

RELATIONSHIPS AMONG NATIVE AND ALIEN PLANTS ON PACIFIC ISLANDS WITH AND WITHOUT SIGNIFICANT HUMAN DISTURBANCE AND FERAL UNGULATES

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ABSTRACT

The native plants of remote tropical islands have been frequently characterized as poor competitors against seemingly more aggressive alien species. Does this "weak competitor" characterization relate to some real adaptive consequences of island isolation and endemism, or does the generally concurrent presence of introduced ungulates and other forms of recurrent human disturbance also act to encourage alien plant dominance? A comparison of tropical islands with and without introduced ungulates suggests that some insular plant species competitively resist alien displacement in the absence of ungulates.

INTRODUCTION

For millions of years remote tropical islands in the Pacific Ocean have provided a variety of ecological opportunities for plant species that reached them through long-distance dispersal mechanisms. Many species that successfully established themselves on far-flung oceanic islands gave rise to extraordinary endemic forms, examples of adaptive radiation, and unusual adaptive shifts. Evolutionary developments occurred on isolated islands largely because of the limited numbers and kinds of colonizing taxa and varying environmental diversity within islands or groups of islands.

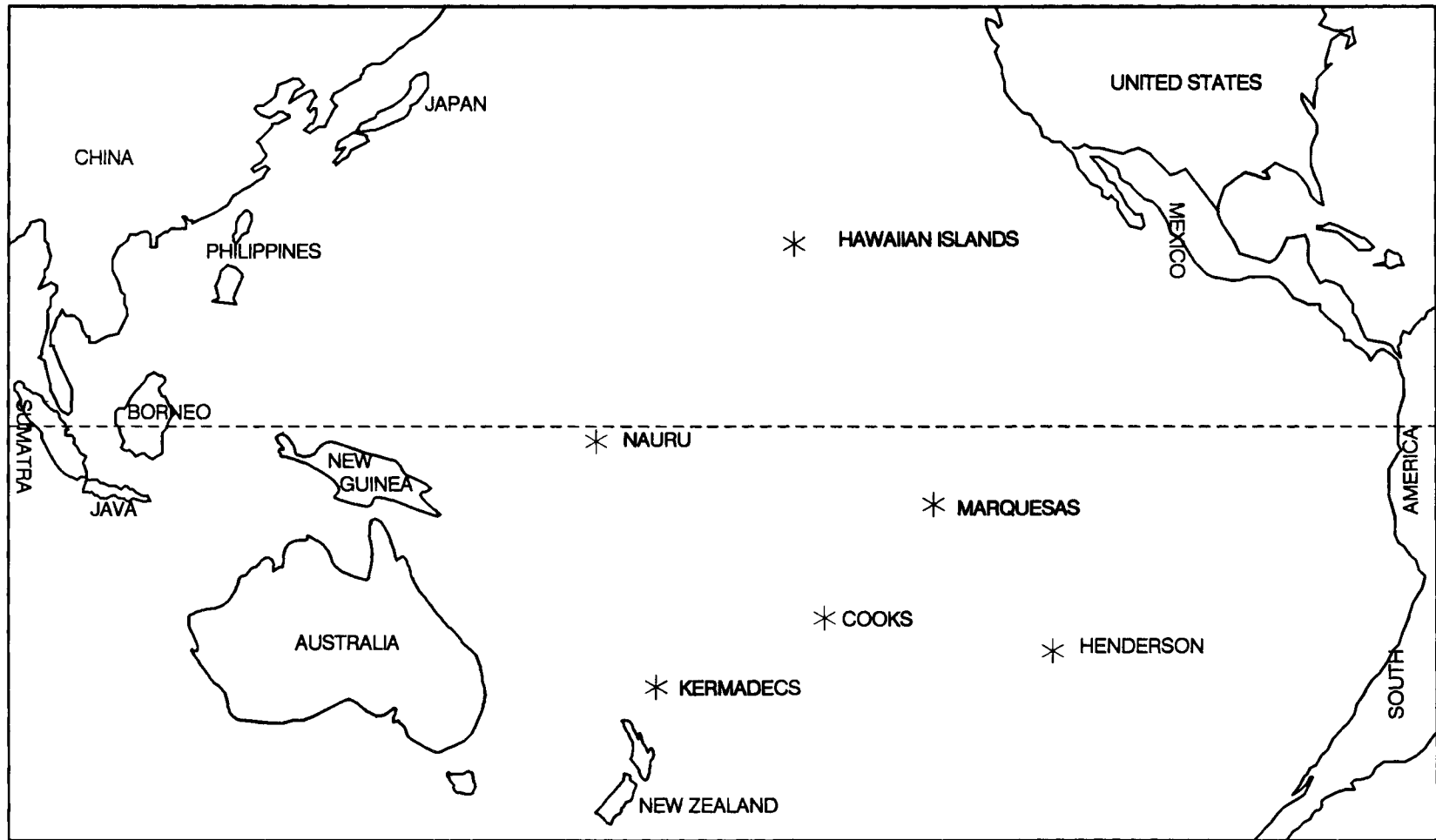
Among the structural and physiological adaptations that frequently occur in remote island environments is the disappearance of typical defensive mechanisms such as poisons, strong odors, thorns, deep tap roots, and tough stems and branches in insular plant species. Some of these adaptations left many species especially vulnerable to a variety of alien ungulates introduced in the historic period (Fosberg 1965; Mangelot 1965; Mueller-Dombois 1975). In the Hawaiian Islands, for example, only a very small fraction of the endemic species of plants produce poisons, thorns, or other defensive strategies against herbivory (Carlquist 1974, 1980).

