Biological Invasions: a Global Perspective
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CHAPTER 10

Characteristics of Invaded Islands, with Special Reference to Hawaii

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10.1 INTRODUCTION

Islands have long fascinated biologists and as a tool have much more yet to contribute in the search for general principles in ecology and evolution (Williamson, 1981). A better understanding of how island ecosystems differ from continental ecosystems may help to clarify the nature of various ecosystem properties. This chapter attempts, within the limits imposed by our current state of knowledge, to answer the question: Why are islands so vulnerable to biological invasions? Because few locations on earth have had such pervasive biological invasions as the Hawaiian Islands, an archipelago that is relatively well studied and the one with which we are most familiar, we will focus most of our discussion there.

10.2 CHARACTERISTICS OF ISLANDS: AN OVERVIEW

Reviews by MacArthur and Wilson (1967), Carlquist (1965, 1974) and Williamson (1981) provide good general coverage to this topic, and it will only be touched upon here. Islands are by definition relatively small and surrounded by water, but otherwise exhibit remarkable individuality. Most islands are geologically young in relation to continents, but the Seychelles are partly underlain by Precambrian granites. Table 10.1 compares selected parameters for various island groups. The islands included in Table 10.1 exhibit substantial topographic and environmental diversity, but many islands of the world are low lying atolls. Islands near continents tend to have more native species and lower endemism than more isolated islands. Older islands, especially those with great environmental diversity, exhibit higher endemism than young islands. Heavily glaciated islands, such as the Faeroes, contain relatively few endemic species.

In relation to the Hawaiian Islands, most archipelagoes of the world are less isolated from continents, geologically younger, have less topographic and climatic diversity, possess lower endemism and relatively few examples of evolutionary adaptive radiation, have had and continue to receive less human

Table 10.1. A comparison of selected archipelagoes of the world

	Hawaiian Islands	Galapagos Islands	Canary Islands	Juan Fernandez Islands	New Zealand
Location	19°–22°N 155°–157°W	0°–2°N 90°–92°W	28°–29°N 14°–18°W	33°S 79°–81°W	33°–47°S 167°–178°W
Distance from nearest continent (km)	3200	800	115	665	2000
Age of oldest islands in group (in millions of years (m.y.))	ca. 70	ca. 3	ca. 80	ca. 6	200 +
Total area of islands (km^2)	16,500	7900	7300	140	268,000
Highest elevation (m)	4206	1707	3718	1650	3765
Range of mean annual precipitation (mm)	200–13,000	< 750	50–1000	1000 +	350–8000
No. of endemic angiosperm genera	31	8	19	10	39
No. of native angiosperm spp.	970–1400	434	ca. 1700	146	1996
% endemism in angiosperm flora	91–96 +	51	28	66	81
No. of invasive introduced spp.	800	240	700	many	ca. 500
References	Table 2	Porter, 1984	Kunkel, 1976	Perry, 1984 Stuessy *et al.*, 1984	Kuschel, 1975

Table 10.1. (*cont*)

	Tristan da Cunha group	Granitic Seychelle Islands	Faeroe Islands	Channel Islands California
Location	37°–40°S 11°–13°W	4°–5°S 55°–56°E	62°N 7°W	33°–34°N 119°–120°W
Distance from nearest continent (km)	3000	1600	300	21
Age of oldest islands in group (in millions of years (m.y.))	20	650	50–60	ca. 20
Total area of islands (km^2)	160	260	1400	900
Highest elevation (m)	2060	914	882	753
Range of mean annual precipitation	ca. 1000	1250–2540	ca. 1500	250–400
No. of endemic angiosperm genera	0	9	0	1
No. of native angiosperm spp.	41	222	310	621
% endemism in angiosperm flora	37	31	0	22
No. of invasive introduced spp.	97	165	30	227
References	Moore, 1979 Williamson, 1981	Stoddart, 1984	Rutherford, 1982	Wallace, 1985

influence, and have suffered fewer extinctions. Most of them have probably been affected by biological invasions to a lesser extent than the Hawaiian Islands, although definitive data are lacking.

10.3 CHARACTERISTICS AND INVASIONS OF THE HAWAIIAN ISLANDS

The Hawaiian Archipelago, the most isolated island group of comparable size and topographic diversity on earth, is located over 3000 km from the nearest continent. The Hawaiian Islands consist of eight major high islands (Figure 10.1). These islands are part of a much longer island chain which was produced by the northwestward movement of the Pacific Plate over a hot spot in the earth's mantle over a 70 million year period (Figure 10.2, Macdonald *et al.*, 1983). Islands of the chain extending to the northwest are eroded and submerged remnants of what were once high islands. The area of the present high islands totals 16 500 km^2, with the largest and youngest island (Hawaii) comprising 63% of the total area. Their elevations range from sea level to over 4000 m. Average annual precipitation, strongly influenced by topography in relation to the northeast trade winds, varies from 200 mm to over 10 000 mm.

