ALIEN SPECIES AND THEIR CONTROL

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Summary

Transport and establishment of species outside their native ranges have become a worldwide ecological problem in the past century or so, with both the earliest and greatest destruction being visited on oceanic islands. The effect of this unprecedented biotic mixing ranges from minor reduction in populations of native species, to their extinction, to wholesale replacement of native biotas with novel foreign ones. The sum effect on oceanic islands has been gross impoverishment of native biodiversity.

Alien species degrade insular communities in a variety of ways, with the most severe effects resulting from changes to the ecosystem's functional properties such as rates of resource supply and cycling, disturbance regimes, and trophic structure. Those aliens most adept at altering insular ecosystems seem to be taxa that are ecologically dominant in continental areas but were formerly absent or poorly represented on islands. Ecological degradation does not come solely from such invasive species, however; population-level changes, such as result from hybridization between alien and native species, can also drive biotic loss on oceanic islands.

A variety of solutions for reducing problems with alien species are available and work best when used jointly as a series of filters that multiplicatively provide the greatest level of protection against unwanted introductions. These filters include prevention systems that provide certification, inspection, quarantine, and screening of proposed introductions or arriving goods; programs of rapid-response eradication that seek to remove newly established pest species before they expand out of control; and long-term control programs to mitigate the worst effects of widely established invaders. In the final analysis, all these methods will simply serve to slow the rate of alien-species establishments in the absence of profound changes in the human attitudes and behavior that drive the current homogenization of the world's biota.

1. Introduction of Alien Species

Alien species are those species established outside their native ranges by the activities of humans, whether done intentionally or not. This definition does not imply that human-mediated dispersal of species is inherently unnatural, but it recognizes that the temporal and spatial scales at which humans are homogenizing the world's diverse biota is occurring at a scale previously absent in the earth's evolutionary history. For example, it has been estimated that the rate of establishment of new species in the Hawaiian Islands was approximately 1/35 000 years prior to human arrival there; it is now on the order of 20–30 species/year, an approximately million-fold increase in rate. Similar changes have occurred on other oceanic islands, although perhaps not of this extreme magnitude. This overwhelming increase in the introduction of alien species has profound effects on native insular species and ecosystems.

It is important to note that for at least the past two centuries the rate of alien species introduction worldwide has been rising at approximately exponential rates for a diversity of taxonomic groups. The reasons for this are various, but include human population growth (see Figure 1), growth in international trade, and the widespread dissemination of certain utilitarian cultural attitudes. Currently, a host of pathways serves to introduce alien species to new environments, including oceanic islands. Unintentional introductions largely result from species hitchhiking rides in cargo or on the vehicles used in international transport. Intentional introductions occur for a variety of reasons, but primarily because a species is perceived to provide an amenity or use-value to humans. As a rule, some taxonomic groups, such as marine invertebrates, insects, and landsnails are largely dispersed via unintentional pathways. Others, primarily plants, fish, birds, and mammals, have largely been intentionally dispersed by humans. A few groups, such as reptiles and amphibians, arrive via a mixture of pathways, with the pathway of importance varying geographically. Most introductions of these last two groups to oceanic islands have been as unintentional hitchhikers in cargo.

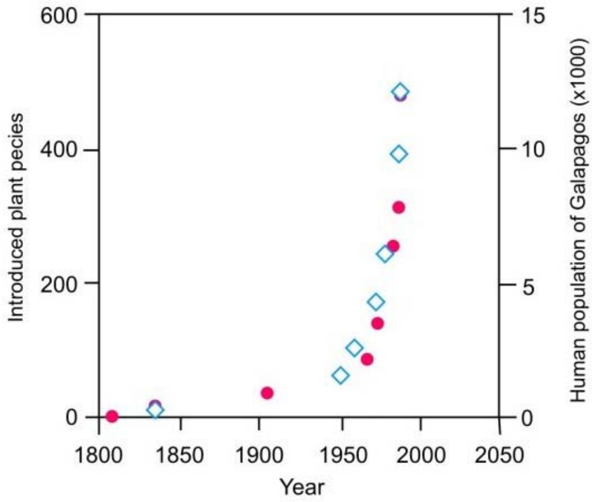

Figure 1. The growth of alien introductions tracks human population growth (*Source*: Reprinted by courtesy of Blackwell Science, from A. Mauchamp, *Conservation Biology* **11**(1) (1997), 261)