The depredations of introduced hooved mammals in isolated, tropical island ecosystems are well documented in the literature (e.g., Skottsberg 1957; Cuddihy and Stone 1990) and are starkly exemplified in many island ecosystems by an array of habitat deterioration and soil erosion problems. What is less clear is the role of competition (without associated disturbance by humans or introduced animals) among alien and native plants in insular ecosystems. In other words, do differential survival rates generally occur for native and alien plants without the influence of free-ranging ungulates and other forms of direct or indirect human environmental disturbance?

If native island plant communities (especially those with high percentages of endemism) contain intrinsically weak competitors, then aggressive alien plant species should ultimately prevail under competition even without sustained human disturbance or alien herbivores (Dasmann *et al.* 1973; Gade 1985). By contrast, if insular ecosystems are reasonably resilient and native plants are well adapted and competitive, these communities should generally persist in the face of continued alien plant introductions as long as alien herbivores are absent or controlled (Mueller-Dombois *et al.* 1981; Merlin 1985, 1991). Research in the Hawaiian Islands (Egler 1942; Hathaway 1952; Mueller-Dombois 1975; Wirawan 1978), and on the raised coral island of Nauru (Manner *et al.* 1985) has shown that native vegetation can sometimes regain dominance after the removal of unnatural disturbance.

The question of alien-native plant competition in the absence of ungulates is of more than theoretical interest; it has important implications in developing management strategies for protection of intact native ecosystems and rehabilitation of disturbed insular environments. If lack of adaptation to grazing results in the replacement of native plant species by aliens, then animal removal may be sufficient to promote native ecosystem regeneration (barring irreversible changes caused by ungulates, e.g., severe soil erosion, extinction of pollinators, or altered nutrient cycles derived from alien plants that fix nitrogen (Allan 1936; Bates 1956; C.W. Smith, pers. comm. 1990). However, if the native flora is composed of comparatively weak competitors, then management of alien plants will pose a continuing problem even after ungulate removal.

In many contemporary oceanic island settings, environmental conditions appear to be stacked heavily on the side of alien biota. Alien plants are often strongly adapted to survival in association with direct human disturbance and browsing, grazing, and rooting ungulates. In this paper, we review the literature and describe our own comparative field work on islands where plant competition among alien and native species may be assessed in the absence of free-ranging ungulates or other forms of continual human disturbance. Our present analysis is based on the following Pacific island cases (Fig. 1): Nihoa and Kaho'olawe in the Hawaiian Islands; Hatuta'a and Eiao in the northern Marquesas; the Kermadec Islands; Henderson and Nauru Islands; and the southern Cook Islands. These island pairs were chosen to contrast disturbed and relatively undisturbed (by ungulates) regimes.



* RELATIVE LOCATIONS OF ISLAND GROUPS

Figure 1. The Pacific Basin, showing relative positions of the island groups and islands discussed in this paper.

