

## Why Do Introduced Species Appear to Devastate Islands More Than Mainland Areas?<sup>1</sup>

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**ABSTRACT:** Island biotas are viewed popularly as much more fragile than those of mainland areas and much more prone to damage from invaders. There are far too few data to assess this view thoroughly; for example, failed invasions are often unrecorded, and claims that an introduced species has displaced a native one are often based on correlated population changes rather than experiment and/or detailed field observations. If there is a tendency for invasions to affect island communities more than mainland ones, it is far from universal; virtually every kind of damage wrought by invaders on islands has also been wrought in mainland areas. It is unlikely that, by virtue of their reduced species richness alone, island communities pose less "biotic resistance" to invaders than mainland communities do. Rather, certain entire groups of species, like terrestrial mammals, are often missing from islands, and these absences can predispose certain invaders to be especially likely to survive and to produce particular impacts.

CONVENTIONAL WISDOM (e.g., Elton 1958, Carlquist 1965, Wilson 1965) is that islands are more easily invaded than mainland areas, and ecological effects of invasions are greater on islands than in mainland situations, because island biotas are somehow fragile and the species weaker than those of the mainland. Yoon (1992:88) eloquently expressed this view with respect to the Hawaiian Islands: "But the isolation of these gentle islands from mainland predators and diseases created a flora and fauna ill equipped to handle the rigors of competition with the outside world. Hawaii is home to thistles without prickles, blackberries without thorns and many flightless insects and birds."

The idea is that island species have been subjected to much less intense selective pressures. In particular, the smaller number of species on islands suggests that competition is less intense, so island species evolve to be less "competitive." Mayr (1965) found island avifaunas to offer "far less resistance" to immigrants than mainland faunas do. Preston

(1968) saw islands as evolutionary "backwaters and dead ends," populated by species whose relatives had long ago been extinguished in mainland areas. Greuter (1979) depicted islands as repositories for old relicts, relatively unimportant in plant evolution. Williamson (1981) believed that slower anagenetic evolution on islands leaves island endemics likely to be extinguished by competition from introduced mainland species. In addition to the susceptibility of island biotas engendered in the long term by evolutionary processes, the small number of species and supposedly simplified food web structures were believed to make island communities particularly invulnerable (e.g., Wilson and Bossert 1971). This belief was part of the dogma that diverse ecosystems are more stable by virtue of their diversity (MacArthur 1955, Elton 1958). The notion that introduced species would be much more likely to survive on islands than in mainland areas even has management implications. For example, Imms (1931) felt that introducing natural enemies for biological control would be an effective method only in the simplified communities of islands.

Nowadays, key aspects of the arguments

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underpinning this conventional wisdom are questionable on numerous empirical grounds. First, is competitive pressure really stronger on the mainland? Though Crowell (1962) and MacArthur et al. (1972) have seen competition among species in bird communities as lower on islands, Schoener (1965), Grant (1968), Keast (1970), and others have argued that competition on islands may be stronger than in mainland areas because the resource base is reduced and that this more intense interspecific competition is reflected in greater morphological divergence of close relatives on islands than in mainland situations. Perhaps generic statements about the relative intensity of competition on islands and the mainland are not very useful, and one must always speak of a specific island and mainland and also determine the relevant resource base empirically.

Second, the relationship between stability and diversity or complexity is now seen as complicated and not monotonic (Begon et al. 1990, and references therein); some diverse, complex systems are very fragile and some simple ones seem stable. That islands tend to have fewer species than mainland areas is likely to be far less important, from the standpoint of invasibility, than the nature of those species that are present (Goodman 1975).

Aside from assessing the underlying reasons for believing that island communities are more likely than mainland ones to be disrupted by introduced species, it is also worth examining whether empirical data really demonstrate this heightened susceptibility.

