be applied to make predictions and understand ecosystems' responses to perturbations. Therefore, the focus in this book has been on the deduction of generalities in processes, properties, and patterns between the many types of ecosystems.

12.3 RECAPITULATION OF THE PHENOMENOLOGICAL ECOSYSTEM THEORY

This theory integrates and extends the abovementioned initiatives, building on those contributions. As stated in the first chapter and carried throughout the book, the Ecosystem Theory presented here rests on seven basic principles we observe in ecosystems:

1) Ecosystems have thermodynamic openness,
2) Ecosystems have ontic openness,
3) Ecosystems have directional development,
4) Ecosystems have connectivity,

5) Ecosystems have hierarchic organization,
6) Ecosystems have complex dynamics: growth and development, and
7) Ecosystems have complex dynamics: disturbance and decay.

Physical—chemical systems can usually be described by matter and energy relations, while biological systems in addition need to include information relations. Biological systems can be characterized using four growth and development forms: (1) increase of material across the system boundary, (2) structural (biomass) growth, (3) network growth and development, and (4) information growth and development. Note the difference between growth and development: growth terms are quantitative and extensive, while development aspects are qualitative and intensive. Both occur within an ecosystem (and also in socioeconomic systems, which is a story for another book). The last two forms give complex systems, including ecosystems, possibilities to move further from thermodynamic equilibrium under the same resource flow constraints. This ability to utilize energy flows to create and maintain structure and functioning is referred to in Chapter 1 as the physically driven biological aspect. Moreover, the synergistic effects of networks give ecosystems the possibility to utilize available resources better (see Chapter 4), and thereby move further away from equilibrium. In addition to purely physical driven energetic considerations, ecological systems are adapting and evolving, which is the principle of biologically driven biological aspect. Through evolution, genetic, biochemical, environmental, and cultural information yields better utilization of the available resources to move the system still further from equilibrium. While material biomass growth form is conservation limited, network and information development are not and are far from their possible limits.

It was demonstrated in Chapter 9 that the seven ecosystem properties presented in Chapters 2—8 can be applied to explain a number of ecosystem rules and observations. We do not propose that we have a complete or finished theory (no scientific discipline has a complete theory), but one that is adequate to explain many of our observations and may have practical value in addressing our many environmental symptoms. Chapters 10 and 11 show that the theory can be applied to assess ecosystem indicators useful in environmental management.

12.4 ARE THERE BASIC ECOSYSTEM PRINCIPLES?

Jørgensen and Fath (2004a) have discussed eight basic principles of ecosystems, their properties and processes, and later Jørgensen (2006, Jørgensen et al., 2007) added two more. Here, as stated in Chapter 1, we hone this down to nine key principles, which are implicitly covered by the general phenomenological properties of ecosystems in Chapters 2—8. To the extent possible, we will mention how each of the principles are rooted in the seven ecosystem properties presented in Section 12.3. Interpretation of the principles has, however, to be subject to the recognition that ecosystems are ontically open—too complex to allow accurate and complete predictions in all details. Nevertheless, let us try to set up the principles because they can, together with the properties presented in Chapters 2—8 and applied in Chapters 9—11, suggest new avenues to understand ecosystems. Our research and experience have converged on this list of nine basic ecosystem principles:

1. *Mass and energy are conserved.* This principle is used again and again in ecology since it allows one to write balance equations at the core of ecosystem modeling, such as with a basic box-and-arrow diagram in which change in mass or energy = input—output.
2. *All ecosystem processes are dissipative and therefore irreversible* (this is probably the most useful articulation of the second law of thermodynamics). Environmental systems are open systems, embedded in an environment from which they receive energy—matter input and to which they also discharge energy—matter output. This relates to property 1, thus requiring open systems to recharge and replenish the dissipated energy, and also contributes to the eventual collapse and decay of ecosystems described in property 7.
3. *All life uses largely the same biochemical constituents and processes.* This simply states the relevance of many biochemical compounds which can be found in all living organisms. They have therefore almost the same elemental composition derived from about 25 elements (Morowitz, 1968) where the "six-pack" of C, H, N, O, P, and S plays the central role. This principle is widely used when stoichiometric calculations are made in ecology, i.e., an approximate average composition way to express the Second Law of Thermodynamics in ecology.
This principle establishes a dependence between the ecosystem and its reliable, external of living matter is applied.

4. *An ecosystem uses surplus energy to move further away from thermodynamic equilibrium (physically driven biological aspect).* As an open system, and as described in detail throughout this book, the ecosystem uses the energy flows to create and maintain complex structures and functions. This accords with the idea of directional development (Property 3).
5. *Ecosystems coevolve and adapt to prevailing conditions (biologically driven biological aspect).* Evolution and directionality, implicit in autocatalysis, can only be understood in light of the irreversibility principle rooted in the Second Law of Thermodynamics. Evolution is a stepwise, path-dependent development based on previously achieved outcomes for surviving in a changeable and very dynamic world (contributes to Properties 3 and 6).
6. *Ecosystems have diversity of structure and function.* Due to the principles above, planetary development has moved in the direction of ever more complexity and diversity in terms of the type and kind of life—environment interactions at all scales. This leads us to the next principle.
7. *Ecosystems have many levels of organization and operate hierarchically.* This principle is used again and again when ecosystems are described: atoms, molecules, proteins, genes, cells, organs, organisms, populations, communities, ecosystems, biomes, and the ecosphere (Property 5).
8. *Ecosystems work together in networks that improve the resource flow utilization.* Simply put, this states that connectivity is a basic property that, through transactions and relations, binds ecosystem parts together as an interacting and often integrated and interdependent system. Both observations and ecological network analysis show the synergistic effect of these interactions: an ecosystem is more than the sum of its parts (Property 4).
9. *Ecosystems have an enormous amount of genetic, biochemical, and process information.* As a result of the above principles, ecosystems are rich with information contained in the genetic codes, but also the chemical interactions and ecological structure and functioning. This summarizes many of the properties expressed throughout the book and is key to ecosystem sustainability.

