CHAPTER 20

DIVERSITY AND BIOLOGICAL INVASIONS OF OCEANIC ISLANDS

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To date, human-caused species extinctions are more an island-based than a continental phenomenon. Of the 94 species of birds known to have become extinct worldwide since contact with Europeans, only 9 were continental (Gorman, 1979). Currently, more endemic Hawaiian bird species are officially listed as endangered or threatened than are listed for the entire continental United States. Where information is available on other groups of animals, it indicates that human-caused extinctions are invariably more frequent on islands.

Heywood (1979) summarized the causes of extinction on islands as deforestation and fire, the introduction of grazing mammals, cultivation, and the introduction of weedy plants. All these factors can be important on continents as well, but species introductions (deliberate or accidental) are disproportionately important on islands (Elton, 1958). Isolated islands and archipelagos often lack major elements of the biota of continents, and their native species often lack defenses against grazing or predations.

Biological invasions are not the only factor leading to elevated extinction rates for island species. Extinction rates are also higher on islands because island species generally have small populations, restricted genetic diversity, and narrow ranges prior to human colonization, and because human alterations of land through use destroy an already-limited critical habitat. The plant and animal hitchhikers and fellow travelers who accompany humans to isolated islands interact with these other causes of extinction, however, and biological invaders endanger native species in reserves and other protected lands.

The fact that biological invasions decrease diversity on islands is paradoxical, because, as pointed out by Lugo in Chapter 6, the introduction of alien species generally increases the total number of species on an island, often spectacularly. However, most of the introduced species are cosmopolitans that are in no danger of global extinction, whereas most species on isolated islands are endemic. Biological invasions can therefore cause a net loss of species worldwide and a homogenization of the biota of Earth (Mooney and Drake, 1986).

SCOPE OF THE PROBLEM

The disproportionate effects of human colonization and attendant biological invasions on island ecosystems are well known (Carlquist, 1974; Darwin, 1859; Elton, 1958; Wallace, 1880); they can be demonstrated even on large islands such as Madagascar and Australia (Carlquist, 1974). The most severe consequences are experienced on old, isolated, mountainous, tropical, or subtropical islands or archipelagos. Islands located near continents receive organisms from those continents and rarely develop unique species. Truly oceanic islands have rates of evolution and speciation greater than those of immigration; hence, their biota contains many endemic species. Low islands (such as atolls) lack the range of environments that permits evolutionary radiation, while islands at high latitudes are subjected to strong climatic fluctuations (Bramwell, 1979), which prevent radiation.

Together these factors suggest that the Hawaiian Islands, the most isolated archipelago in the world, should have a large number of exotic species and a large potential for loss of endemic species as a consequence of biological invasions. The very large number of endemic species on these islands is well documented (Carlquist, 1974); the importance of biological invasions can also be demonstrated. For example, a survey of exotic plants on National Park Service lands (Loope, in press a) shows that island parks have a much larger proportion of alien species in their flora than do continental parks (Table 20–1). Moreover, in most continental parks alien species are largely confined to roadsides and areas occupied by humans before the park was established. In contrast, Channel Islands National Park in California, Everglades National Park (an island of tropical vegetation at the tip of the Florida peninsula), and the Hawaiian parks contain alien species that establish themselves in otherwise undisturbed native ecosystems and change the nature of the sites they occupy (Ewel, 1986; Stone and Scott, 1985; Stone et al., in press a).

The problems in the Hawaiian parks reflect in part the overall abundance of exotic species in Hawaii. As many as 1,765 native species of vascular plants (probably fewer as taxonomic revisions take hold) existed in the islands when the Polynesians arrived, and 94 to 98% of them were endemic (Kepler and Scott, 1985). Polynesians brought additional species, perhaps 30 of them (Nagata, 1985), when they colonized Hawaii and journeyed among the Pacific islands. The advent of more rapid transportation from distant areas and especially the occupation of Hawaii by people from diverse western and eastern cultures, each with its distinctive food, medicinal, and ornamental plants, greatly increased the number of species present. More than 4,600 species of introduced vascular plants are now known to

grow in Hawaii, and at least 700 of these are reproducing successfully and maintaining populations in the field (Smith, 1985; Wester, in press). At the same time, more than 200 endemic species are believed to be extinct, and another 800 are endangered (Jacobi and Scott, in press). Most sites below 500 meters elevation, and many higher ones, are entirely dominated by alien species (Moulton and Pimm, 1986).