The Hawaiian biota started to evolve as much as 70 million years ago in nearly

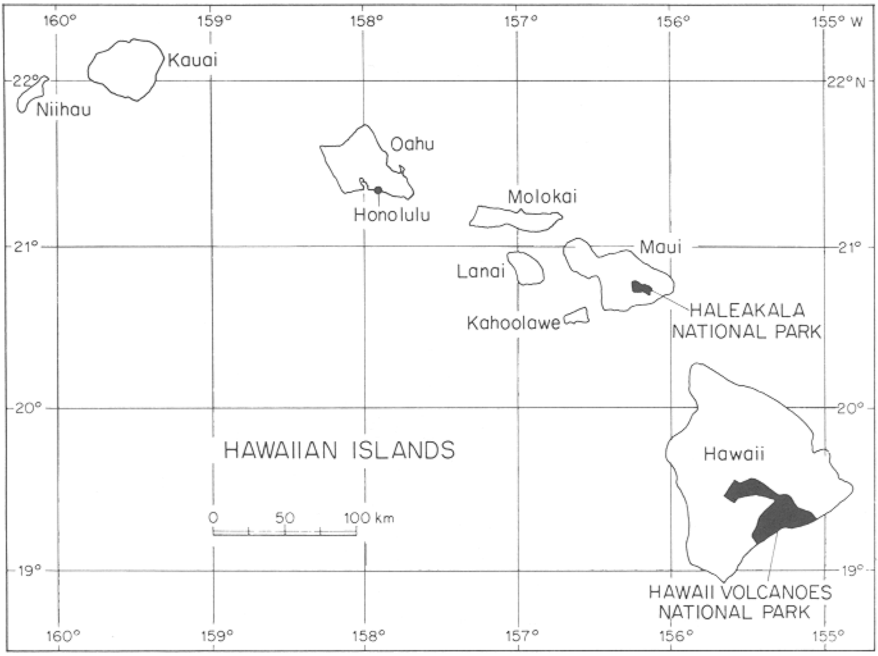

Figure 10.1. The eight major high islands of the Hawaiian Archipelago

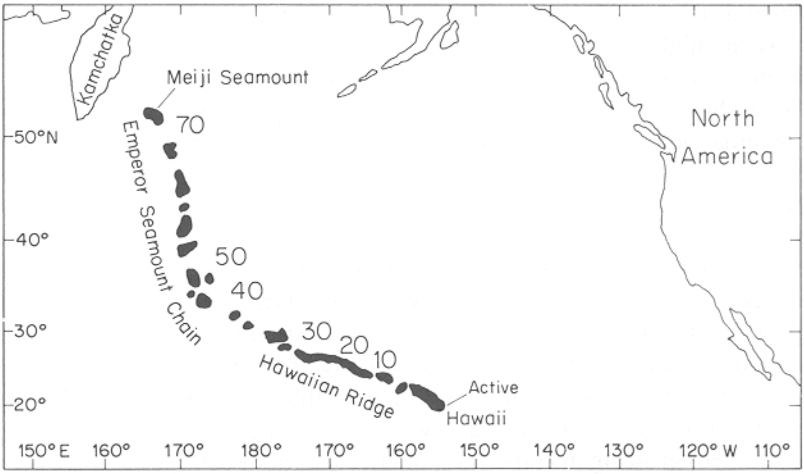

Figure 10.2. Map showing the Hawaiian–Emperor island chain with approximate ages given in millions of years. The islands were formed by northwestward movement across the active 'hot spot' now near the eastern side of the island of Hawaii. (Adapted from Macdonald *et al.*, 1983.)

total isolation—with persisting colonization through long-distance dispersal for major taxonomic groups occurring at very infrequent intervals. In only a few very efficiently dispersed groups (e.g. diatoms, McMillan and Rushforth, 1985) have dispersal and establishment not been major factors limiting the development of the Hawaiian biota. In general, the percentage of endemism is very high. The known terrestrial endemic Hawaiian vascular flora and macroscopic metazoan fauna are thought to have evolved from fewer than 1000 colonizing ancestors. A flora of 1000–1500 species of flowering plants (St John, 1973; Wagner, in Gentry, 1986) evolved from about 272 colonizing ancestors (Fosberg, 1948); 168 pteridophyte taxa developed from about 135 original immigrants (Fosberg, 1948); a native arthropod biota of 6000–10 000 species evolved from about 300–400 ancestral immigrant species (Gagné and Christensen, 1985; Hardy, 1983); a native mollusc biota of *ca* 1000 species evolved from as few as 22–24 long-distance immigrants, probably carried by birds (Zimmerman, 1948); and about 100 known species of endemic land birds (including species known only as fossils) evolved from as few as 20 ancestors (Olson and James, 1982).