#### *Probability That an Introduced Species Survives on an Island*

A problem in assessing the likelihood that an introduced species survives on both mainland and islands is general lack of information on failed introductions (Simberloff 1981, 1986a). Approximately 3000 surviving introduced insect species are known from the contiguous United States (Anonymous 1986), and about 2500 are known from the Hawaiian Islands (Funasaki et al. 1988, Nishida

1992). But these are only *surviving* introduced species; who knows how many propagules of other species landed but did not lead to populations or produced small populations that went extinct before being recorded? Surely the number must be greater for the contiguous United States, but how much greater? Probably a lot, so it seems as if the probability of an introduced insect's surviving in Hawai'i is greater. Because Hawai'i has about 5000 described native species (Nishida 1992) and the contiguous United States has about 90,000 (Arnett 1983), the probability of survival seems greater in the site with fewer species. Is this probability of survival greater because there are fewer species there to resist the invader?

An order-by-order examination of the introduced insects of Hawai'i is not consistent with this hypothesis (Simberloff 1986a). For example, Hawai'i has proportionally more surviving introduced Coleoptera and Lepidoptera species than does the contiguous United States, but it also has proportionally more native Coleoptera and Lepidoptera. By and large, even though the native insect orders are very differently represented in Hawai'i than in the contiguous United States (many orders are even missing), the relative proportions of surviving introduced species in the different orders are very similar in the two sites. Without knowing how many species of each order were introduced in each place, we cannot even say where the probability of survival is greatest, so we cannot really assess the hypothesis as we would wish to, but the data on surviving species suggest that the question is not trivial.

Probably the best published data for survival and disappearance of introduced species come from the literature on biological control, although even here there have been many unrecorded, more or less ad hoc introductions (F. G. Howarth, pers. comm., 1991). From an encyclopedic list of biocontrol introductions (Clausen 1978), I found six genera (five parasitic wasp genera and a beetle genus) with the largest number of species that had been introduced, in various directions, among islands and mainland, with Australia considered a mainland (Simberloff

1986a). I tabulated successes and failures of introductions from mainland to island, mainland to mainland, island to island, and island to mainland. If there were less biotic resistance posed by island biotas and island species were generally less competitive, one would expect mainland-to-island introductions to have survived far more frequently than island-to-mainland ones, with the other two classes intermediate. These six genera produced 281 introductions; although the probabilities of survival are in the order predicted, the probabilities are all very close. For example, 49% of mainland-to-island introductions survived, and 33% of island-to-mainland ones. A multiway contingency test does not reject the hypothesis that survival or disappearance of a propagule does not depend on whether source or target areas are island or mainland.

The general relevance of this result is lessened because most biological control efforts on both islands and mainland are in agricultural communities, which are both far from pristine and more similar to one another, no matter whether on island or mainland, than pristine communities would be. Thus the species introduced to islands for biological control purposes were not, by and large, faced at the outset with competition and other interactions from the entire native community. Rather, resistance was from a small subset of it (that lives in anthropogenous habitats), as well as from other introduced species. This same problem obtains when one considers introduced birds, for which some data exist for failures as well as successes. At least 50 passeriform species have been introduced to the Hawaiian Islands, of which 30 survived on all islands to which they were introduced, 17 failed on all islands to which they were introduced, and 3 survived on some islands and failed on others (Simberloff and Boecklen 1991). However, for the most part the introduced birds are found in agricultural lands, exotic forests, and built-up areas, and these were also typical habitats of those species that failed. The native land birds are primarily found in the native forests, almost wholly restricted to uplands (Berger 1981, Moulton and Pimm

1983). There are probably some competitive interactions between introduced birds that *do* invade native forest (especially *Zosterops japonicus* Temminck & Schlegel) and native birds (Scott et al. 1986). But habitat restrictions surely greatly reduce potential competition between introduced species and native ones, so that it is unlikely that resistance or lack thereof by native birds is the reason for success or failure of species introduced to Hawai'i.