As seen from this short overview of the nine principles, they may be considered a useful organization of the basic systems ecology needed to understand the ecosystem reactions and processes.

We, the nine authors, conclude that we do have a workable ecosystem theory that can be presented in different ways but under all circumstances can be used to explain and understand ecological observations, properties, and processes (Chapter 8) and even be applied in environmental management (Chapters 10 and 11). The theory should be considered an early attempt to present working hypotheses about how ecosystems function from a thermodynamic and complex systems perspective. Ecology is not just an accounting of the abundance and distribution of species, but rather a science that investigates the interrelations and interconnections between life and environment. The principles described herein most likely will be changed in the coming years as we gain experience by using it. We welcome collaboration and criticism to help further improve these ideas, particularly to develop good strategies for ecosystem management.

12.5 CONCLUSION

The earth is a nonisolated system. There is almost no exchange of matter with outer space (the earth loses a little hydrogen and receives meteorites). The matter on earth is reused and recycled many times on times scales as different as organismal, ecological, and geological. The rate of decomposition in cycling implies that the ecosystem components are linked in an interacting network (Chapter 4).

Ecosystems must be, as the earth, nonisolated because otherwise they could not receive the energy needed to maintain them far from thermodynamic equilibrium and even move further away from thermodynamic equilibrium. Ecosystems are actually open systems (Chapter 2) because they need to exchange at least water (precipitation and evaporation) with their environment. In addition, it is practical that evolutionary adaptations in one ecosystem can be exported to other ecosystems (for instance, species with new emergent properties that facilitate survival under a combination of new and emergent conditions). Moreover, it is easy to observe that ecosystems *are* open systems.

The flow of energy from the sun to the ecosystems is also limited. It is important that an ecosystem captures as much sunlight as possible to supply its energy needs. Therefore, in early stages of succession, ecosystems increase biomass to increase net primary productivity. However, even the best photosystems can only capture a certain part of the solar radiation, which is limited to about 10^{17} W on average. Therefore, moving further away from thermodynamic equilibrium requires that an ecosystem develop better utilization of the usable work capacity that it is able to capture. Network development, where the interdependent components coevolve together, provides improved efficiencies. Another possibility is to increase information in the form of better process efficiencies. Increased sizes of the organisms also imply that the work energy capacity lost for respiration decreases relatively to the biomass. While matter and energy flow limit growth, the amount of information is far from its limit. Therefore, it is understandable that information embodied in genes and in ecological networks has increased throughout evolution.

The development of life on earth has been possible because of the presence of the necessary elements to build the biochemical compounds that support life. These include water that is essential to most life and an ideal solvent for most biochemical reactions. In addition, the earth has a suitable temperature range such that the biochemical reactions proceed with a certain rate and decomposition of particularly proteins is moderate. These conditions provide the right balance between formation and destruction of high molecular weight proteins that are the enzymatic compounds controlling life processes.

Life-environment processes take place in cells because they have a sufficiently high specific surface to allow an exchange rate with the environment that is suitable. Cells are therefore the biological units that make up organs and organisms. Nature must therefore use a hierarchical construction: atoms, molecules, cells, organs, organisms, populations, communities, ecosystems, and the ecosphere. The addition of units in one hierarchical level to form the next level gives the next level new and emergent properties.

The variability of life's conditions in time and space is very high. When an ecosystem has adapted to certain conditions, it can still be disturbed by catastrophic events. Ecosystems have the adaptability and flexibility to meet these changed conditions and still maintain their systems far from thermodynamic equilibrium. The disturbances call for new and creative solutions for life to survive. Disturbances may therefore also be beneficial in the long term for ecosystems.

We can explain ecosystem processes, responses, and evolution with the principles and hypotheses presented in this book. The discussion throughout the book has tried to show that the principles are sufficient and the discussion in this last section has demonstrated that the properties are also necessary. It may, however, not be the only possible explanation of life in general. We cannot exclude that we will find other life forms somewhere else in the universe, for instance, based on silica or based on carbon but with another biochemistry, better suited for a different situation. However, the properties presented above are very consistent with both direct and indirect observations, which render them a good basis for an ecosystem theory applicable on Earth. Chapters 9—11 have shown that the ecosystem theory presented in this book can be used to explain other ecological rules and hypotheses and have potential for application in environmental management, which hopefully can inform our quest to manage our planet toward sustainability.

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