The differential dispersal and establishment of various taxonomic groups as colonizers of Hawaii has allowed adaptive radiation (Carlquist, 1974). Beginning with a single ancestral population, certain groups have undergone spectacular adaptive radiation, resulting in a diverse assemblage of closely related species occupying a wide range of habitats. The silversword alliance (Asteraceae: *Argyroxiphium–Dubautia–Wilkesia*, Carr, 1985), lobeliads (Lobeliaceae:

Clermontia–Cyanea–Delissia–Rollandia, Carlquist, 1970), the avian honeycreepers (Fringillidae: Drepanidinae, Raikow, 1976), tree snails of the family Achatinellidae (Cooke and Kondo, 1960), pomace flies (Drosphilidae, Carson and Kaneshiro, 1976), a group of predacious caterpillars (Geometridae: *Eupithecia*, Montgomery, 1982), and wood-boring beetles (Cerambycidae: *Plagithmysus*, Gressitt, 1978) are among the groups that have undergone adaptive radiation in the Hawaiian Islands.

The rate of establishment of new immigrant species in the Hawaiian Islands has increased markedly since arrival of the Polynesians. The Polynesians brought 40–50 species of animals and plants with them during their own colonization (Kirch, 1982; Nagata, 1985), an average of three to four introductions per century for a period of about 1400 years. In contrast, Beardsley (1979) found that 15–20 species of immigrant insects alone become established in Hawaii each year. St John (1973) listed 4275 introduced flowering plant species (a conservative figure, now outdated) growing in cultivation in Hawaii; about 800 species have become invasive (Wagner, personal communication).

The Hawaiian Islands have had more bird species become established than any other area on earth (Long, 1981). Moulton and Pimm (1986) found that 63% of the documented intentional or unintentional introductions of bird species to individual Hawaiian Islands have resulted in establishment. For mammals and reptiles the success rate was assessed at 93% and 91% respectively (Moulton and Pimm, 1986). Table 10.2 provides the most currently available assessment of the number of native and introduced species in the various taxonomic groups of Hawaiian biota.

10.4 WHY DO INVADERS OF ISLAND ECOSYSTEMS HAVE SUCH A HIGH RATE OF SUCCESS?

Darwin (1859) attributed the vulnerability of island biota to invasions to the fact that only small numbers of indigenous species occur on islands. Much biological work has been done on islands since. Although the broad patterns are evident, the details are not yet fully clear. We can class probable reasons into four general categories as follows.

10.4.1 Evolution of island organisms in isolation

The Hawaiian biota and its ecosystems have evolved with disturbance from several sources including volcanism, windthrow, and landslides, but without grazing and trampling of ungulates and with a reduction in frequency and intensity of fire relative to most continental systems (Mueller-Dombois, 1981). Disturbance has been such an important evolutionary force in continental situations that opportunistic species have evolved that are adapted to persistence, dispersal and colonization of unoccupied areas (Pickett, 1976). The Hawaiian

Table 10.2. Statistics for various taxonomic groups in the Hawaiian Islands

Taxonomic Group	No. of Native Species	No./% of Endemic Species	No. of Invasive Species	Reference
Flowering plants	1442	1394 (97%)	326	St. John, 1973
	970	883 (91%)	800	W. Wagner in Gentry, 1986 and pers. comm.
Ferns and allies	143	105 (73%)	21	Lamoureux pers. comm.
Hepaticae (liverworts)	168	ca. 112 (67%)	2	Miller, 1956. Yoshida and Smith, 1976
Musci (mosses)	233	112 (48%)	3	Hoe, 1979
Lichens	678	268 (38%)	0	Magnusson, 1956. Smith pers. comm.
Resident birds	57	44 (77%)	38	Pyle 1983
Mammals (on land)	1	0 (0%)	18	Tomich, 1986
Reptiles (on land)	0	0	13	McKeown, 1978
Amphibians	0	0	4	
Freshwater fish	6	6 (100%)	19	Maciolek, 1984
Arthropods	6000–10,000	98%	ca. 2000	Gagné and Christensen, 1985 Hardy, 1983. Howarth, 1985
Molluscs	ca. 1060	99%	9	Zimmerman, 1984. Howarth, 1985

biota is well adapted locally to disturbances related to volcanism (e.g. Smathers and Mueller-Dombois, 1974; Winner and Mooney, 1985). Grazing and trampling of ungulates are assumed to comprise a major evolutionary force, at least in certain savanna and grassland ecosystems of the world (e.g. McNaughton, 1985), but were entirely lacking in Hawaii before 1778 AD. In most terrestrial environments of the world, fire has been the most pervasive disturbance. In areas long influenced by frequent fire, the entire flora has become closely attuned to this type of disturbance (Naveh, 1975). In any given fire-influenced area, the plants and animals have evolved a broad spectrum of adaptations to deal with this aspect of their environment (Gill, 1981; Keeley and Zedler, 1981).

Fire does not appear to have played an important role in most native ecosystems of Hawaii (Mueller-Dombois, 1981), since few native plants of the Hawaiian Islands possess adaptations to fire. Lightning is relatively uncommon on islands because their small land mass is not conducive to convective buildup of thunderheads. Many native Hawaiian ecosystems may have lacked adequate fuel to carry fires that may have been ignited by lightning or vulcanism. Humans were not present as an agent of ignition until the 4th century AD, but subsequently Polynesian colonizers undoubtedly used fire in clearing for agriculture (Kirch, 1982). Fires in modern Hawaii, carried mainly by introduced grasses, are generally highly destructive to native plant species. Opportunistic invasive plant species, on the other hand, spread rapidly following fire or other disturbance, notably on mineral soil exposed by pig-digging (Spatz and Mueller-Dombois, 1975).

