

Succession

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Introduction

This article explores the notion of ecological succession, one of ecology's oldest and most controversial concepts. Simply stated, succession is the orderly changes in communities of a specific place over a period of time. More formally, it is the orderly progression of directional community development that results from modification of the physical environment by the community and culminates in an ecosystem in which maximum biomass and interactions among component organisms are maintained. Many workers relate succession to disturbance (fires, hurricanes, drought, etc.), such that succession refers to changes in a community after a perturbation opens up ecospace. Most of the earlier work on succession (dating back to 1899!) described the sequential invasion of species invading a particular site; later studies deal with a whole range of community characteristics from both empirical and theoretical standpoints (Table 1). Most of the work on succession has been dominated by forest communities, but successional studies also exist for a number of other ecosystems including benthic and pelagic marine ecosystems.

Different Kinds of Succession

Two kinds of succession have been proposed. 'Autogenic' succession refers to sequential changes in the community that are brought about by the influence and activities of the organisms themselves upon the environment or habitat. 'Allogenic' succession occurs to communities through the influence of factors external to the organisms themselves. The utility of allogenic succession may be limited because it may be too broadly applicable to any temporally repetitive change. Most of the debates surrounding succession, and studies which provide detailed examples are concerned with autogenic succession.

'Primary' succession refers to the colonization of sites where a severe disturbance has left no trace of the preexisting community, or where entirely new ecospace has been created. These might include a terrestrial or submarine lava flow, glacial recession, or the movement of submarine or subaerial sand dunes. Harsh environments usually characterize the earliest phases of primary succession, and communities tend to develop more slowly than with more minor disturbances to the ecosystem. 'Secondary' succession refers to colonization of sites which did have a previous community established, but a perturbation has removed a portion of it or all of it over a limited area. Here again, much of the debate surrounding succession and most of its examples come from secondary succession. However, most unassailable instances of succession are examples of primary succession.

Expected Community Trends of Succession

The expected community trends of succession are explicit and detailed (Table 1). They rely on an early-successional community that ultimately leads to the 'climax' community, or the most stable state for the successional sequence. This climax community is maintained until an extrinsic disturbance resets the successional clock. The attributes are grouped according to community energetics, community structure, life-history characteristics, cycling of nutrients, selection pressure, and overall homeostasis. These trends follow from the notion that the climax community is a steady state maintained by internal feedback control mechanisms. But they break down if it is not, and there is little evidence so far that they are.

In forests there are a variety of aspects of production ecology which vary over the successional sequence including forest floor depth, chemistry and content of decaying wood, nutrient availability, leaf area, carbon allocation, species composition and their nutritional adaptations, the relative roles of trees and minor vegetation, the relative importance of geochemical, biogeochemical and internal cycles, rate of soil organic matter accumulation, and total ecosystem organic matter. Early-successional forest species generally are shade intolerant, require a mineral seedbed, may be fast-growing, can generally utilize nutrients that occur in newly formed gaps, may be nitrogen-fixing, are tolerant of microhabitats in newly disturbed settings, and are superior competitors in such settings. Late-successional forest species generally are shade tolerant where they are able to grow slowly, may require a more organic seedbed, and are generally poorly adapted to newly disturbed settings where they are poor competitors. Nutrients are generally gained from litter decomposition and mycorrhizae.

Models of Succession

Three alternative models have been proposed for determining the sequence of species that might occur after a perturbation. The first is the facilitation model in which only certain species ('early successional') are able to arrive immediately following a

Table 1 Predicted changes that occur in major structural and functional characteristics of a developing ecosystem during ecological succession

<i>Ecosystem attributes</i>	<i>Developmental stages</i>	<i>Mature stages</i>
<i>Community energetics</i>		
1. Gross production/community respiration (<i>P/R</i> ratio)	Greater or less than 1	Approaches 1
2. Gross production/standing crop biomass (<i>P/B</i> ratio)	High	Low
3. Biomass supported/unit energy flow (<i>B/E</i> ratio)	Low	High
4. Net community production (yield)	High	Low
5. Food chains	Linear, predominantly grazing	Weblike, predominantly detritus
<i>Community structure</i>		
6. Total organic matter	Small	Large
7. Inorganic nutrients	Extrabiotic	Intrabiotic
8. Species diversity – variety component	Low	High
9. Species diversity – equitability component	Low	High
10. Biochemical diversity	Low	High
11. Stratification and spatial heterogeneity (pattern diversity)	Poorly organized	Well-organized
<i>Life history</i>		
12. Niche specialization	Broad	Narrow
13. Size of organism	Small	Large
14. Life cycles	Short, simple	Long, complex
<i>Nutrient cycling</i>		
15. Mineral cycles	Open	Closed
16. Nutrient exchange rate, between organisms and environment	Rapid	Slow
17. Role of detritus in nutrient regeneration	Unimportant	Important
<i>Selection pressure</i>		
18. Growth form	For rapid growth (' γ -selection')	For feedback control (' K -selection')
19. Production	Quantity	Quality
<i>Overall homeostasis</i>		
20. Internal symbiosis	Undeveloped	Developed
21. Nutrient conservation	Poor	Good
22. Stability (resistance to external perturbations)	Poor	Good
23. Entropy	High	Low
24. Information	Low	High