2. Characteristics of Islands That Make Them Susceptible to Ecological Invasion

Three of the physical characteristics leading to distinctive and remarkable biotic communities on islands are important in making island biotas especially susceptible to ecological invasion by aliens. First, island biotas are often disharmonic, meaning they have an uneven sample of those taxonomic groups to be found on mainland source areas. This results from the differential ability of the various mainland taxa to disperse successfully over marine barriers and leads to the absence on many oceanic islands of taxa that are ecologically dominant on mainlands. Examples of such taxa include ungulates (hooved animals), social insects like ants and some bees and wasps, and fire-promoting grasses. When these species are subsequently introduced to islands by humans they often change ecological relations to the detriment of native species, frequently leading to the long-term loss of native communities and ecosystems. Second, the small size of most oceanic islands allows for relatively rapid penetration of alien species across the entire landscape, leaving no refuge for native species to escape their impact. Third, island isolation leads to the development of native communities adapted to only occasional colonizations of new species. When humans then introduce alien species, native communities are simply overwhelmed by the sheer numbers of new competitors, predators, and disease organisms, at least some of which will bring to the islands new ecological attributes with which the native species cannot cope.

3. The Nature of Alien Species Problems on Oceanic Islands

Alien species negatively affect native island communities in many ways, including a variety of forms of direct and indirect competition with natives. The most threatening aliens are those that alter ecosystem-level processes, which can be done in at least three ways: (1) alteration of rates of resource supply and cycling for plants, (2) alteration of disturbance regimes, and (3) alteration of trophic structure.

3.1. Alteration of Rates of Resource Supply and Cycling

Physiological adaptations of alien plants may alter community structure by changing the rate at which nutrients or water are cycled through the ecosystem and, therefore, available to native plants. The mechanics of these processes have been worked out in several continental situations but have not yet been widely studied on islands. However, the ecological principles remain the same, making it likely that these mechanisms serve to degrade some native island ecosystems. One insular example comes from Hawaii, where nitrogen cycling in early-successional plant communities on lava fields is well studied. In that situation it has been determined that no native plants that pioneer on young volcanic sites have the capability of fixing atmospheric nitrogen, but some alien species, such as firetree (*Myrica faya*), have efficient symbioses with actinorhizal fungi that allow them to do so. This capability affords a competitive advantage to these aliens, such that they can often physically dominate and change the successional characteristics of the areas they colonize. The long-term effects of these changes are unknown, but may facilitate the establishment of additional alien species, many of which only invade relatively fertile soils.

Nutrient-cycling regimes are largely based on the recycling of fallen or recently dead plant tissues, which can vary widely in their resistance to decay. Production of slowly decaying litterfall, by plants such as Australian pines (*Casuarina*) and true pines (*Pinus*), can alter nutrient-cycling regimes by sequestering important nutrients for long periods in a form unavailable to native plants. This may serve to enhance the competitive ability of those alien species that produce the litterfall and that are adapted to slow nutrient accumulation rates, while starving adjacent native species unadapted to the newly imposed shortage of resources. The wide introduction of *Casuarina* and *Pinus* to a variety of oceanic islands suggests this could serve as an important means of altering some native insular communities.

Plants primarily affect water cycling through ecosystems in two ways. First, some rain is captured by the leaves and stems of plants where it remains until it evaporates. Because this rain does not reach the ground, it is unavailable for use by the plant community or to recharge groundwater reservoirs. Plants with highly dissected leaves have a relatively greater leaf surface area that captures more rain, serving to decrease the ability to recharge groundwater. Second, water absorbed by plant roots flows upward to the leaves, where it is eventually transpired back to the atmosphere. Plants with higher water-use requirements remove water from the soil at higher rates and are consequently capable of lowering the depth of the water table and increasing the rate at which soil dries out after a rainfall relative to plants with low requirements for water.

Figure 2. Suppression of plant regeneration by a carpet of *Casuarina* leaves
(*Source*: Photo courtesy of R. Palmer)

Certain commonly introduced alien plants are known to have relatively high evapotranspiration and/or rainfall-interception rates and, consequently, are capable of lowering water tables and reducing stream flows when introduced outside their native ranges. Several tree species planted on tropical islands, especially pines (*Pinus*), wattles (*Acacia*), and saltcedar (*Tamarix*), have led to these problems on a widespread scale in mainland situations and seem likely to exert similar drying effects when transplanted to islands. Conversely, it is possible for other alien plants to increase, instead of decrease, water runoff during rains if the primary period of rainfall in their introduced range occurs at a season different from that in their native range. This can lead to increased erosion and siltation instead of soil desiccation.