Similarly, 20 passeriforms have been introduced to the Mascarene Archipelago, of which nine survived on all islands to which they have been introduced, nine failed wherever introduced, and two survive tenuously on La Réunion but disappeared from Mauritius after more than a century (Simberloff 1992a). As in the Hawaiian Islands, there is general habitat separation between the introduced species and the native ones, with the native species in upland native forest and the introduced species in lowland open anthropogenous habitat. Only *Zosterops borbonicus borbonicus* (Boddaert) among the natives invades open lowland habitats, and only *Fou-dia madagascariensis* (L.) among introduced species is found in forests; for both species the anomalous habitat is a very secondary one (Barré 1983). The species whose invasions failed were also primarily species of open habitat; it is difficult to believe that their failure was caused by competition from native birds.

The smaller number of species on islands than in nearby mainland areas is the most widely known characteristic of island biotas. Invasion by a new species of a new site, island or mainland, is often viewed in terms of the species' having to find an "empty niche" (Udvardy 1969, and references therein). Although the static "niche" that this view entails has given way to a more dynamic conception, the general idea still surfaces frequently and has management implications. For example, many game species are introduced to fill supposedly empty niches on islands (Ebenhard 1988). The vacancy of niches is notoriously hard to prove (Herbold and Moyle 1986). Further, since resources are ultimately metabolized in some way or

other, even if only by decomposers, the depiction of a niche as empty can always be construed as simply a different way of defining the niches of a particular community (Simberloff 1991).

Nevertheless, it is clear that the reduced number of species on islands often leads to the absence of entire ways of making a living. The literature on disharmony of island biotas (e.g., Carlquist 1974, Begon et al. 1990) depicts this same absence. So it is not surprising that certain types of species are especially likely to survive on islands if introduced. The African dung beetles introduced to Australia found a resource (300 million cowpats produced each day) that was not used in the way they use it, because the native dung beetles are not adapted to this resource. And, of course, the numerous successful introductions of predatory mammals such as rats, small mustelids, and the small Indian mongoose, *Herpestes auropunctatus* Hodgson, to small islands lacking such species but containing abundant potential prey (often birds and their eggs) can be viewed in this light (cf. King 1984, Atkinson 1989).

Thus, there may be a generic tendency for certain types of introductions to be more likely to survive on islands than in mainland areas. About 1.6 times as many mammal species and three times as many bird species have been successfully introduced to islands than to mainland areas (Atkinson 1989). Without a tabulation of how many attempts were made in each setting, one cannot say with certainty that the rate of survival was greater on islands, but I think it is likely that many of these island successes were facilitated by absence of native species with similar "niches."

### *Ecological Impacts of Surviving Introduced Species*

With respect to degree of ecological impact, the published record on introduced species is deficient on two counts. First, it is more likely that dramatic effects will be noticed, and the introduced species associated with them thus recorded, than if there is minimal ecological impact. Second, inter-

specific interactions can be very difficult to elucidate without a controlled experiment or very detailed observations, yet such data are usually lacking. Suggestive observations can be very misleading. For example, the rapid spread of the North American mink (*Mustela vison* Schreber) in Great Britain in the 1950s coincided approximately with the decline of the otter. This synchrony led many to infer a causal nexus; however, pesticide pollution is the chief reason otter populations have declined (Chanin and Jeffries 1978).

The subtlety of effects of introduced species on natives, even some devastating effects, and the absence of detailed study in the vast majority of cases make any discussion of this phenomenon highly anecdotal. For example, it is often said that introduction of natural enemies, especially insect parasitoids and predators, for biological control is environmentally friendly. There is good reason to be skeptical (Simberloff 1992b). Gagné and Howarth (1985) and Howarth (1985) argued that such introduced insects might have caused the unintended extinction of several endemic Hawaiian moth species, a charge contested by Funasaki et al. (1988). The specifics of this case cannot be resolved with available data (see Simberloff 1992b for details), but it is difficult to believe that enough attention was paid to species of pristine environments, especially relatively rare insects of no obvious economic importance, to support the general conclusion of Funasaki et al. (1988) that biological control introductions are not harming native nontarget species (Simberloff 1992b).