Analysis of these parameters provides empirical tests of the expected development of ecosystems during succession.

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disturbance. The most important factor governing succession in the facilitation model is the degree to which early-successional species alter the environment for later-successional species. Later species can only colonize after these early-successional species have sufficiently modified the environmental conditions. For example, in forest communities the amount of net primary production of the plant community will influence its ability to alter the site. This model implies a high degree of organization in ecological communities. However, it may still operate in communities where such organization is not apparent, for example, in heterotrophic successions or primary successions.

The second is the tolerance model in which the sequence of species to inhabit an ecosystem after a disturbance is determined exclusively by their life-history characteristics. The species that occur are simply those that are most efficient in exploiting resources in a given time or place. Thus, the success of later species is unrelated to the species composition of the earlier community. Two circumstances have been forwarded where this model of succession might be most prevalent. The first is with certain groups of animals, such as large vertebrates or insects that display a high degree of social integration, that have evolved a high degree of independence from both biotic and physical environments. The second is in situations where populations are limited more by resources than natural enemies or environmental stress. In the tolerance model, life-history characteristics such as the relative longevity, growth form, reproductive mode, and size of the early versus later species becomes paramount. A further elaboration of this model is given below in the section titled 'The role of competition and life history'.

The third is the inhibition model in which early-successional species inhibit the success and growth of later-successional species. Those species that happen to occupy the site first maintain their membership in the community until their populations are damaged or die, only then enabling later species to invade. As such, the species composition gradually shifts to species with greater longevities. No special mechanism need be invoked for the inhibition model of succession.

Most models of succession have been criticized. Some authors treat them as purely descriptive and, like the entire successional process, a particular manifestation of the outcome of interacting individual life histories. In fact, one of the original authors of these three models has recently acknowledged that directional species replacement is only one change that might occur after a disturbance, and is often not the most likely change.

Some authors have taken these three models and related them to the search for ecological assembly rules during succession and compared them with a fourth alternative, the random colonization model, where chance survival of different species initiates the successional sequence; subsequent associations occur as a result of subsequent random colonization by new species. The search for assembly rules in ecology has a rich and controversial history that parallels that in succession. In fact, successional changes in community composition might be viewed as a special case of an overall search for deterministic processes in the maintenance and diversity of ecological communities.

Factors Influencing Succession

There are a number of factors that can influence the way in which community succession proceeds, if at all. Probably the most important of all are differences in life-history traits such as dispersal, ability to establish in open sites, shade tolerance, etc. The tradeoff between the availability of seeds and propagules of later-successional species versus the degree to which the early-successional community is resistant to invasion will influence the degree to which the former can increase at the successional site. Invasion success itself is dependent upon a large number of factors including, but not limited to, changes in microclimate or microhabitats, the composition of the seedbed, diseases, predators, and competition. Superimposed upon all of these are factors external to the organisms themselves, such as precipitation, temperature, salinity, and disturbance regime which can serve to reset the successional sequence.

The Role of Competition and Life History

Patterns from succession are numerous and varied, and have been mainly reported from the population and ecosystem level. However, a generalized theory of succession has been proposed for plants based on individual organisms. It is based on a model with three features: (1) the demographic history (birth, growth, death) of each individual is tracked through time; (2) every individual is assigned a suite of species-specific life-history traits (e.g., size, maximum age, and shade tolerance); and (3) competition and resource availability (light) is modeled explicitly through varying each individual's growth and mortality based on its degree of shade tolerance and light availability. The model successfully produces a significant portion of the variability in successional patterns using the mechanism of competition. Again, the importance of life-history traits among interacting plants is manifested.