Island biotas have proved vulnerable to many other types of changes in conditions after the arrival of man. Unquestionably, the lack of such ecologically important groups as ants, rodents, mammalian carnivores, and herbivorous ungulates in the Hawaiian Islands and other isolated island groups has increased the vulnerability of endemic species when members of these groups are introduced. Certain introduced ants are voracious predators and have obliterated most of Hawaii's endemic lowland arthropod fauna (Zimmerman, 1978). Rodents are selective feeders, eat great quantities of seeds, and may prevent reproduction of certain plant species that have not evolved mechanisms to protect even a fraction of their seeds from rodents (e.g. Clark, 1981). Rodents may also be devastating to the reproductive success of endemic birds (Atkinson, 1977, 1985). Predators such as the mongoose (*Herpestes auropunctatus*) are especially destructive to birds with conservative reproductive strategies such as the Hawaiian dark-rumped petrel (*Pterodroma phaeopygia*), a long-lived species that has low natural mortality of its single, well cared for, chicks (Simons, 1983). Flightlessness in birds is a condition that has evolved independently on many islands and usually proves to be a fatal condition when predators are introduced (James and Olson, 1983). Evolution in the absence of large mammalian herbivores, which consume large quantities of vegetation and cause perpetual disturbance through trampling and digging (in the case of pigs), has resulted in high vulnerability to damage by introduced ungulates. Hawaiian plants are relatively nonpoisonous and free from many other characteristics that deter mammalian herbivores (Carlquist, 1970, 1974), although they retain physical and chemical defenses against insect herbivory. Evolution in the absence of exposure to avian malaria has resulted in high susceptibility of the surviving Hawaiian land bird fauna to the mosquito-borne protozoan, *Plasmodium relictum* (van Riper *et al.*, 1986).

Loss of coevolved organisms may further hasten the demise of island species. Some of the many extinct birds of the Hawaiian Islands (Olson and James, 1982) may have been important in dispersal and/or scarification of seeds. From East Maui, there is evidence that necessary scarification of seeds of the native shrub *Styphelia tameiameiae* is provided by passing through the digestive tract of introduced pheasants (*Phasianus colchicus*) (A. C. Medeiros, personal communication). Successful alien plant species in Hawaii are often dependent upon introduced dispersal vectors as well.

Pollination is an essential process for which many plant species are dependent upon insects, birds, or other animals. Even when appropriate pollinators are present, seed set is often limited by a suboptimal quantity of pollinators (Bierzychudek, 1981). At least some island plants, including the silversword (*Argyroxiphium–Dubautia*) alliance of the Hawaiian Islands, have evolved obligate outcrossing mechanisms (Carr *et al.*, 1986) and are thus vulnerable to extinction of pollinators. Pollinators of the Haleakala silversword (*Argyroxiphium sandwicense macrocephalum*) may indeed be vulnerable to elimination by the Argentine ant (*Iridomyrmex humilis*) (Medeiros *et al.*, 1986).

10.4.2 Modification of island environments by humans

The Hawaiian Islands have been heavily exploited by the colonizing Polynesians (Kirch, 1982; Olson and James, 1982) and much more so by continental man after 1778 (Gagné, 1975; Daws, 1968, Cooper and Daws, 1985). The small land area in relation to its potential (augmented by products from the sea) for supporting a self-sustaining large human population contributed to the Polynesian impacts. In Polynesia in general, dispersal of human populations through voyaging during the past several thousand years was apparently triggered by large population pressure (Jennings, 1979). Throughout the Hawaiian Islands, most land below 600 m with even moderately good soils was cultivated by the Hawaiians in the 13th–18th centuries (Kirch, 1982). The pre-contact Hawaiians also eliminated over half the species of endemic birds of the islands through habitat alteration and hunting (Olson and James, 1982). Archeological reconstruction of the prehistory of the Hawaiian island of Kahoolawe may illustrate an extreme case of a broad pattern. Now an uninhabited and barren wasteland used as a bombing range by the US military, Kahoolawe is unique in that the archeological evidence for settlement has been preserved intact (Kirch, 1985). Colonization of Kahoolawe

(117 km^2 area) is inferred by Hommon (1980) to have taken place about 1000 AD, with initial exploitation of the coastal zone. The inland central plateau zone (up to 450 m above sea level), initially a 'dryland forest or parkland', was occupied and extensively used for agriculture (sweet potatoes, etc.) from 1400 to 1550 AD. Hommon (1980) proposed that agricultural clearance and burning led to 'island-wide degradation', leading to a rapid decline in human population during 1550–1650 AD. The island area was completely abandoned after about 1750 AD. At the time of Western contact, the island's population was estimated at about 60 persons, dwelling entirely along the coast. Although environmental degradation was much less on other Hawaiian Islands, there is relatively good archeological evidence on western Hawaii for a human population decline, presumably due to attainment of a population level exceeding carrying capacity and accompanying resource deterioration, prior to Western contact (Kirch, 1985).