Similarly, Groves (1989) claimed that no insect introduced to control an invasive plant has affected a native congeneric plant, but this claim is incorrect and, in any event, there has not been nearly enough field study of native plants, especially in pristine environments, to justify lack of concern. A candidate endangered species, the semaphore cactus (*Opuntia spinosissima* Miller), was found in the United States only on Little Torch Key, Florida. All individuals there have been destroyed or are under attack by caterpillars of the moth *Cactoblastis cactorum* (Berg), which was deliberately introduced to the island of



Nevis in the Lesser Antilles to control another cactus and island-hopped over about 30 yr all the way to Florida. The important lesson from this introduction is that the cactus would have gone quietly extinct but for a very unlikely set of circumstances. It inhabited an area favored by plant collectors and botanists, in an intensively studied hammock that is part of a Nature Conservancy refuge, and a local botanist was tipped to the possibility of the moth's presence by a colleague who had noticed it at Guantanamo Bay, Cuba (Simberloff 1992*b*). How many species have been reduced or even extinguished without anyone's having thought to look?

Granted that our knowledge of the true extent of ecological effects is very poor, what do the anecdotes suggest? We can begin by looking at one dramatic effect, extinction.

The number of known extinctions apparently caused by introduced species is much greater on islands (Atkinson 1989). Probably the best-known reason is predation on island species that had not evolved in the presence of predatory mammals like cats, rats, and the small Indian mongoose, the key culprits aside from humans (Atkinson 1989). Absence of direct antipredatory behavior combined with habits such as nesting on the ground to predispose such species to extinction.

In fact, destruction of habitat by browsing and grazing by introduced pigs, rabbits, sheep, cattle, horses, and other species has probably led to more island extinctions than predation has, either by direct elimination of an entire plant species or by reducing habitat quality and amount so much for animal and plant species that they are more prone to extinction from the various factors that place very small populations at risk (outlined by Simberloff [1986*b*]). Although such habitat destruction is often depicted as far greater on islands than on the mainland (e.g., Atkinson 1989), there is really no thorough study of this matter. For example, pigs devastated plant communities of Auckland Island, restricting some species to sites inaccessible to pigs (Atkinson 1989). Pigs have also greatly affected plant communities and several species of animals in the Great Smoky Moun-

tains National Park (references in Simberloff [1991]). Mack (1986, 1989) explained the destruction of the native plant communities of the North American intermountain West and their replacement by introduced Old World plant species as a consequence of the introduction of large congregating grazers, to which American plant species were not adapted. A similar fate befell South American and Australian grasslands when faced with Eurasian invaders. Is the ecological impact of grazers more severe on Auckland Island than in the intermountain West? No one has addressed this issue.

It is difficult to find ironclad examples on either island or mainland in which introduced species have replaced native ones by competition, rather than by occupying a changed habitat (Udvardy 1969, Ebenhard 1988). Ebenhard (1988), acknowledging that many of the cases he tabulated are not strongly supported by empirical evidence, found that, of 1559 introductions of 330 species of birds and mammals worldwide, 79 introductions *may* have manifested competition between the invader and one or more native species, in that at least resources were jointly used. There were relatively more such cases in mainland areas than on islands, but, for introduced mammals (not birds), documented decreases in the population of the native species (whether or not caused by competition) were more common on oceanic islands. The inferences about real impact for most of these cases are so weak that it seems impossible to say whether introductions are more likely to lead to competition on islands than in mainland areas. This is a surprising result considering the conventional wisdom described at the beginning of this paper. All one can really say for mammals and birds is that competition seems to result from an introduction very infrequently, yet both island and mainland examples are known.

Disease vectored by introduced species is often viewed as a key element in the devastation wrought by invasions (e.g., Crosby 1986). Some of the introduced Asian passeriform birds may have contributed to the decline of native Hawaiian species by vectoring avian malaria (Ralph and van Riper 1985,

Van Riper et al. 1986), and a similar scenario, though with no supporting data, was suggested for native Mascarene birds by Cheke (1987*a,b*). In neither instance, however, does the evidence suggest that these diseases facilitated the survival of surviving invaders. Rather, the more likely scenario is that habitat modification created favorable circumstances for survival of at least some introduced species, simultaneously reducing native populations, and the introduction of new diseases may have worsened the plight of the natives.

