

# The evolutionary impact of invasive species

H. A. Mooney\* and E. E. Cleland

Department of Biological Sciences, Stanford University, Stanford, CA 94305-5020

Since the Age of Exploration began, there has been a drastic breaching of biogeographic barriers that previously had isolated the continental biotas for millions of years. We explore the nature of these recent biotic exchanges and their consequences on evolutionary processes. The direct evidence of evolutionary consequences of the biotic rearrangements is of variable quality, but the results of trajectories are becoming clear as the number of studies increases. There are examples of invasive species altering the evolutionary pathway of native species by competitive exclusion, niche displacement, hybridization, introgression, predation, and ultimately extinction. Invaders themselves evolve in response to their interactions with natives, as well as in response to the new abiotic environment. Flexibility in behavior, and mutualistic interactions, can aid in the success of invaders in their new environment.

**The Nature of the Problem.** Those of us alive today are witnessing the consequences a number of truly grand, but unplanned, biological experiments. They are the result of the activities of a massive human population that is still growing and increasing its impact on the Earth. Because there are no controls on these experiments, as such, we must look to biological patterns through time for perspective on the consequences of the mixing of biotas. This is a challenge because environments of the past also changed, sometimes abruptly.

These historical fluctuations in climate and biota of the past have led some to say that nothing new is happening that has not already happened before. The response to this proposition is yes, but the *rate of change* in the composition of the atmosphere today exceeds anything of the past, as will the consequent rate of climate change. This is also true to a large degree in the extent of migration of species among continents. Before the Age of Exploration, dispersal of organisms across these great biogeographic barriers was a low-probability event; however, today this is routine. In this paper we briefly summarize the consequences of the massive movement of organisms across these barriers in terms of the course of future evolution.

We start this essay with two quotes providing perspectives on the problem. One is from the pioneering work of Charles Elton (1), who stated, “We must make no mistake: we are seeing one of the great historical convulsions in the world’s fauna and flora.” Elton certainly had no doubts of the magnitude of the invasive species issue. More recently, Geerat Vermeij (2) remarked specifically about the evolutionary consequences of this convulsion, “. . . if newcomers arrive from far away as the result of large-scale alterations in geography or climate, the change in selective regime and the evolutionary responses to this change could be dramatic.” We examine here some of the evidence for this potentially dramatic scenario.

**The Changing Evolutionary Landscape.** It is commonly acknowledged that the abiotic environment is being greatly altered because of massive land-use alteration and emerging climate change (3, 4). However, an equally drastic alteration is occurring in the composition of biotic communities. The kinds of physical

and biotic environments that exist now are quite different from those that have existed in recent geological times.

International commerce has facilitated the movement of species; this is true globally and across taxonomic groups. Ironically, this has increased species richness in many places where new species are introduced. The actual numbers of individuals and species being transported across biogeographical barriers every day is presumably enormous. However, only a small fraction of those transported species become established, and of these generally only about 1% become pests (5). Over time however, these additions have become substantial. There are now as many alien established plant species in New Zealand as there are native species. Many countries have 20% or more alien species in their floras (6). There are few geographic generalities to these trends; the strongest is that islands, in particular, have been the recipients of the largest proportional numbers of invaders. Biotic homogenization within continents is equally as striking as mixing among oceans. As one example, Rahel (7) notes that in the United States pairs of states on average now share 15 more species than they did before European settlement. The states of Arizona and Montana, which previously had no fish species in common, now share 33 species in their faunas.

Mack (8) estimates that over the last 500 years, invasive species have come to dominate 3% of the Earth’s ice-free surface. Vast land or waterscapes, in certain regions, are completely dominated by alien species, such as the star thistle *Centaurea solstitialis* in the rangelands of California, cheatgrass (*Bromus tectorum*) in the intermountain regions of the western United States, and water hyacinth (*Eichornia crassipes*) in many tropical lakes and rivers.

**The Rates of Exchange.** As the volume of global trade increases, one would expect the rate of establishment of alien species to increase also; data support this prediction. Cohen and Carlton (9) noted that the rate of invasion into San Francisco Bay has increased from approximately one new invader per year in the period of 1851–1960, to more than three new invaders per year in the period of 1961–1995. In the United States the numbers of fish introductions, either from foreign sources or across watershed boundaries, has increased dramatically. In the period between 1850 and 1900, 67 species were introduced, between 1901 and 1950, 140 species, and between 1951 and 1996, 488 species (ref. 10 and the web site referred to therein).