Human-related prehistoric extinctions have now been documented throughout the world, both on islands (e.g. Olson, 1975, 1977; McCoy, 1979) and continents (e.g. Martin, 1984). Massive deforestation has been demonstrated in prehistoric Mesoamerica (Turner and Harrison, 1981). Effects of prehistoric man in altering island environments may have been more consistently severe largely because of their smaller size and lack of alternative land for exploitation.

Westernization has led to unprecedented resource exploitation and degradation throughout the oceanic world (e.g. Greenway, 1958; Holdgate and Wace, 1961; Millot, 1972; Lee, 1974; Wace, 1976; Coblentz, 1978; Melville, 1979; Rauh, 1979; van der Werff, 1979; Cronk, 1980, 1986; Perry, 1984; Gade, 1985). For example, the portion of New Zealand covered by forest has been reduced from 68% to 14% by human activity over the past 200 years (Kuschel, 1975). Again, continental environments, though subjected to the same types of devastating damage that have occurred on islands, have proved relatively resilient because at least until recently, possibility existed for exploiting an area and moving elsewhere.

10.4.3 Invasibility of island ecosystems

Island biotas typically have low species numbers in certain groups in relation to their relative proportions in continental areas of the world. 'Disharmony' is a term often used in the context of island biology to denote a taxonomic balance that differs from continental norms. For example, the Hawaiian Islands have only four native species of orchids, one of the largest angiosperm families worldwide, particularly in warm and moist climatic regions. The native biota also lacks representatives of the following taxa important on continents: gymnosperms, Aceraceae, Araceae, Betulaceae, Bignoniaceae, Cunoniaceae, Fagaceae, *Ficus, Piper*, reptiles and amphibians. Mammals are lacking except for a single species of bat. Two-thirds of the world's insect orders have no representatives in Hawaii. On the other hand, the Hawaiian Drosophilidae comprise about 600 species, a large percentage of the total species worldwide in this family (Carson and Templeton, 1984).

Simberloff has justifiably questioned whether the taxonomically disharmonic nature of the Hawaiian entomofauna has been responsible for the large number of invading insect species there. He shows (Simberloff, 1986, Table 1.1) that the insect orders in Hawaii with the largest numbers of natives (Coleoptera, Lepidoptera, Hymenoptera) are also those with large numbers of introductions.

In some instances, nevertheless, some of the same factors that have promoted adaptive radiation over evolutionary time appear to promote vulnerability to invasion in modern time. The absence or near absence of a taxonomic group or ecological guild on an island will often result in minimum resistance to invading continental species of that group until saturation is approached. An example is the successful purposeful introduction of 19 species of freshwater fish in Hawaiian waters, which were occupied prior to 1800 only by six species of native gobiids, freshwater-tolerant fish derived from ancestors that spent their entire life cycles in the sea (Heere, 1940; Maciolek, 1984). Absence of native mammalian herbivores and ants has undoubtedly facilitated the highly successful invasion of those groups. On the other hand, invasive species are not necessarily responding in most cases to 'vacant niches waiting to be filled.' A common pattern is creation and exploitation of new niches through multiple invasion. For example, the extremely successful invading tree *Myrica faya* is able to establish and thrive on nutrient-poor young volcanic substrates on the island of Hawaii; it is aided by an introduced microbial nitrogen-fixing symbiont (*Frankia*) and introduced birds that disperse its seeds (Walker *et al.*, 1986). Feralization of pigs in the Hawaiian Islands has been facilitated by invasion of introduced earthworms and of such introduced plants as *Psidium cattleianum* and *Passiflora mollissima* (Stone and Loope, 1987). In turn, massive invasion of forest understories by numerous introduced plant species is made possible by exposure of mineral soil by pig digging.

The total number of species per unit area is smaller on islands than in continental situations. MacArthur (1972) states the principle that 'no island has nearly the number of species it would have if it were part of the mainland.' The central equation of MacArthur and Wilson's (1967) theory of island biogeography, presenting island species number as a balance between immigration rate and extinction rate, might seem to shed light on island vulnerability to invasions, with accelerated immigration driving up extinction rates or increased extinction rates facilitating establishment of immigrants. Although this theory has stimulated much thought and numerous investigations regarding island ecology, it would seem to have little to do with an isolated oceanic island system such as Hawaii where pre-Polynesian immigration rates were exceeded by rates of evolution of new species (Williamson, 1981). Now that immigration rates have been accelerated from one introduction per 50 000 years to 20 or more introductions per year, there is little indication that species numbers *per se* have much immediate relevance to forcing species extinctions or retarding establishment of further immigrants. However, individual introductions (e.g. the ant *Pheidole megacephala*, the feral goat, the feral pig, etc.) can be crucial in this regard.