Exactly why island species should be more prone than mainland ones to contract pathogenic diseases from mainland invaders is unknown. Similarly, mainland species are relatively impervious to island diseases. Though I know of no statistical study of these propositions, they are surely true. In addition to the Hawaiian bird story, other anecdotes about island populations devastated by introduced diseases are numerous (e.g., Ebenhard 1988, Pimm 1991), but I cannot identify an example of a disease endemic to an island that has devastated a mainland species. Of course, introduced diseases have devastated rich continental communities—rinderpest from Asia invaded large parts of Africa in the late nineteenth century with enormous, lasting impact on the ruminants and, through them, entire ecosystems (Dobson and May 1986, Barbault 1992, and references therein). The phenomenon may not be only a mainland-island effect, but may be wholly or partly a statistical tendency for Eurasian diseases to be more devastating in other areas. Only syphilis among New World human diseases has invaded the Old World, whereas no human diseases have been exported from Australia to elsewhere (Crosby 1986). Almost all devastating plant disease epidemics have been caused by Eurasian pathogens introduced to other continents (von Broembsen 1989). The pathogenicity of Eurasian human diseases and resistance by Eurasian humans might be a result of greater Eurasian human population densities, but the analogous trend for plant pathogens cannot be so explained.

Di Castri (1989) suggested generic rea-

sons, relating to the geological history of Eurasia and the long association of this region with human activities, that might predispose its species to be particularly adept at invading other regions, including islands. One must always consider the opportunities for dispersal to and from various sites before postulating a hypothesis of greater likelihood of inherent superiority of species from one biota over those of another (Simberloff 1989). It may well be that far more species of both disease and free-living organisms are transported from mainlands to islands than vice versa and that the per-capita probability of surviving does not differ. The same argument may hold for disease organisms from Eurasia compared with those from elsewhere.

Perhaps disease susceptibility on islands is a probabilistic phenomenon related to the species-area relationship. One can ask if there is a null per-species probability that a parasite will be severely pathogenic, so that regions with more species have, on average, more pathogenic species and potential hosts in such regions experience more natural selection for resistance. Another possibility is that the smaller size of island populations means that total genetic diversity is, on average, lower than in mainland situations. Carson (1981) argued that total genetic diversity of continental species is far greater than that of island species, by virtue of the larger number of local populations. Thus the probability that resistant genotypes exist is lower on islands, and they will evolve more slowly once an introduced species arrives. Carson (1981) saw the reduced genetic base as responsible for a generic tendency for island species to be less "aggressive," not well-adapted "general purpose genotypes" that typify invaders from the mainland. He pointed out (H. L. Carson, pers. comm., 1993) that this pattern is far from universal. For example, among the endemic Hawaiian picture-winged *Drosophila*, most species are monophagous, but five are so polyphagous that each feeds on at least five host plant families, including some introduced plant species (Montgomery 1975). There has been no precise quantification of aggressiveness

and general purpose capability, much less a comprehensive comparison of all island and mainland species to see if these traits are more frequent among the latter.

One possible generic reason why island ecosystems may be more prone to damage from introductions is that their species' populations are perforce smaller and more geographically restricted, and so less likely to have some refuge, some regions not exposed to predators, diseases, grazers, and so forth, than would mainland species exposed to similar invaders. Thus, extinction of a native species is more likely for a given introduction on an island, and, after extinction has occurred, reinvasion and succession as means of repairing the ecological damage are foreclosed. On the mainland, by contrast, even if vast areas are devastated, some areas are more likely to be unaffected by an introduced species, and, if the introduced species is removed or controlled, reinvasion is possible.