Two-species simulations from the model were classified into five groupings based on the temporal patterns of species divergence (**Fig. 1**). The first was classical successional replacement where one species was able to dominate early in succession and the other species later, and is due to the correlation among life-history parameters of the two species. Divergence occurs when competitive ability starts out the same, but then one species outcompetes the other whereas convergence is the opposite: species are unequal in competitive ability early in succession but this equals out later in succession. Total suppression occurs when one species has the competitive advantage throughout the entire successional development. Finally, pseudocyclic replacement occurs when a temporary period of dominance or co-dominance by the initial cohort of species 2 results during the period between the senescence of the initial cohort of species 1 and the maximum lifespan of species 2. Thus early succession is characterized by the establishment of both species, but the initial cohort of species 2 persists longer than that of species 1. Species 2 is later replaced by the competitively superior species 1. The outcomes of the simulations depend more upon the equality of the life-history characteristics among species as opposed to the absolute values of the characteristics themselves; thus outcomes are governed by the qualitative relationship between the species with respect to their competitive abilities through time. Results of the simulations were similar to the two-species models when more than two species were considered and when multiple resources were considered. To summarize this important model to the concept of succession, the summary of the authors is quoted:

An approach based on competition among individual plants is presented as an explanation for species replacements during plant succession. Inverse correlations among life-history and physiological traits that confer competitive ability under different environmental conditions are shown to be sufficient to produce successional replacements but not sufficient for understanding the complex variety of successional patterns unless they are applied at the individual rather than at the population level or higher. With models based on competition among individual plants, various combinations of life-history and physiological traits can produce the great variety of population dynamics found in natural successions. The classic successional pattern of species replacement results from a particular structure of correlations among life-history and physiological characteristics. Atypical patterns of succession result when this correlation structure is altered. Both primary and secondary succession are modeled as nonequilibrium processes capable of interacting with disturbances to produce steady-state communities whose properties depend on abiotic conditions, such as temperature and resource levels, and on the type and frequency of disturbances. (Huston and Smith, 1987, p. 193)

Before leaving the subject of competition, it must be noted that there may well be a role for positive interactions among species comprising a community. There is increasing evidence that direct positive interaction, or facilitations, among species can play a vital role in ecological communities. While relatively unexplored in successional studies, the role of facilitations might provide an important context for testing the importance of successional patterns and processes in the maintenance of communities.

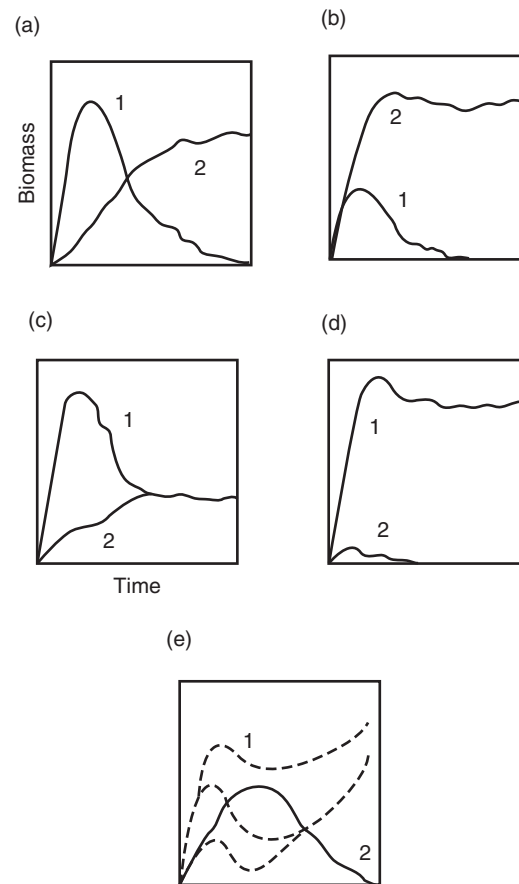


Fig. 1 General patterns of species interactions in a two-species succession. Competitive dominance occurs as a result of differing life-history traits. (a) Classical successional replacement that results from an inverse relationship between the two species in the attributes that confer early and late competitive advantage; (b) divergence that results when competitive abilities are equal early on, followed by a competitive advantage by one of the species; (c) convergence, the inverse of (b), that results when one species has a competitive advantage that equals out during the succession; (d) total suppression that results from one species having a competitive advantage over the other throughout succession; and (e) pseudocyclic replacement that results from alternating periods of dominance or co-dominance between the two species. From [Huston MH and Smith T \(1987\)](#) Plant succession: Life history and competition. *American Naturalist* 130: 168–198.

Is Succession Real?

Many models of succession are based on the idea that species that occur early in the successional sequence facilitate their own replacement by altering the environment to be more favorable to later species. Of course, this is anathema to natural selection – no species would ‘intentionally’ create more favorable circumstances for any other species than itself (the ‘evolutionary paradox’ of succession). For this reason the whole idea of succession has been questioned, and some authors consider it to be no more than the result of the passage of time, with no real mechanistic basis.