TABLE 20–1 Proportion of Alien Plants in the Vascular Flora of Selected U.S. National Parksa

National Park	Alien Species (% of total)
Sequoia-Kings Canyon	6–9
Rocky Mountain	7–8
Yellowstone	11–12
Mount Ranier	12–14
Acadia	21–27
Great Smoky Mountain	17–21
Shenandoah	19–24
Channel Islands	16–19
Everglades	15–20
Haleakala	47
Hawaii Volcanoes	64

[a]From Loope, in press a.

Similar patterns of introduction of alien insects, mammals, reptiles and amphibians, and birds have been described (Carson, in press; Moulton and Pimm, 1986). The birds are probably the best documented (Moulton and Pimm, 1986; Olson and James, 1982), although mammals are the most spectacular (from 1 native bat to at least 18 species of alien mammals). At least 86 species of land birds are known to have been present in Hawaii 2,000 years ago, and at least 68 of them were endemic passerines. Forty-five species, including 30 passerines, disappeared around the time of Polynesian colonization; another 11 have disappeared since Europeans arrived; and several more are on the verge of extinction (Moulton and Pimm, 1986; Stone, 1985). In contrast, at least 50 species of alien passerines have become established since 1780. Even casual observers of lower-elevation birds in Hawaii have noted a kaleidoscope of shifting dominance by different species of alien birds over the past 30 years; the one constant has been the near absence of natives.

This pattern of successful invasion by cosmopolitan species and the decline of certain native species is not unique to Hawaii. A similar conversion of native-dominated to alien-dominated ecosystems occurs on isolated islands in all the oceans—from the Galapagos to New Zealand to Diego Garcia to Tristan da Cunha and St. Helena (Bramwell, 1979; Carlquist, 1974; King, 1984; Wace and Oilier, 1982). In many cases, the successful invaders are identical—goats *(Capra hircus)* and guava (*Psidium guajava* and *P. cattleianum*) are problems in Hawaii, the Galapagos, and the Rodrigues Islands in the Indian Ocean.

WHY ARE ISLANDS SUSCEPTIBLE?

The reasons why biological invasions are disproportionately successful on islands, and why island species seem more likely to become extinct, have long been debated. Loope (in press b) summarized this discussion with seven possible explanations for the observed patterns:

- Reduced competitive ability due to repeated "founder effects," i.e., chance events during colonization by small initial populations
- Disharmony of functional groups and relative lack of diversity
- Small populations and genetic variability; restrictive specialization
- Relative lack of adaptability to change; loss of resistance to consumers and disease
- Loss of essential co-evolved organisma
- Relative lack of natural disturbance, especially fire, in the evolutionary history of many island biotas
- Intensive exploitation by humans

He also pointed out that the apparent lack of vigor of island species can be overstated, sometimes with negative consequences. For example, Lyon (1909) interpreted a decline of native óhiá *(Metrosideros polymorpha)* in Hawaii as reflecting that species' inability to survive in the modern world, and spearheaded the introduction of many alien species to replace it. In fact, periodic diebacks of natural populations of *Metrosideros* are a natural feature of forest dynamics in Hawaii and elsewhere in the Pacific (Mueller-Dombois, 1983), and *Metrosideros* naturally recolonizes most of these areas. More generally, many native island species maintain themselves quite successfully in mixed native/exotic ecosystems (Mueller-Dombois et al., 1981).

At the other extreme, it has been argued that alien species are merely temporary components of island ecosystems, certain to be replaced by natives in the course of ecological succession (Allan, 1936; Egler, 1942). In fact, some aliens invade intact native ecosystems, whereas others alter the course of succession in already disturbed sites (Smith, 1985) and seem capable of persisting in those altered sites.

Although biological invasions clearly have contributed to the extinction of native species on islands, the importance of direct competition between native and exotic species in causing these extinctions is uncertain. Habitat destruction by humans and feral animals, alterations in basic ecosystem properties caused by newly introduced species, grazing and predation pressure from introduced consumers, and exotic animal diseases (such as avian pox and malaria) appear to be at least equally important.