One may also view access to the soil itself as a resource that may be denied to plants. A variety of alien plants carpets the ground with a thick layer of either living or dead leaves and thereby denies native seeds the access to the soil necessary to stimulate germination. *Casuarina* (Figure 2) and *Pinus* do this with thick carpets of dead leaves, while a variety of grasses, including kikuyu grass (*Pennisetum clandestinum*) and fountain grass (*Pennisetum setaceum*), do the same with a dense mixture of living and dead leaves. The result in either case is a cessation of germination and recruitment of native plants, eventually leading to total replacement of the native community by alien plants.

3.2. Alteration of Disturbance Regimes

Natural disturbance of one form or another is a major force structuring biotic communities everywhere. The geographic scale and frequency at which disturbances occur determine whether their effects are positive or negative. Many disturbance regimes that are important in structuring continental communities are of a type or occur at scales absent on oceanic islands and, hence, these become disruptive when introduced. Two such disturbance agents widely introduced by humans and disruptive to many island ecosystems are ungulate mammals and fire. These foreign agents of disturbance rapidly degrade insular ecosystems because native species typically have no history of exposure to the new agents and, consequently, are not adapted to survive them.

Ungulate hooves provide a disturbance regime of tremendous impact on oceanic islands. In both wet and dry forests, ungulate trampling directly damages roots by cutting and crushing, and compacts the soil, removing air pockets and breaking symbiotic fungal connections needed for proper root function. With time, heavy ungulate usage causes erosion as a direct action of the hooves themselves as well as the loss of consumed understory plants to hold the soil in place. Rooting by pigs has exactly the same effect (Figure 3). Increased erosion reduces soil organic content and rainfall infiltration, fouls adjacent freshwater communities and, in tropical areas, can dump heavy silt loads onto offshore reefs. Comparison of nearby ungulate-free and ungulate-infested islands shows that in the absence of ungulates, native plant communities are remarkably resilient to alien plant invasion. Add ungulates, and the competitive advantage swings to alien plants because many of them are adapted to this disturbance and incorporate it as a condition for successful completion of their life cycles. Native species, being naive to the new disturbance regime, are damaged by its sudden and pervasive appearance.

Fire is a similarly dominant disturbance regime in many continental areas. Consequently, numerous continental plants have adaptations that enhance their ability to survive fire, including morphological attributes, such as thickened bark or placement of growing tips below the soil, and physiological stimulation of seed germination or growth of new shoots by fire. Frequently, such plants require fire to successfully complete their life cycles, and these species often have attributes, such as the retention of dead leaves, that promote the spread of fire.

Figure 3. Effects of pig tillage on rainforest plant community: (A) Soil disturbance and understory loss before fencing and pig removal; (B) Recovery of native plants six years after pig removal
(*Source*: Photos courtesy of Hawaii Volcanoes National Park, Resource Management Division)

Many of the alien grasses brought to tropical islands have these requirements, burn readily, and serve to increase fire intensity and frequency in native dryland ecosystems. Because fire was rare and unimportant in the evolution of many tropical island communities, native insular plants often lack adaptations to survive or capitalize on fire; consequently, fires promoted by alien grasses have a negative impact on native vegetative communities, which gradually become replaced by fire-adapted alien communities with each successive burn. In this way, former forests have been replaced by grasslands in much of Guam and the leeward lowland areas of Hawaii.

Similar concerns apply to water diversions and impoundments on those oceanic islands having sufficient water resources to support such projects. In these instances, disturbance consists of creating an entirely new habitat to which native stream-dwelling species are likely to prove intolerant. Under these circumstances, only such introduced species as may be present and adapted to these formerly absent ecosystems are likely to thrive.

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Biographical Sketch

Fred Kraus received a Ph.D. in biology from the University of Michigan in 1987 for a study on the evolution of salamanders. He subsequently was engaged in two research appointments investigating the molecular evolution of mammals and snakes. In 1991, he co-conducted a conservation project focused on alien species eradication, rare plant restoration, and landsnail surveys on an island in the Virgin Islands. In 1996, he accepted an appointment as invasive species biologist for the Hawaii Department of Land and Natural Resources, Division of Forestry and Wildlife, where his activities included devising and implementing policy and field programs to reduce alien species problems in the State of Hawaii. He now works for Bishop Museum in Honolulu. His research interests in island biology have taken him to the Caribbean, Philippines, Borneo, Palau, and Guam. This interest continues with ongoing studies of New Guinea's herpetofauna and of invasive reptiles and amphibians in Hawaii.