Many of the factors that might influence succession have been called into question, such that many authors believe that it is not a real phenomenon, or if it is, is unimportant in the maintenance of species diversity. Of critical importance is the degree to which communities act in changing the environment. Some reviews of the idea of succession conclude that most purported examples of succession do not fit the predicted trends: changes in structural and functional properties are not consistently associated with changes in species composition; successional stages are not consistently unidirectional; and effects of earlier species might just as easily delay or prevent as facilitate later-successional replacement.

Workers critical of successional theory have also put forward alternatives. One of these relates purported successional changes to consequences of differential growth, survival, and colonizing ability of species adapted to growth at different points on environmental gradients. Differences in taxonomic composition among successional stages are dependent upon interspecific competition while structural and functional changes in the community results in correlations in plants among size, longevity, and growth rate. In fact, successional changes may be exclusively governed by the presence of slower-growing later-successional species during the early phases of succession.

Much of the debate stems from the classic divergence in opinion about the influence of factors that result in the way in which species are maintained within ecological communities. On the one hand there may only be a loose association of species who

happen to inhabit the same habitat at the same time. In this model, species do not 'feel' each other or interact much, or if they do, the effects of these interactions are minor in comparison with their shared environmental tolerances. In the extreme view, communities are just haphazard associations of species and any spatial or temporal continuity in the composition of a community is either minimal, or determined solely by environmental parameters.

A completely different view holds that biological communities are tightly integrated units composed of species that not only respond together to environmental changes, but also maintain linkages among each other that result in continuity of occurrence over broad spatial and temporal scales. Some caricatures of this model have even referred to the community as a 'super-organism' with emergent properties that extend beyond individual species. While this view is probably overstated, there is a large amount of evidence that species interactions within communities result in spatial and temporal continuity of species assemblages within habitats. It is these interactions and other biological properties that have led many authors to believe that succession is a very plausible model for understanding changes in species composition over time.

Some Examples of Succession

Regardless of the continuing debates on whether there is any mechanistic basis for explaining directional patterns in species occurrences, excellent examples of the latter occur in nature. One of the best studies of primary succession was a test of the mechanisms involved in succession following deglaciation at Glacier Bay, Alaska. The main conclusion from this work was that no single factor or mechanism can totally account for primary succession. Plant life-history traits, such as seed size, growth rate, age at first reproduction, maximum height, and longevity played a fundamental role, but competition among species, and facilitation by addition of soil N and organic matter were also important. Although the relative importance of these factors was influenced by resource availability and environmental stress, they varied predictably through the successional sequence. The authors concluded that (1) life-history traits and availability of propagules determine the pattern of succession, (2) the mechanism for changes in species abundance patterns that accompanies succession is competition, and (3) the rate of change and nature of the climax community depends upon initial site conditions and the role of facilitation.

Perhaps one of the most famous and long-standing successional stories comes from the Krakatau Islands of Indonesia. The volcanic eruptions between May and August 1883 resulted in the almost complete 'sterilization' of the islands. A classic primary successional sequence has been documented for the main volcanic island of Rakata which continues uninterrupted, whereas the other islands display characteristics of secondary succession (Fig. 2). On Rakata, a number of different successional pathways are being expressed (Fig. 2a). A similar diversity of succession characterizes the other islands, but eruptive activity of Anak Krakatau – a new volcano that was established in the center of the group between 1927 and 1930 – disrupted the vegetation of some of the other islands such as Serung and R. Kecil. There, varying disturbance events have reset the successional sequence (Fig. 2b).

Differences in vegetation and in the curves of species colonization among the Krakatau Islands have been attributed mainly to intermittent disturbances of varying intensities from Anak Krakatau. The importance of succession in viewing the history of terrestrial ecosystems of the Krakatau Islands is summed up by Whittaker *et al.*

Neither the pattern of change in the flora, nor that for some groups of fauna, e.g., the birds and butterflies... can be understood without reference to vegetation succession and the key period in the 1920s when the savanna vegetation of the interiors gave way to forest. ... a successional model of island recolonization is required, involving evaluation of habitat and dispersal mechanisms. (Whittaker *et al.*, 1989, p. 103)

Succession in the Fossil Record

One of the great limitations of assessing the frequency or validity of the processes of succession is that the complete successional sequence might take longer than the period of time over which most ecosystems are studied within scientific research programs. Since succession is by its very nature a process that occurs over time, it is not surprising that paleontologists have investigated the degree to which it can be understood from evidence in the fossil record. In contrast to modern ecologists working on mainly terrestrial forest communities, paleoecologists have focussed more on marine systems, studying succession in fossil coral reefs, marine hardgrounds, and some sandy substrates. A critical debate for paleoecologists is the degree to which species replacements in communities are ecological versus evolutionary phenomena.