Comparisons of bird communities on oceanic islands with those of comparable mainland habitats suggests to some workers that as a result of lower species numbers on islands, competition is often reduced and niches are broader (Crowell, 1962; MacArthur *et al.*, 1972). Williamson (1981) questions whether niche expansion on islands has really been demonstrated, but concludes from his review of island ecology that 'isolated islands have a distinctive biota, and the number of species per unit area is less than on an equivalent area of the mainland, or of less isolated islands.' Mountainspring and Scott (1985), working in relatively undisturbed upland habitats of Hawaii, Maui and Kauai, found only sporadic interspecific competition between native and introduced bird species and virtually none among native species or among introduced species. Competition among native Hawaiian species would be expected to have been drastically reduced by massive extinctions in the past 1500 years related to habitat destruction or disturbance (Olson and James, 1982; Kirch, 1982; Gagné, 1975) and by severely negative effects of avian pox and malaria, introduced within the past century (van Riper *et al.*, 1986). There appears to be at least some evidence that upland Hawaii is not presently saturated with bird species, making it highly vulnerable to continued invasion.

On the other hand, Moulton and Pimm (1983) inferred substantial competitive interaction in the Hawaiian Islands among introduced bird species below 600 m elevation. Since most inadvertent introductions occur at low elevations in areas of high human population density, the most effective barrier against further bird invasions may be the relative saturation of lowland habitats with introduced bird species.

Likewise, invasion of low and middle elevation areas in the Hawaiian Islands by about 40 species of alien ants has produced alien ant communities that appear relatively resistant to further invasions (Huddleston and Fluker, 1968; Fluker and Beardsley, 1970). Immigration or introduction of numerous alien parasitoid hymenopterans and ants not only adversely effects native biota (Howarth, 1985), but retards establishment of intentional biocontrol introductions (Howarth, 1983) and depresses populations of introduced pest species (Wong *et al.*, 1984).

Disharmony and low species numbers appear to contribute in at least a minor way to vulnerability of islands to invasions.

10.4.4 Reduced aggressiveness and vulnerability to extinction of island biotas

Numerous workers have noted that native island species have reduced 'aggressiveness' or increased vulnerability to extinction even under optimal environmental conditions. A theory first proposed by E. O. Wilson (1961) in describing this phenomenon for the Melanesian ant fauna is the concept of the taxon cycle. Later, Greenslade (1968) and Ricklefs and Cox (1972, 1978) applied the theory to the avifauna of the Solomon Islands and West Indies respectively. The taxon cycle concept involves the increasing habitat specialization and increasing vulnerability to extinction that a taxonomic group undergoes in the progressive invasion of an archipelago. In Solomon Island birds, for example, recent colonizers (Stage I) are expanding and are present in coastal and cultivated habitats throughout the island group (Greenslade, 1968). In Stage II, there is a fragmentary distribution in tropical rainforests, leading to subspeciation and some local extinction. In Stage III, involving speciation, populations become highly fragmented as a result of habitat shift to montane forests with range contraction and extensive extinction of local populations. Extinctions are due both to invasion by later arriving forms and to over-specialization in small habitats.

Williamson (1981) has reviewed the taxon cycle concept favorably, concluding with the following statement: 'Only a few cases of the taxon cycle have been described, but no studies have been published showing it to be inapplicable. How general a phenomenon the cycle is remains to be determined.' Kruckeberg and Rabinowitz (1985) have, on the other hand, criticized the taxon cycle concept as unfalsifiable. Carlquist (1974) cites the work of McDowall (1969) as suggesting that the older an island endemic is, the more prone it is to extinction. McDowall showed that the higher the taxonomic level of endemism for New Zealand land birds (e.g. endemic family versus endemic subspecies) the more chance of their being extinct or endangered with extinction.

Application of a similar approach to McDowall's to the Hawaiian angiosperm flora and bird fauna yields similar results (Tables 10.3 and 10.4). Among Hawaiian flowering plants (Table 10.3), a taxon in an endemic Hawaiian genus is 1.3 times as likely to be extinct or endangered as one endemic at the species level, 4 times as

Table 10.3. Relationship between vulnerability of taxa in the Hawaiian flora and the taxonomic level of endemism. Computations made based on data in St. John (1973) for numbers of taxa in flora and levels of endemism and in Fosberg and Herbst (1975) for extinction or level of endangerment

	Taxa Endemic at Level of:			
	Genus	Species	Variety	Not endemic
No. of taxa in flora	872	1562	33	43
No. (%) of extinct taxa	135(15%)	133(9%)	0	0
No. (%) of 'endangered' taxa	311(36%)	480(31%)	4(12%)	2(5%)
Total extinct or endangered taxa	446(51%)	613(40%)	4(12%)	2(5%)
No. of 'rare' taxa	25	63	0	1
No. taxa of 'uncertain' status	235	278	4	0
Total extinct or vulnerable taxa	706(81%)	956(61%)	8(24%)	3(7%)

likely as one endemic at an infraspecific level, and 10 times as likely as a native taxon not endemic at any level. The same pattern holds true if taxa classed as 'rare' and 'of uncertain status' (many of which are actually extinct or endangered) by Fosberg and Herbst (1975) are included. In the historically known Hawaiian bird fauna (Table 10.4), no taxon endemic at a level below species is extinct and no nonendemic taxon is classified as 'endangered,' whereas for endemics at the species, genus, and subfamily levels, 32% are extinct and 50% endangered. Such analyses seem to give at least some support to the taxon cycle theory.