The importance of grazing and predation by alien animals deserves special emphasis. Most isolated oceanic islands originally lacked whole groups of organisms; mammals were especially sparse. Even ants were nearly or entirely absent on some islands, including Hawaii (Medeiros et al., 1986).

The introduction of mammals has had enormous effects on island ecosystems throughout the world. Comparisons of islands with introduced ungulates and those without such animals in widely separated Pacific island groups (the Hawaiian

Islands, the Cook Islands, and the Kermadec Islands) demonstrate that native communities often hold their own in the absence of mammals but that invasions by plants are much more common and disruptive of native communities on heavily grazed islands (Merlin and Juvik, in press).

WHAT CAN BE DONE?

Biological invasions of oceanic islands appear to be an immense and largely unmanageable problem. Of the approximately 4,600 species of alien plants on Hawaii, more than 700 reproduce in the wild and 86 are considered serious threats to native ecosystems (Smith, 1985). At present, there are neither the resources nor the will to attack a problem of this magnitude. Moreover, while interception and quarantine systems can slow the further introduction of additional exotic species and stop a few indefinitely, the sheer volume and pace of transport by jet aircraft may overwhelm most controls. Finally, any inspection system detailed enough to be broadly effective would necessarily hinder and annoy tourists that are the major economic support of many oceanic islands. Moreover, many island residents have strong reasons for importing or protecting introduced species as agricultural, timber, or forage crops, medicinal or ornamental plants, watershed protection, domestic livestock, pets, agents of biological control, or targets of sport or commercial hunting or fishing. These economic or cultural attachments to alien species mean that there is little chance of developing broad-based, politically effective support for controlling alien species that are not regarded as weeds in the classical (economic) sense.

There are nevertheless several steps that can be taken to reduce the effects of biological invasions and protect some of the native biological diversity on isolated oceanic islands:

- identification of the aliens most likely to threaten native ecosystems and concentration of control efforts on those species;
- selection of critical habitat areas from which most or all species of aliens are excluded;
- protection of areas from further habitat destruction; and
- study of biological invasion and species extinction on islands to learn how these same processes may affect continents.

IDENTIFICATION OF PROBLEM SPECIES

Identification of the invading species most likely to disrupt native ecosystems requires some understanding of the biology of both the invader and the invaded community. Research designed to obtain that information is now being conducted, and its results are being used in management decisions on many islands. The most disruptive species (not necessarily in order of importance) include herbivorous mammals, vertebrate and invertebrate predators, species that can alter ecosystem-level characteristics of invaded areas, and species that can invade otherwise undisturbed native ecosystems.

Herbivorous Mammals

Grazing and browsing mammals effect islands in such pervasive ways that it is difficult to see how native ecosystems can be protected unless they are eliminated. Studies of whole islands and of exclosures have clearly demonstrated that ungulate populations affect erosion, soil fertility, and the success of invasions by alien plants (Loope and Scowcroft, 1985; Merlin and Juvik, in press; Mueller-Dombois and Spatz, 1975; Vitousek, 1986). Island plants often lack defenses, such as thorns and toxic chemicals, against herbivores, and herbivority reduces total plant cover and selects for better defended alien plants. Moreover, feral pigs (which are widespread on many oceanic islands) directly disrupt soil structure in the course of their feeding. Efforts to eliminate mammals are expensive and difficult, but they have been highly successful in a number of areas (Bramwell, 1979; Stone et al., in press b). In many cases, the removal of grazing animals has been followed by the recovery of native plants and even by the discovery of entirely new species of native plants (Bramwell, 1979; Mueller-Dombois and Spatz, 1975).

Predators

Alien vertebrate and invertebrate predators can have significant effects on island ecosystems both directly, by eliminating natives, and indirectly, by altering community structure. For example, rats and feral cats affect the breeding success of ground-nesting birds in many areas (Clark, 1981; King, 1984; Wace, 1986). Alien ants altered invertebrate communities in the Hawaiian lowlands years ago, and other ant species are now threatening to do so at high elevations (Medeiros et al., 1986). Invertebrate predators are particularly problematic in that they may eliminate important native pollinators from island faunas.