Palaeontologists have used ancient reefs as model ecosystems in the study of succession. Four major phases of succession in eight ancient reefs ranging in age from the Early Ordovician (488 Ma) to the Late Cretaceous (65.5 Ma) have been established: stabilization, colonization, diversification, and domination. The stabilization stage involves the initial colonization of the seafloor that results in the establishment of a firm substrate. The colonization stage is characterized by encrusters and frame-builders, those organisms capable of colonizing a hard substrate and that begin to build three-dimensional structures above the sediment-water interface. Some authors consider the first two of these stages to be the same, equivalent to the pioneering stage of ecologists studying succession in living forest communities. The third stage in the succession of fossil reefs is referred to as the diversification stage, where maximum diversity of the reef community is developed. Diversity then decreases as a 'domination' stage sets in whereby a single functional entity characterizes the reef community. As the communities ascend through the first three stages of succession, species diversity, degree of stratification and pattern diversity, niche specialization, and the complexity of food chains all increase. These successional sequences typically occur through significant intervals of time and are the result of the gradual

In Kenya, 'obligatory succession' in the Pleistocene consisted of an early assemblage of sediment-tolerant corals (dominated by massive or doming corals) that was replaced by predominantly branching and platy/encrusting corals. This kind of succession was mainly confined to the earliest portions of reef development on a bare substrate. Patterns through longer successional phases were varied, but under certain conditions massive or domed-shape corals might replace the branching assemblages. However, clearly defined zones were rare – most temporal changes in reef species associations were random or unstructured.

Applications to Restoration Ecology

The concepts of succession and community assembly have recently been taken up by the field of 'restoration ecology'. The nature of community assembly and the degree to which communities can be expected to return on a path generally directed to their original states (though return to their exact previous state is probably not possible nor desirable) is of primary interest to restoration ecologists interested in mitigating and reversing the effects of human-induced habitat degradation. Because of this central concern and the fundamental questions which each theory provides, it is an important exercise to understand the similarities and differences between community succession and community assembly. Both concepts recognize the importance of historical events in shaping community composition, which develops over time toward a final state, and both recognize competition as a major driving force.

Single or multiple stable states are predicted for both concepts, but the way in which species are maintained in such states is very different. We have already discussed the idea of a climax community – the final stable state of a successional sequence. However, where succession occurs, multiple stable states can be maintained across an ecosystem by disturbances that keep the community in a variety of successional states, so the 'climax' is never achieved at any one site or time. Where these disturbances are generated by the characteristics of the community itself (herbivory or fire) the community may be kept at an 'arrested' successional state. Arrested succession might also arise where early-successional species maintain their advantage over later-successional species for extremely long periods of time. 'Cyclic' succession occurs when there is no one stable successional state and all of the stages yield to others within the successional cycle. Stochastic differences in the arrival and colonization of late-successional species might also result in variability among ecosystems in their community composition.

Community assembly refers to the process by which species colonize, interact with other species and establish a community. This assembly may or may not be affected by 'assembly rules' which predict community composition on the basis of a few key attributes such as size of the species pool, the abiotic environment, or interspecific interactions. Community assembly may also result in either a single community type or multiple stable states. Where there is a strong match between environment and community, then community composition should converge towards a single state where similar environmental conditions hold, regardless of the historical order in which the species invade. But multiple stable equilibria have also been observed with varying historical sequence of species invasions, so that different timing of introduction of species colonization leads to different species composition.

Regardless of whether species are maintained through a successional sequence, or the product of their sequence of invasion into an ecosystem, an understanding of the processes which bring about various community states is fundamental to those wishing to move the system in one direction or another. Even where such processes are particularly opaque, an understanding of the presence of particular states may help in providing goals for management and restoration. Some predictions about the likelihood of the existence of a single or multiple stable states have been put forward. While these need further testing, a single stable community state has been predicted to arise in ecosystems with small species pools, high levels of dispersal, low productivity, and high rates of disturbance; whereas multiple stable states should be more apparent in ecosystems with large species pools, low levels of dispersal, high productivity, and low rates of disturbance. Thus, an integrated approach to understanding the processes underlying the historical trajectory of ecosystems, coupled with an in-depth knowledge of life-history variability, and a few key attributes of the ecosystem can go far in our understanding of how communities are likely to respond in the future to environmental changes today.

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