Nihoa and Kaho'olawe

Nihoa is a small (190 a or 77 ha), steeply sloped volcanic island of the Hawaiian Archipelago that reaches a maximum elevation of 910 ft (277 m). It lies about 155 mi (250 km) northeast of Kaua'i (Fig. 2), is relatively dry, geographically remote, and has very poor landing access. Although ample evidence exists that prehistoric humans used the Island, the duration of their occupation is unknown. Based on observations of archaeological remains, Emory (1928) speculated that as many as 200 people may have lived there at one time. Although Nihoa had been abandoned prior to European contact, there can be little doubt that prehistoric Polynesians transformed much of the ecosystem, given the small size of the Island and the abundance of archaeological sites. However, in spite of early human impacts (burning, farming, and possible pig (*Sus scrofa*) rooting), the present recovered condition of the native ecosystems on Nihoa is especially noteworthy.

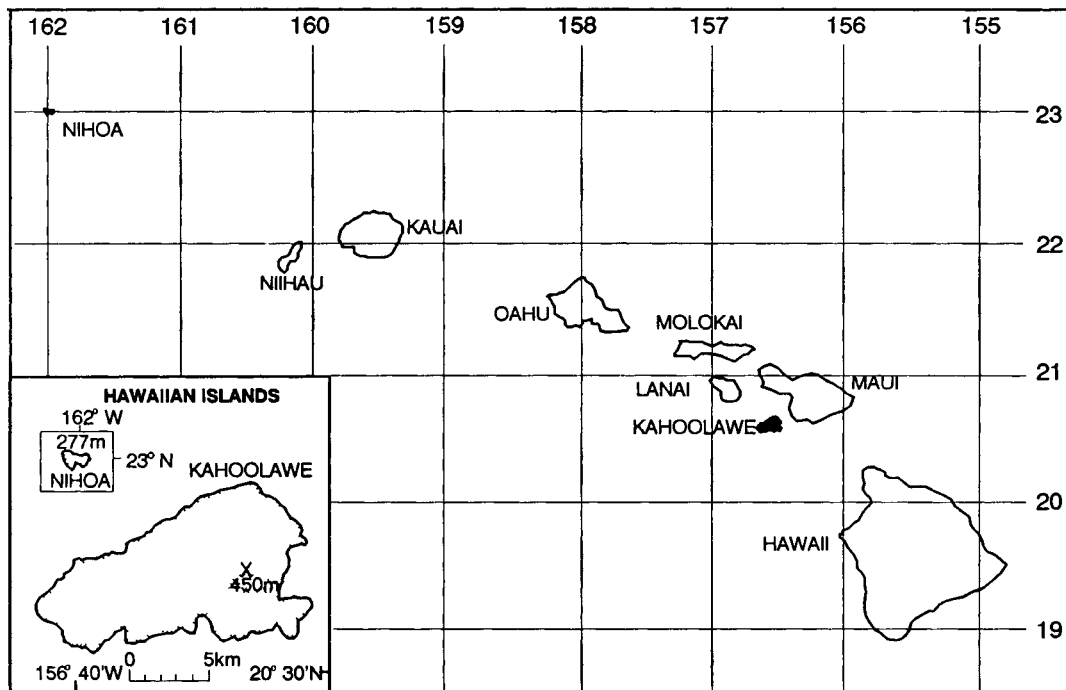


Figure 2. The southeastern Hawaiian Islands (Nihoa to Hawai'i), showing placement of Nihoa and Kaho'olawe in relation to the others.

Nihoa has apparently been little, if at all, disturbed by ungulates, and consequently it has retained a good deal of its native biota. According to Conant (1985), Nihoa not only has the greatest integrity and variation in native species composition of any of the Northwestern Hawaiian Islands, it is also probably "one of the only places remaining in the entire Hawaiian Archipelago where there is a diverse and relatively intact low-elevation dry-land ecosystem, with its complement of native terrestrial plants,

arthropods, and birds" (Fig. 3). Conant's recent research on Nihoa indicates that 21 plant species are now found on the Island, of which five are endemic; most of the rest are indigenous. Six alien species have been recorded, and only one of these (a small herbaceous plant, *Portulaca oleracea* or pigweed) is considered common on the Island. The predominantly native plant communities of Nihoa support many endemic animals, including numerous terrestrial arthropods, several land snails, and two land birds, as well as large populations of breeding seabirds (Conant *et al.* 1984).