Ecosystem-Level Effects

Any alien species that alters ecosystem-level characteristics (such as primary productivity, nutrient availability, hydrological cycles, and erosion) of the area it invades alters the living conditions for all organisms in that area (Vitousek, 1986). It may also alter the kind or quality of the services that natural ecosystems provide to human societies (Ehrlich and Mooney, 1983). Alien animals clearly alter ecosystem properties in a number of ways (as described above), and it is becoming clear that alien plants can do so as well. In Hawaii, for example, the exotic nitrogen-fixing fire tree *(Myrica faya)* increases the availability of the soil nitrogen in nitrogen-limited volcanic ash deposits (Vitousek, in press). Similarly, the alien grasses *Andropogon virginicus* and *A. glomeratus* provide fuel for fires and also sprout rapidly following fires, thereby greatly increasing both their abundance and the overall frequency of fires to the detriment of native species not adapted to fire resistance (Smith, 1985).

Invasion of Intact Native Ecosystems

Alien animals are frequently (not invariably) able to invade intact native ecosystems, but plants species that can do so are not common. Most often, alien plants invade undisturbed native ecosystems in association with alien animals. In Hawaii,

alien birds and mammals consume and disseminate the fruit of the aggressive alien plants strawberry guava *(Psidium cattleianum)* and banana poka *(Passiflora mollissima)* throughout native forest areas. Interactions between feral pigs and these invading plants are particularly severe: pigs disseminate seeds of these fleshy-fruited aliens, mix them with organic fertilizer, and deposit them into seedbeds, which are cleared by the pigs' rooting activity. The pigs' descendants then use fruit of the daughter plants as a major food source (Smith, 1985; Stone, 1985). Similar interactions between cattle and common guava *(Psidium guajava)* occur in the Galapagos (Bramwell, 1979). These interactions between alien plants and animals further illustrate why control of alien animals is fundamental to protecting the native ecosystems of islands.

IDENTIFICATION OF CRITICAL HABITATS

A second strategy for limiting the effects of biological invaders is to control manageable alien species in selected critical habitats. This process is expensive and time-consuming, but it does lead to the maintenance of areas as close to their natural state as possible (although birds, flying insects, and microorganisms are of course difficult or impossible to control). Management in “Special Ecological Areas” of Hawaii Volcanoes National Park has been designed to protect areas that represent the major ecosystems in the park by minimizing the influence of alien species. These areas can then act as refugia for threatened native biota and as areas for ecological study and education (Stone et al., in press a; Tunison et al., 1986).

HABITAT DESTRUCTION

Control over habitat destruction is also essential to protecting biological diversity on oceanic islands. Land clearing or fire in native systems can both destroy individuals of threatened native species and lead to the establishment of alien-dominated successional ecosystems. Conflicts in achieving this objective are inevitable; most islands are neither museums nor biological preserves, and one person's “habitat destruction” will certainly be another's source of food or income. Destruction of critical habitat on islands is perhaps most severe on Madagascar, but it is not a problem confined to developing countries. Nearly half of Hawaii's largest native-dominated lowland rain forest was cleared during 1984 and 1985 in a subsidized endeavor to generate electricity from wood chips.

ECOLOGICAL RESEARCH ON ISLANDS

Controlling the effects of biological invasions on islands is paramount, but there is also a great deal to be gained from studying their effects carefully. The relative simplicity of the biota of many islands perhaps enables invading species to have greater effects on native communities than they would in continental areas; it certainly facilitates a much more complete evaluation of those effects. Better understanding of biological invasions and their consequences for biological diversity on islands will contribute to the development and testing of basic ecological theory

on all levels of biological organization. Few of the effects of biological invasions described here are unique to islands; they are only more highly developed and occur most rapidly there, as demonstrated by the invasion of European wild boars into Great Smoky Mountains National Park (Singer et al., 1984). An understanding of the effects of invasions on biological diversity in rapidly responding island ecosystems may give us the time and the tools needed to deal with similar problems on continents; it may even contribute to the prediction and evaluation of the effects of environmental releases of genetically altered organisms.

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