In addition to the greater number of species crossing borders there is also a buildup in the invasive potential of those nonnative species already established in a region, as immigration increases their population sizes. “Introduced species” may stay at a fairly low population size for years and then explode at some later date—the so-called lag effect. This lag effect may simply be the result of the normal increase in size and distribution of a population. For instance, *Bromus tectorum* was introduced to

This paper was presented at the National Academy of Sciences colloquium, “The Future of Evolution,” held March 16–20, 2000, at the Arnold and Mabel Beckman Center in Irvine, CA.

\*To whom reprint requests should be addressed. E-mail: hmooney@jasper.stanford.edu.

intermountain western North America around 1890, and remained in localized populations for 20 years. This lag phase was followed by 20 years of logistic range expansion; by 1930 *B. tectorum* was dominant over 200,000 km<sup>2</sup> (11).

Crooks and Soule (12) note that in addition to the normal population growth lag phase there are other mechanisms that can keep newly introduced species at low levels for decades before they become invasive. These include environmental change, both biotic and abiotic, after establishment and genetic changes to the founder populations that enable subsequent spread. Evidence for the former cases is abundant but scarce for the latter.

In summary, the biotic background for evolution has been changing since the Age of Exploration, and at an ever-accelerating pace because of accumulative effects of the numbers of species involved, the increased rate of exchange, and the lag debts that communities have amassed.

**Looking to the Past.** There are examples from the past of sudden mixing of biotas that were formerly isolated; one of these is fairly recent and instructive. The biota from the Red Sea and the Mediterranean Sea were reconnected, after a separation of millions of years, by the construction of the Suez Canal in 1869. The pathway for movement between these water bodies has changed since 1869 because of the varying salinity of a lake in the canal system; that is, there has not been totally free exchange without barriers. Nonetheless, over 250 species, 34 new genera, and 13 new families have moved into the Mediterranean Sea from the Red Sea, yet there has only been one documented extinction (13). These invasions have primarily been accommodated by niche displacements through competitive interactions among the congeners (14). Many of the native fish in the Mediterranean have maintained their preinvasion feeding habits but have been displaced in depth by the Red Sea invaders, which prefer the shallower, warmer, waters at the surface (15). Two nocturnally foraging fish (*Sargocentron rubrum* and *Pmpheris vanicolensis*) have shown large population increases after invading the Mediterranean from the Red Sea. Night foraging is an uncommon strategy among native Mediterranean fish (only one feeds at night), hence these migrants were probably successful because this novel behavior allowed them to exploit resources that the native fauna had not yet used.

There have been a number of spectacular population explosions of the Red Sea immigrants through time, most of which have eventually become reduced in size (14). An exception is *Rhopilema nomadica*, a large Red Sea jellyfish that experiences population explosions and crashes each summer off the coast of Israel.

The Great American Interchange of biota, the result of the isthmian land bridge that formed during the Late Pliocene, provides further information on the consequences of the mixing of previously isolated biota. However, the course of temporal resolution of the information available does not make it possible to say with certainty whether the losses of biota that occurred subsequent to the bridge were due to competition with new arrivals, although it appears likely (16). The effects of the interchange apparently were asymmetrical, with the immigrants from the south “insinuating” into the northern biota, whereas the northern immigrants to the south may have caused extinctions and undergone subsequent evolutionary radiation (17).

What we lack is detailed information on the impacts of the exchanges of biota on time frames greater than centuries but less than millions of years. In the century time frames we have processes that are still in a state of flux at the community level and ones that have been that have not been studied in detail. In the geological time frame, the poor temporal resolution does not permit us to clearly understand the mechanisms that have led to what we see in the fossil record.

## The Direct Evolutionary Consequences of Mixing

**Evolutionary Adjustments of Invaders and of the Invaded.** We turn to contemporary studies to give us some indication of the evolutionary impact of invasive species. Recent studies have shown that invaders can rapidly adapt to the new environments in which they find themselves. Huey *et al.* (18) demonstrated how an introduction of a new fruit fly into the west coast of North America resulted in the evolution, in only 20 years, of an apparently adaptive cline related to wing size, throughout the vast new latitudinal range extending from southern California to British Columbia. The cline that developed in North American female flies was similar to that found in the European native populations. Interestingly, the developmental basis for the cline of wing size was different in Europe than for the invader in North America, although the functional result was the same, providing additional evidence for the adaptive advantage of this set of traits.

*Drosophila subobscura* were introduced into North America in 1982; shortly thereafter Ayala *et al.* (19) described the invasion as “a grand experiment in evolution.” This was certainly an accurate prediction, given the results of Huey *et al.* 10 years later, and only 20 years after the beginning of the invasion event.