The genetic basis of the phenomenon of reduced aggressiveness with progressive island evolution is virtually unexplored, but the extensive work with Hawaiian drosophilids by H. L. Carson and colleagues provides a basis for educated speculation. To begin with, we must emphasize that Carson's work shows no evidence for genetic impoverishment of local drosophilid populations in Hawaii. Carson (1981, pp. 471–2) summarized studies of genetic variation in Hawaiian *Drosophila* as follows:

> The genetic data presented here provide no evidence that there are unique properties to the genetic variation systems of insular species. Thus the levels of genetic variation found within a series of endemic and introduced species of *Drosophila* are basically similar to their continental counterparts. Perhaps the most important point is that island species, even some with quite small total populations, are capable of carrying as much genetic variability in a local population as are species with very large populations.

In spite of comparable variability of local populations, termed 'the growing point of evolutionary change,' insular and continental species differ in their gross population size (Carson, 1981). Continental species have many local populations; island populations have few. Carson continues (p. 474):

> Accordingly the total genetic variance carried in a continental species should be far greater than that found in insular ones. A continental deme will be able to draw variability from adjacent demes, given a capacity for gene flow between demes. Any deme is limited in the amount of genetic variability it can carry. Continental demes... have the advantage of being able to be enriched continually by gene flow. This probably represents an important difference between island and continental populations. The isolated nature of most island demes may be conducive to the evolution of restrictive specializations, whereas continental conditions are capable of giving rise to the genetic basis of a generalism, wherein the organism is homeostatic. This difference may underlie the observed failure among island organisms to evolve aggressive weedy organisms that have genotypes adapted to general purposes.

Table 10.4. Relationship between vulnerability of taxa in the historically known Hawaiian resident bird fauna and the taxonomic level of endemism. Computations made based on taxonomic status and status on Federal List of Endangered Species given in Pyle (1983).

	No. of Species Endemic at Level of:				
	Subfamily	Genus	Species	Subspecies	Not endemic
Phaethontidae					
Non-endangered	—	—	—	—	1
Sulidae					
Non-endangered	—	—	—	—	3
Fregatidae					
Non-endangered	—	—	—	—	1
Ardeidae					
Non-endangered	—	—	—	—	1
Anatidae					
Endangered	—	1	2	—	—
Acciptridae					
Endangered	—	—	1	—	—
Rallidae					
Extinct	—	—	2	—	—
Endangered	—	—	—	2	—
Recurvirostridae					
Endangered	—	—	—	1	—
Laridae					
Non-endangered	—	—	—	—	3
Strigidae					
Non-endangered	—	—	—	1	—
Corvidae					
Endangered	—	—	1	—	—
Muscicapidae					
Endangered	—	—	3	—	—
Non-endangered	—	—	1	—	—
Melaphagidae					
Extinct	—	4	—	—	—
Endangered	—	1	—	—	—
Fringillidae					
Extinct	8	—	—	—	—
Endangered	13	—	—	—	—
Non-endangered	7	—	—	—	—
Totals					
Extinct	8	4	2	0	0
Endangered	13	2	7	3	0
Non-endangered	7	0	1	1	9

Recent investigations of allozyme variation in several island groups that have undergone extensive adaptive radiation shed additional light on the genetic structure of island taxa. Lowrey and Crawford (1985) examined allozyme divergence in Hawaiian *Tetramolopium*, a morphologically and ecologically diverse group in the Asteraceae occupying habitats from sea level to above 3000 m. They found that 'the mean genetic identity for pairwise comparison of 19 populations from seven species is 0.95, a very high value normally obtained for conspecific plant populations.' This type of pattern has been found in Hawaiian *Bidens* (also Asteraceae) by Helenurm and Ganders (1985) as well as in such diverse island groups as Hawaiian *Drosophila* (Diptera: Drosophilidae) (Carson and Kaneshiro, 1976), Galapagos finches (Fringillidae: Geospizinae) (Yang and Patton, 1981), and the snail genus *Partula* in Moorea of French Polynesia (Johnson *et al.*, 1977).

Another genetic factor, although a highly controversial one (e.g. Charlesworth *et al.*, 1982), that could lead to increased vulnerability of island species through evolutionary time is the repetition (and compounding) of founder events in the genetic history of many island species. The Hawaiian Islands have an ancient insular biota which has established by long-distance dispersal (Fosberg, 1948; Carlquist, 1974; Gressitt, 1978; Carson and Templeton, 1984) and undergone adaptive radiation on an archipelago much older than the currently existing islands. Whereas the oldest current high island, Kauai, has no dated rocks more than 6 million years old, geological evidence suggests an age of 30–40 million years for the now largely eroded older islands in the Leeward Hawaiian chain and up to 70 million years for the islands in the adjacent Emperor Seamount Chain (Macdonald *et al.*, 1983). Biological evidence from DNA and protein 'clocks' suggests that the ancestral forms of Drosophilinae and Drepanidinae arrived in the island chain prior to the existence of the current high islands (Sibley and Ahlquist, 1982; Beverley and Wilson, 1985). The rigor of natural selection in such an evolving insular system may be relaxed by the large number of genetic bottlenecks (founder events) many groups have undergone in island-hopping.