Introduced species can have enormous impacts on target ecosystems without directly causing extinctions. Species that constitute entirely new habitats can entrain major changes in a biota. For example, native mangroves cover soft intertidal substrates in most tropical bays and estuaries, but there were none in the Hawaiian Islands until an introduction in 1902. Now mangroves, especially *Rhizophora*, have spread, largely on their own, to many suitable sites throughout the archipelago, forming substantial forests in some areas where none had previously existed. There has been little study of the terrestrial or marine ecology of these forests, but the effect of this introduction on some ecological functions must be enormous (Simberloff 1991). For example, mangrove swamps typically drop about 10,000 kg of leaves per hectare per year and accumulate sediment that builds land (Holdridge 1940). They are major fishery nurseries (Hutchings and Saenger 1987, and references therein). Thorough modification of an existing habitat can also cause community-wide changes. For example, the invasion of young volcanic areas of Hawai'i by the Atlantic plant *Myrica faya* Aiton, which fixes nitrogen, poten-

tially has enormous ecosystem consequences, as do the introductions of some plants that enhance fire frequency in various Hawaiian ecosystems (Vitousek 1986).

It is not clear, however, that introduced species are more likely to play such "key-stone" habitat-modification roles on islands than in mainland areas. The introduction of salt cedar (*Tamarix* spp.) and Russian olive (*Eleagnus angustifolia* L.) along rivers in the American Southwest has created new forests even more extensive than those of Hawaiian mangroves with major ecological impact (references in Simberloff [1991]). And introduced nitrogen-fixers are a major threat to dune plant communities in northern California (references in Simberloff [1991]). Most of the northeastern coast of North America has been changed from mud flats and salt marshes to rocks by an introduced European periwinkle snail, *Littorina littorea* L. (references in Simberloff [1991]), and native forests of much of South Florida have been replaced by *Melaleuca quinquenervia* (Cav.) from Australia and *Schinus terebinthifolius* Raddi from South America (Ewel 1986). The latter two species are particularly inimical to the native biota because of the enhanced fire regimes they foster.

However, the same reduced number of species and disharmony noted above as characteristic of islands, especially small islands, would probably make it more likely that an introduced species would "fill an empty niche" in such a way as to become a new habitat on an island than on the mainland.

### Conclusions

The data are inadequate to draw strong conclusions about the relative invasibility and fragility of islands and mainland. In particular, one would have to know much more about frequency of different types of introductions and number of failed introductions. For example, the fact that no island bird species has invaded continents to the extent that species like the house sparrow or the Java sparrow have invaded islands may

be wholly or partly a consequence of the fact that such introductions of island species to mainland areas have never been performed. Virtually all attempts to introduce island birds have been from one small island to another, usually in the same region, and many have survived (Long 1981).

Despite the paucity of quantitative data, it appears that introduced species *are* more likely to survive on islands than in mainland areas, and *are* more likely to produce major ecological impacts, but there are many counterexamples. If this tendency exists, it is probably *not* generated by an inherent, community-wide "biological resistance" posed by mainland communities to invaders but vitiated on islands. It is not simply a matter of greater species richness in mainland areas conferring greater ecological stability. Rather, it seems that the absence of entire groups of species from islands may have predisposed certain invaders from the mainland to be likely to survive on islands and certain introductions to be likely to have greater ecological effects. In other words, the proximate factor in determining the trajectory of an introduction may be the specific type of species and the specific community it is introduced to, rather than simply the size of the island community. However, over the long term, the size and composition of the island community may have led to the evolution of a community likely to be susceptible to certain types of damage from invasions. It is also possible that, if there is some inherent invasibility and fragility of island communities, at least part of it is really an aspect of an inherent invasibility and fragility of all communities when faced with Eurasian introductions.

This is not a very satisfactory conclusion to a paper about the supposed vulnerability of island species and communities to invasion. Species of some native island communities seem to have resisted invasion as well as continental ones do. For example, in Hawai'i, the plants of upland native forests are not greatly affected by exotic plants (Mueller-Dombois 1981), and plant communities of extreme habitats seem not to be easily invaded (Loope and Mueller-Dombois 1989).

It would be worth exploring whether this pattern extends to other archipelagoes. In general, it is far from clear that island species *do* tend to be weak, unaggressive, uncompetitive evolutionary incompetents; if there is such a tendency, it is far from universal, and the reasons are still unknown.

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