There are other documented instances of an invading species adapting to its new environment. For example, Johnston and Selander (20) described the evolution of apparently adaptive clines in body size and feather color in English sparrows that were introduced into North America in 1852 and that subsequently established a large geographical range. Further, Cody and Overton (21) described the reduction in distance of dispersability for wind-dispersed seeds of invasive species onto islands in just a few generations in small isolated populations. Similarly, Losos *et al.* (22) demonstrated that within 10–14 years species of lizards introduced onto a series of island in the Caribbean showed adaptive morphological adjustments.

There are also examples of relatively rapid, nonadaptive, genetic change of invaders as seen in house mice introduced into Madeira; localized differentiation of chromosomal races is the result of genetic drift in isolated valleys (23). Similarly, genetic drift has been responsible for geographic genetic patterns found in the introduced *Bufo marinus* in Australia (24).

**Evolution in Response to an Invader.** There are also examples of rapid evolution in native species in response to an introduced species. Carrol and Dingle (25) indicate that populations of the soapberry bug (*Jadera hematoloma*) have evolved differing beak lengths in response to the introduction of new invasive hosts, within only 50 years time. Singer *et al.* (26) have shown rapid evolution in the feeding preferences of the *Euphydryas* butterfly for the invading herb, *Plantago lanceolata*.

Zimmerman (27) documents an interesting case of evolution in response to an introduced crop species. At least five species of host-specific moths (*Hedylepta*) have evolved since the introduction of banana into Hawaii ≈1,000 years ago. These species were threatened at the time of Zimmerman’s study by parasitic wasps and flies introduced for agricultural pest control.

There is a large literature on the evolution of weeds in response to human activities, including agricultural practices. Harlan (28) noted that some weeds have evolved to be crop mimics. Not only are they similar in their phenological development and morphological appearance to the crops with which they have co-evolved, but also their seeds have evolved a similar appearance so they are not sorted and discarded during harvesting. For example, the lentil mimic (*Vicia sativa*) has evolved a seed shape and color comparable to the lentil (*Lens culinaris*). This trait is under control of a single gene. Similarly, *Echinochloa crus-galli* has evolved mimics to rice, *Oryza sativa*, which are very difficult to distinguish from the crop.

De Wet and Harlan (29) surmised that many plant weeds might have evolved from natural pioneer species associated with continuous disturbance by humans. Some weeds that have developed in association with agriculture have become crop mimics as described above. Weeds are also derived from hybridization and introgression with crops as happened with Johnson grass (*Sorghum halepense*) and the cultivated *Sorghum bicolor*. Weeds have also evolved from abandoned domesticated plants.

Thus there are many cases that have been documented of the evolutionary response to the new environment that an invasive species may encounter as well as cases of the adaptive response of organisms to a new invader.

**Hybridization and Introgression.** In addition to direct evolutionary responses of organisms involved in invasions there are also very important indirect effects through changes in the genetic structure of invasive species in relation to the new organisms that they encounter. These major effects are related to hybridization and introgression. Rhymer and Simberloff (30) have recently summarized our knowledge in this area. There are many examples extending over many different taxonomic groups, a few of which are noted below. These authors conclude that in the case of invasive species hybridization with native species can cause a loss in fitness in the latter and even a threat of extinction. McMillan and Wilcove (31) have documented that of 3 of 24 species listed as Endangered in the United States and that subsequently went extinct, 3 were the result of hybridization with alien species.

**Birds**—Mallard ducks (*Anas platyrhynchos*) that have been introduced into various regions of the world have had large genetic effects. They have hybridized and reduced populations of the New Zealand gray duck (*Anas superciliosa superciliosa*), the Hawaiian duck (*Anas wyvilliana*), and the Florida mottled duck (*Anas fulvigula fulvigula*) (30).

**Mammals**—Sitka deer (*Cervus nippon*) were introduced into Great Britain from Japan over a hundred years ago. They have hybridized with the native reed deer (*Cervus elephas*) although they are different in body size. It appears that the genetic integrity of the native red deer is threatened in some regions (32).

**Fish**—There are a number of cases of hybridization and subsequent introgression in fish, primarily game fish where there are massive introductions of foreign stock. These include trout in western and eastern United States as well as in Europe (33, 34). It has been shown, however, that even small introductions of nonnative species can have large impacts on the genetics of native species through hybridization and introgression, as was found for native pupfish in Texas (33).

**Plants**—Abbott (35) notes that of 2,834 species listed in the New Flora of the British Isles 1,264 are aliens. There are 70 recognized hybrids between native and alien species and 21 between aliens. About half of these hybrids show some degree of fertility.