Carson (1981), referring to the founding of populations of Hawaiian *Drosophila* on geologically new islands (often by a single gravid female) states: 'At each of these events, drastic effects on the genetics of the new species resulting from founders would be expected. Species that inhabit a moderately old archipelago such as Hawaii have populations that both ancestrally and currently have been and are being rent by forces of chance to which no specific adaptational response is possible.' Natural selection operates, of course, on these populations and the island forms achieve a high level of adaptation to their new local environment—but in many instances may not be so well adapted as the 'general purpose genotypes' of invasive introduced species.

In summary, there are suggestive patterns and some interesting genetic evidence possibly related to the relative lack of aggressiveness and tenacity of some island species. However, further work is needed before definitive statements can be made. Granted that some island species exhibit reduced aggressiveness and increased vulnerability to extinction, we wish to emphasize that by no means all island species suffer such restriction. For example, the native fern *Dicranop-*

teris linearis aggressively colonizes disturbed areas, in some cases displacing aggressive non-native woody plants. *Metrosideros polymorpha*, the dominant tree in many Hawaiian forests, exhibits a number of ecotypes, some of which are successful colonizers of recent lava flows, others are better adapted to older, more mesic soils, and still others to bogs (Stemmermann, 1983). Aggressive non-native plants notably lack competitive superiority over natives in extreme habitats such as on new lava flows (Smathers and Mueller-Dombois, 1974), on soils with aluminum toxicity (Gerrish and Mueller-Dombois, 1980), and in montane bogs (Canfield, 1986).

10.5 ISLAND INVASIONS AND CONSERVATION

The inference that conservation of island ecosystems is a hopeless task because of their vulnerability to invasions has been often used as a rationalization for either wholesale destruction of island biotas or benign neglect of their protection. For example, an early influential figure in Hawaiian botany and forestry, H. L. Lyon, noted (1909, 1918, 1919) the widespread dieback of native *Metrosideros* rainforest on northern East Maui (termed the 'Maui forest disease') and concluded that Hawaiian native forests could not be maintained or restored and that a new forest flora must be built from introduced species in order to save the Islands' watershed (Holt, 1983). Lyon's interpretations led to massive introductions of introduced trees to Maui with limited positive results and much subsequent damage from aggressive invasive species. Similarly, Burgan and Nelson (1972) and Petteys *et al.* (1975) interpreted large-scale *Metrosideros* dieback on the island of Hawaii as a progressive disease-induced decline which would ultimately lead to the demise of most *Metrosideros*-dominated native forests. An obvious implication of this work was that these native forests should be exploited commercially before their natural demise took place. However, work by Mueller-Dombois and his co-workers (summarized in Mueller-Dombois *et al.*, 1981; Mueller-Dombois, 1985) has largely contradicted interpretations of earlier workers on the demise of *Metrosideros* forests, and has shown that in most instances forest dieback is followed by vigorous regeneration (e.g. Jacobi *et al.*, 1983). Mueller-Dombois (1983) interprets *Metrosideros* dieback in Hawaii as a recurring natural phenomenon that may be related to similar phenomena in New Zealand, Australia, and New Guinea.

Studies of vegetation response within fenced exclosures in Hawaii indicate that at least partial recovery of native vegetation occurs in most instances after the influence of alien ungulates is removed (Loope and Scowcroft, 1985). The synthesis volume of work in Hawaii as part of the International Biological Program's Island Ecosystems project (Mueller-Dombois *et al.*, 1981) took a positive view of the ability of island organisms to survive, given reasonable human assistance. Increasingly active management by the US National Park Service in Hawaii's national parks in the past two decades has yielded some success (Stone and Loope, 1987). With active management, primarily involving control of feral ungulates and some of the more aggressive plant invaders, chances appear good for preservation of the still largely intact systems at high elevations and on specialized sustrates.

10.6 SUMMARY AND CONCLUSIONS

Isolated oceanic islands were predisposed to certain types of human-related invasions because of long isolation from the continual challenge of some of the selective forces that shape continental organisms—including such forces as virulent diseases, browsing and trampling of herbivorous mammals, ant predation, and frequent and intense fire. In spite of their very limited resources, islands (particularly tropical ones) have fascinated and attracted humans, resulting in severe direct and indirect human impacts. The structure of island ecosystems, generally comprised of relatively few species in comparison to comparable mainland habitats, and certain genetic properties of island taxa may also contribute significantly to their vulnerability to invasion. Much remains to be understood. Island biology has played a major role in the development of evolutionary theory. As native island species continue to be lost to the onslaught of invaders, accompanied by the further loss of dependent coevolved species, opportunities are lost for important studies that can continue to contribute to the mainstream of biological theory. Well planned, scientifically based efforts at active management of strategically selected island ecosystems appear highly worthwhile. At the very least, they will greatly prolong the time that these systems will be available for study.

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