There are many examples of the large populations of invading species swamping small populations of native species by hybridization, but in certain cases small populations of an invader can threaten native species that have much larger populations. This is the case with the invading *Spartina alterniflora* into the San Francisco Bay. It hybridizes with the native *Spartina foliosa*. The invader has a higher pollen output, and greater male fitness, than the native species and the hybrids and it occupies lower intertidal habitats. In time introgression will threaten the native species (36). Conversely, small populations of rare species can be threatened by hybridization in a number of ways (37), including infertility of the hybrids.

Small populations on islands are particularly vulnerable to extinction by hybridization because they are often less genetically divergent than mainland species and have weak crossing barriers as well as unspecialized pollinators. Levin *et al.* (37) describe a

number of cases of extinction by hybridization on islands, including the endemic shrub *Cercocarpus traskaei* with the widespread *Cercocarpus betuloides* and the endangered *Lotus scoparius traskiae* with the *Lotus argophyllus ornithopus*. They specifically note that introductions may threaten rare species on islands and give a number of examples from around the world, including threats to the rare *Arbutus canariensis* and *Senecio teneriffae* on the Canary Islands, *Gossypium tomentosum* on the Hawaiian Islands, and *Pinguicula vulgaris* and *Linaria vulgaris* in the British Islands. They posit that the threat of extinction of rare species by hybridization is very high and that habitat disruption and invasive species are increasing this threat to the degree that conservation programs should strive to isolate rare species from cross-compatible congeners.

**The Origin of New Taxa Through Hybridization and Introgression.** While hybridization with invaders can be a threat to species integrity, it can also be a source of new variation and the origin of new species. *Spartina alterniflora* from the east coast of North America was introduced into Southampton in shipping ballast in the early 19th Century. It subsequently hybridized with the local *Spartina maritima*, producing a sterile hybrid. The hybrid in turn underwent chromosome doubling to produce the new fertile species, *Spartina anglica*. *Spartina anglica* has become very aggressive and occupies large areas of the coastline of the British Isles while at the same time the original invader, *Spartina alterniflora*, and the native *Spartina maritima* have maintained limited distributions. The new polyploid evidently has characteristics that enable it to occupy bare tidal flats that were not available to the parents (38). This event was apparently serendipitous and has not been replicated artificially (39).

In addition to the *Spartina anglica* there are other cases of allopolyploids that have originated from hybridization of native and invasive species. These include species of *Tragopogon* in North America and *Senecio* in Great Britain (35).

There are also examples of introgressive hybrids between native and weedy species becoming stabilized to form new taxa. The introduced *Helianthus annuus* hybridized with native *Helianthus debilis*. The hybrids adapted to the new conditions it encountered to form the subspecies *Helianthus annuus texanus*. Abbott (35) cites six such cases of origins of new taxa.

### The Indirect Evolutionary Consequences of Mixing

**Behavioral and Trait Shifts.** In addition to the evolution of traits to adapt to new environments and to new invaders there are cases of behavioral shifts in the invaders themselves or in response to invaders. Holway and Suarez (40) give examples of shifts in behavior of populations of invading species from that found in their native ranges. Two ant species originating from Argentina (the fire ant *Solenopsis invicta* and the Argentine ant *Linepirtma humile*) both exhibit these shifts. It is not known whether these shifts are founder effects or adaptive. These authors make the case that behavior should be more fully incorporated into research as we build an understanding of the invasion process.

The introduction of brown trout into the streams of New Zealand started in the mid-1800s. They have driven to extinction some local populations of native fish and, in addition, they have evidently resulted in changed behavior of native mayfly nymphs and, to a certain extent, crayfish (41).

In addition to behavioral shifts, either in response to an invader or in response to the new biotic community that an invader encounters, shifts in traits have been observed in an invader in a new environment. Blossey and Notzold (42) note that in populations of invasive species, the individuals are often larger in their new territory than in their native land. They compared plants from populations from the United States and as well as those from Europe where they are subject to natural predation in their native habitat. They attributed the size dif-

ferences to the consequences of natural selection for greater competitive capacity after release from herbivore attack and the need to produce defensive compounds. Although this particular explanation has been challenged (43), others have noted similar cases of this phenomenon in comparing invading plants from Australia into California (44) and comparing invasions from South Africa into Australia and *vice versa* (45).

Invasive ants may also benefit from release from native pathogen populations, leading to larger colony size that confers greater exploitative competitive capacity, as discussed in Holway (46) and Human and Gordon (47) (see below). Colonies of invasive Argentine ants are larger in areas where they invade than they are in their native habitat.

**Niche Displacement.** Gray squirrels (*Sciurus carolinensis*) from North America have displaced the native red squirrel (*Sciurus vulgaris*) throughout most of the deciduous and mixed woodlands of Britain. This displacement apparently has resulted from food competition between these species, with gray squirrels favored by high quantities of oaks in the canopy. Recent decline of hazelnuts over oaks has evidently contributed to the demise of the red squirrel (48).

There has been a detailed study of the interaction between a California native mudsnail, *Cerithidea californica*, and an invasive mudsnail, *Ilyanassa obsoleta*, from the American Atlantic. Populations of *Ilyanassa* have locally displaced *Cerithidea* from the open tidal flats, restricting its distribution to the upper intertidal area. *Cerithidea*'s former functional role has been taken over by *Ilyanassa* (49).

Douglas *et al.* (50) have described the apparent niche shift in the native fish *Meda fulgida* when they co-occur with the introduced red shiner (*Cyprinella lutrensis*).

**Competitive Exclusion.** Some invasive species completely eliminate native species through competitive exclusion. The invasive fire ant (*Solenopsis invicta*), for example, has had a devastating effect on the arthropod biota that it encounters. In a detailed study in Texas, it was found that this fire ant reduced native ant diversity by 70% and the total number of native ant individuals by 90%, apparently by competitive exclusion. Similarly, overall non-ant arthropod diversity was reduced by 30% and the numbers of individuals by 70% (51). It should be noted, however, that while the fire ants excluded some native species from the invaded areas, the natives persisted in nearby uninvaded areas, such that no extinctions were observed.

The Argentine ant (*Linepithema humile*) is a widely distributed invasive species that displaces native ants throughout its introduced range. It does so by being a better competitor for food resources than the native species (46, 47).

There are accumulating studies examining the mechanisms of competitive displacement of native species by invaders. As examples, superior competition for food resources has resulted in the replacement of the native gecko, *Lepidodactylus lugubris*, by the invading *Hemidactylus frenatus*, throughout the Pacific (52). A higher resource-use efficiency of the available food resources has been implicated in the competitive superiority of the introduced snail *Batillaria attramentaria* over the native mud snail *Cerithidea californica* in the salt marshes and mud flats of northern California (53). Studies have also shown that behavioral differences in aggression and predation between a native and an invading amphipod explain competitive displacement (54). Competition for space by the invading mussel *Mytilus galloprovincialis* from southern Europe has displaced native mussels in California and South Africa (55).

Studies of such new interactions, brought about by invaders, are particularly revealing on the nature of competition because in "stable" ecosystems, with a long history of competition among

its members, the resulting evolution of niche displacement makes it more difficult to observe the direct competitive process.

**Mutualisms.** In any ecosystem there is a web of interaction among the biotic components of differing specificities. Mutualisms, the tightest of such interactions, would seem to be a barrier to the success of a single player of a partnership becoming an invasive species. There is some evidence for this in the fact that nonmycorrhizal (i.e., do not depend on mutualistic root fungi) plant taxa, such as the Brassicaceae and the Chenopodiaceae, are particularly successful weeds. However, quite often the tightness of mutualisms is not as great as supposed and other species in the new habitat can play the required role for the invader (e.g., pollination). There are also examples of the arrival of one nonnative species, and the subsequent arrival of a co-evolved facilitator, thereby increasing the success of each in its new environment. This has happened with *Pinus* spp. and their mutualistic mycorrhizal fungi in the Southern Hemisphere; Richardson *et al.* (56) describe these as well as other examples.

With the mixing of biota and thus new interaction potentials there is the great possibility of new kinds of mutualistic relationships evolving. Richardson *et al.* (56) note several such cases, including the dispersal of North American and European pine seeds, which are normally wind-dispersed, being dispersed into new areas by cockatoos and European pines being dispersed in South Africa by alien American squirrels. Simberloff and Von Holle (57) also note cases of one invading species facilitating the success of another, including a bird of Asian origin being the prime disperser of a shrub from the Canary Islands, all in their new Hawaiian home.

There are also instances of an invasive species disrupting mutualistic relationships (58). Native seed-harvesting ants disperse the seeds of certain proteas in South Africa. These native ants have been displaced by Argentine ants that are not successful in dispersing the *Protea* seeds to suitable germination microsites, thus potentially leading to the extinction of rare and endemic *Protea* species.

Finally, there are striking examples of host shifts as species are mixed through invasions and a parasite of one infects the other which is less able to cope with the parasite, as is happening with the parasitic mite *Varroa jacobsoni*, which evolved as a brood parasite of the Asian hive bee, *Apis cerana*, but which has now also switched host to the western honeybee, *Apis mellifera*, with disastrous results (59).

**Extinctions.** Invasive species not only alter competitive interactions and reduce native populations within a community but they can also lead to extinctions. Overall they are considered the second greatest threat to imperiled species in the United States (60). Carlton *et al.* (55) make the useful distinction among extinction events as local, regional, or global extinctions. They also recognize functional extinctions where individuals of a species are so reduced in numbers that they no longer play a major role in ecosystem processes. Thus there is a large continuum of impacts, with the main concern and statistical information available on the total global extinction of a species whereas, of course, local extinctions and population reductions are important in ecosystem functional considerations as noted by Carlton *et al.*

The literature abounds with examples of invasive species driving local native species to extinction, primarily on islands, and especially involving predators. Rodda *et al.* (61) detail the particularly dramatic case of the impact of the invasive brown tree snake (*Boiga irregularis*) on the biota of Guam, which has caused a major conservation crisis through negative effects on birds, reptiles, and mammals. In a review of the impacts of introduced species on reptiles on islands Case and Bolger (62) note that, "Although competition has led to changes in abun-

dance and has caused habitat displacement and reduced colonization success, extinctions of established reptile populations usually occur only as a result of predation.” They do note the large number of examples of the latter that have occurred as a result of predation by rats, feral cats, and mongooses.

It has been well documented that of all ecosystems lakes and streams have been most modified by invasive species, mainly because of the persistent efforts of humans to stock with game fish. Many of the introductions into these bodies result in species enrichment rather than extirpation (63). However, one of the most spectacular example of species extinctions in lakes comes from the introduction of the Nile perch into Lake Victoria, resulting in the loss of hundreds of species of cichlid fish (64). Ricciardi and Rasmussen (65) call attention to the fact that the freshwater fauna of temperate North America has extinction rates matching that of tropical forests, in part because of invasive species. Ricciardi *et al.* (66), for example, note a global pattern, that within 4–8 years after invasion by zebra mussel (*Dreissena polymorpha*) local native mussel populations are extirpated. Over 60 endemic mussel species of the Mississippi River Basin are threatened with global extinction by the effects of zebra mussel and environmental degradation.

Although the introduction of an organism into a new environment always provides risks and surprises as to the impact it will have on other organisms, it is particularly disconcerting when organisms that are introduced to control the activities of an unwanted invader instead do collateral damage to other species, even driving them to extinction. This is apparently the case with the introduction of the rosy wolf snail, *Euglandina rosea*, which was imported into Hawaii in 1958 to control the giant African snail, *Achatina fulica*. Unfortunately, *Euglandina* did not restrict its predatory activity to the African snail but also attacked rare native Hawaiian snails (67), apparently driving some to extinction. Between 1977 and 1987 *E. rosea* pushed the endemic tree snails of the island of Moorea to extinction (68). There is another extinction crisis in the making with the movement of *Cactoblastis cactorum* from its point of introduction for the control of *Opuntia* in the Caribbean, to a trajectory that will bring it to a center of diversity of *Opuntia* in Mexico (H. G. Zimmermann, personal communication).

There have been attempts to give us some sense of the ultimate result of the mixing of the biota of world. Brown (69) has calculated, based on species–area relationships, the worst-case scenario for the impact of free exchange of biotic material across former biogeographic barriers. This was done assuming the Earth’s land surface was contained into one supercontinent but that the current climates and geological features were maintained. With these assumptions there would be massive decrease in species, amounting to 65.7% for land mammals, 47.6% for land birds, 35% for butterflies, and 70.5% for angiosperms. McKinney (70) has made similar calculations for the ocean and concludes that there would be a reduction of about 58% in the current diversity. McKinney points out, however, that for the

theory to be fulfilled there would have to be unfiltered faunal exchange around the world and the lack of physical variability. McKinney notes that it is because these conditions are not fulfilled that we have not seen extinctions in relation to the Suez Canal exchanges.

### Concluding Remarks

In the course of this review we have discussed the mechanisms by which invasive species evolve in response to their new biotic and abiotic environments, and how invasive species have altered the evolutionary trajectory of native species with which they interact. While it is not surprising that an invasive species would evolve in their new habitat in response to a new set of selective pressures, it is surprising that there are a number of clear examples of evolutionary shifts in native species in response to the presence of invaders, given the small number of generations involved in interactions, and the short period for which such interactions have been studied by ecologists and evolutionary biologists. Much of the evidence we have reviewed has been observed in islands, reinforcing what we know of islands as evolutionary hotspots. While few generalizations can be made across taxa and across environments, we can venture a few tentative conclusions. First, invasive predators may have the most dramatic effects, as the extinctions they cause represent an irreversible removal of evolutionary potential. Second, few examples of extinction have been associated with competitive interactions. This indicates either that extinction by competition is a slower process than extinction by predation, such that the end product of the process is not likely to be observed on the time scale of most scientific studies, or that communities are not as “full” as most ecological theories presume. Third, interactions between invasive and native biota demonstrate how global changes that alter community structure can have persistent and unexpected consequences.

The biota of the Earth is undergoing a dramatic transformation. The spatial patterning, structure, and functioning of most of the ecosystems of the world have been altered by the activities of humankind. There is every indication that these trends will intensify as the size of the human population continues to grow, even in systems that have been set aside for protection, because of the global changes that have been set in motion that are affecting the atmosphere and the climate. Although some aspects of global change, such as climate change, may be reversed by societal actions, this will not be possible for biotic exchange. The mixing of formerly separated biota, and the extinctions these introductions may cause, are essentially irreversible. Since the beginnings of the Age of Exploration, humans have purposefully and inadvertently moved biological material across barriers that, for recent evolutionary time, have separated the unique biotic realms of the continental land masses. We are now developing a whole new cosmopolitan assemblage of organisms across the surface of the Earth with large consequences not only for the functioning of ecosystems but also for the future evolutionary trajectory of life.

1. Elton, C. S. (1958) *The Ecology of Invasions by Animals and Plants* (Methuen, London).
2. Vermeij, G. J. (1996) *Biological Conservation* **78**, 3–9.
3. Vitousek, P. M., Mooney, H. A., Lubchenco, J. & Melillo, J. M. (1997) *Science* **277**, 494–499.
4. Sala, O. E., Chapin, F. S. I., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., *et al.* (2000) *Science* **287**, 1770–1774.
5. Williamson, M. (1996) *Biological Invasions* (Chapman and Hall, London).
6. Vitousek, P. M., D’Antonio, C. M., Loope, L. L. & Westbrooks, R. (1996) *Am. Sci.* **84**, 468–478.
7. Rahel, F. J. (2000) *Science* **288**, 854–856.
8. Mack, R. N. (1985) in *Studies in Plant Demography*, ed. White, J. (Academic, London), pp. 127–142.
9. Cohen, A. N. & Carlton, J. T. (1998) *Science* **279**, 555–558.

10. Nico, L. G. & Fuller, P. L. (1999) *Fisheries* **24**, 1–27.
11. Mack, R. N. (1981) *Agro-Ecosystems* **7**, 145–165.
12. Crooks, J. A. & Soule, M. E. (1999) in *Invasive Species and Biodiversity Management*, eds. Sandlund, O. T., Schei, P. J. & Viken, A. (Kluwer, Dordrecht, The Netherlands), pp. 103–125.
13. Por, F. D. (1978) *Lessepsian Migration* (Springer, Berlin).
14. Spanier, E. & Galil, B. S. (1991) *Endeavour* **15** (New Series), 102–106.
15. Golani, D. (1993) *Isr. J. Zool.* **39**, 391–402.
16. Simpson, G. G. (1980) *Splendid Isolation: The Curious History of South American Mammals* (Yale Univ. Press, New Haven, CT).
17. Webb, S. D. (1991) *Paleontology* **17**, 266–280.
18. Huey, R. B., Gilchrist, G. W., Carlson, M. L., Berrigan, D. & Serra, L. (2000) *Science* **287**, 308–309.
19. Ayala, F. J., Serra, L. & Prevosti, A. (1989) *Genome* **31**, 246–255.
20. Johnston, R. F. & Selander, R. K. (1960) *Evolution* **14**, 548–550.

21. Cody, M. L. & Overton, J. M. (1996) *J. Ecol.* **84**, 53–61.
22. Losos, J. B., Warheit, K. I. & Schoener, T. W. (1997) *Nature (London)* **387**, 70–73.
23. Britton-Davidian, J., Catalan, J., Ramalhinho, M. D., Ganem, G., Auffray, J. C., Capela, R., Biscoito, M., Searle, J. B. & Mathias, M. D. (2000) *Nature (London)* **403**, 158–158.
24. Easteal, S. (1985) *Evolution* **39**, 1065–1075.
25. Carroll, S. P. & Dingle, H. (1996) *Biol. Conserv.* **78**, 207–214.
26. Singer, M. C., Thomas, D. & Parmesan, C. (1993) *Nature (London)* **366**, 681–683.
27. Zimmerman, E. C. (1960) *Evolution* **14**, 137–138.
28. Harlan, J. R. (1965) *Euphytica* **14**, 173–176.
29. De Wet, J. M. J. & Harlan, J. R. (1975) *Econ. Bot.* **29**, 99–107.
30. Rhymer, J. M. & Simberloff, D. (1996) *Annu. Rev. Ecol. Syst.* **27**, 83–109.
31. McMillan, M. & Wilcove, D. (1994) *Update* **11**, 5–6.
32. Abernathy, K. (1994) *Mol. Ecol.* **3**, 551–562.
33. Echelle, A. A. & Echelle, A. F. (1997) *Conserv. Biol.* **11**, 153–161.
34. Lariagder, C. R. & Scholl, A. (1996) *Mol. Ecol.* **5**, 417–426.
35. Abbott, R. J. (1992) *Trends Ecol. Evol.* **7**, 401–405.
36. Anttila, C. K., Daehler, C. C., Rank, N. E. & Strong, D. R. (1998) *Am. J. Bot.* **85**, 1597–1601.
37. Levin, D. A., Francisco-Ortega, J. & Jansen, R. K. (1996) *Conserv. Biol.* **10**, 10–16.
38. Thompson, J. D. (1991) *BioScience* **41**, 393–401.
39. Gray, A. J. (1986) *Philos. Trans. R. Soc. London B* **314**, 655–674.
40. Holway, D. A. & Suarez, A. V. (1999) *Trends Ecol. Evol.* **14**, 328–330.
41. Townsend, C. R. (1996) *Biol. Conserv.* **78**, 13–22.
42. Blossey, B. & Notzold, R. (1995) *J. Ecol.* **83**, 887–889.
43. Willis, A. J., Thomas, M. B. & Lawton, J. H. (1999) *Oecologia* **120**, 632–640.
44. Crawley, M. J. (1987) in *Colonization, Succession and Stability*, eds Gray, A. J., Crawley, M. J. & Edwards, P. J. (Blackwell, Oxford), pp. 429–453.
45. Noble, I. R. (1989) in *Biological Invasions*, eds Drake, J. A., Mooney, H. A., di Castri, F., Groves, R. H., Kruger, F. J., Rejmanek, M. & Williamson, M. (Wiley, Chichester, U.K.), pp. 301–313.
46. Holway, D. A. (1999) *Ecology* **80**, 238–251.
47. Human, K. G. & Gordon, D. M. (1996) *Oecologia* **105**, 405–412.
48. Kenward, R. E. & Holm, J. L. (1993) *Proc. R. Soc. London Ser. B* **251**, 187–194.
49. Race, M. S. (1982) *Oecologia* **54**, 337–347.
50. Douglas, M. E., Marsh, P. C. & Minckley, W. L. (1994) *Copeia* **1994**, 9–19.
51. Porter, S. D. & Sagivnano, D. A. (1990) *Ecology* **71**, 2095–2106.
52. Petren, K. & Case, T. J. (1996) *Ecology* **77**, 118–132.
53. Byers, J. E. (2000) *Ecology* **81**, 1225–1239.
54. Dick, J. T. A., Elwood, R. W. & Montgomery, W. I. (1995) *Behav. Ecol. Sociobiol.* **37**, 393–398.
55. Carlton, J. T., Geller, J. B., Reaka-Kudla, M. L. & Norse, E. A. (1999) *Annu. Rev. Ecol. Syst.* **30**, 515–538.
56. Richardson, D. M., Allsopp, N., D'Antonio, C. M., Milton, C. M. & Rejmanek, M. (2000) *Biol. Rev. Camb. Philos. Soc.* **75**, 65–93.
57. Simberloff, D. & Von Holle, B. (1999) *Biol. Invasions* **1**, 21–32.
58. Bond, W. & Slingsby, P. (1984) *Ecology* **65**, 1031–1037.
59. Oldroyd, B. P. (1999) *Trends Ecol. Evol.* **14**, 293–332.
60. Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A. & Losos, E. (1998) *BioScience*, 607–615.
61. Rodda, G. H., Fritts, T. H. & Chiszar, D. (1977) *BioScience* **47**, 565–574.
62. Case, T. J. & Bolger, D. T. (1991) *Evol. Ecol.* **5**, 272–290.
63. Moyle, P. B. & Light, T. (1996) *Biol. Conserv.* **78**, 141–161.
64. Worthington, E. B., Lowe, M. C. & Connell, R. (1994) *Environ. Conserv.* **21**, 199–213.
65. Ricciardi, A. & Rasmussen, J. B. (1999) *Conserv. Biol.* **13**, 1220–1222.
66. Ricciardi, A., Neves, R. J. & Rasmussen, J. B. (1998) *J. Anim. Ecol.* **67**, 613–619.
67. Stone, R. (1999) *Science* **285**, 1837.
68. Strong, D. R. & Pemberton, R. W. (2000) *Science* **288**, 1969–1970.
69. Brown, J. H. (1995) *Macroecology* (Univ. of Chicago Press, Chicago).
70. McKinney, R. L. (1998) *Global Ecol. Biogeogr. Lett.* **7**, 297–301.