Kaho'olawe is the eighth-largest of the Hawaiian Islands (Fig. 2), with an area of 45 mi² (117 km²) and a maximum elevation of 1,490 ft (450 m). Located in the leeward rain shadow of the larger island of Maui, Kaho'olawe possesses a semiarid climate similar to that of Nihoa. Recent botanical surveys indicate that the vegetation of the Island is overwhelmingly alien (Environmental Impact Study Corporation 1979). The disappearance of the great majority of native plant life can probably be explained by the lengthy presence of domesticated and feral ungulates on Kaho'olawe; their ecological impact has undoubtedly imperiled all native plants save those in the most steeply-sloped cliff-face refugia.



Figure 3. The island of Nihoa, despite an early period of Polynesian settlement (note stone wall in center left of photo), today remains one of the few places in the Hawaiian Islands with an intact native dry coastal ecosystem (note thickets of the endemic *Pritchardia* palm). Feral ungulate populations were never established on Nihoa. (Photo: S. Conant.)

Recent archaeological research on Kaho'olawe indicates that significant human alteration of the native vegetation and soils probably started during the prehistoric period. A distinctive, widespread layer of burned grasses and ash up to 0.8 in. (2 cm) thick has been identified; this layer was probably produced through a series of different events over a time span of as much as 200 years before the arrival of the first Europeans: "It is suggested that dryland swiddening practices, wherein large areas of virgin forest were burned off to make room for the cultivation of plants, may have been the primary initiating factor in the degradation of the interior island soil cover" (Barrera 1979). Subfossil land snail assemblages found in erosional deposits or associated with the widespread burn layer on Kaho'olawe have also been used to support the assumption that prehistoric Polynesians severely altered dry forest ecosystems on this island (Hommon 1980). Fires that appear to have caused significant alteration of the pristine dry forest ecosystems may have been initiated purposefully to promote slash and burn agriculture. Fires may also have been used to extend (and later maintain) the range of pili grass (*Heteropogon contortus*), a culturally important thatch and mulch source (Yen *et al.* 1972; Kirch 1982).

Even if the prehistoric occupants converted much of the original dry forest ecosystem on Kaho'olawe into anthropogenic grassland, alien hoofed mammals introduced in the Post-Cook period were also responsible for "the massive erosion and landscape degradation" of the Island (Spriggs 1986). Devastation of the soil and vegetation (especially on the higher parts of the Island) occurred primarily during the last part of the 19th and the early 20th centuries, when large herds of livestock and feral animals consumed much of the remaining vegetation and exposed the Island to increased soil erosion.

The first ungulates to reach Kaho'olawe were probably goats (*Capra hircus*) given to a Maui chief by Captain George Vancouver. The chief is said to have sent some animals to Kaho'olawe in 1800 with hopes that they would multiply (Barrera 1979). Pigs were also reported on Kaho'olawe during the first half of the 19th century. These alien mammals had developed sizable populations by the 1850s (Allen 1858).

By the late 1890s, about 15,000 sheep (*Ovis aries*) and a large number of goats were present. Less than 20 years later (1909), the territorial legislature of Hawaii voted not to renew a 50-year lease that had been granted to two ranchers using the Island. The justification was severe deterioration of the vegetation and related soil erosion attributed to ungulate populations that were by then ravaging the remaining vegetation on Kaho'olawe (Lebarron and Walker 1970). Limits were subsequently set on a new ranching lease, which required that goats and sheep be eradicated and that the number of cattle, horses, and mules (*Bos taurus*, *Equus caballus*, *Equus caballus x asinus*) that could be brought to Kaho'olawe be restricted. Between 1912 and 1918, about 5,000 goats were eliminated. However, even with these new measures, there was little evidence of vegetation regeneration. As of 1918, large-scale removal of the native vegetation by alien ungulates had opened up the greater part of the central plateau (area above 600 ft or 200 m) to massive soil erosion, exposing the

reddish, saprolitic hardpan one still encounters in this part of the Island (Barrera 1979). Although sheep, cattle, and horses were eliminated from Kaho'olawe during this century, a few goats still inhabit the Island, even after a number of concerted, but unsuccessful, efforts to eradicate them.

The impoverished vegetation found on Kaho'olawe today is dominated by alien species with defense mechanisms against herbivory. Defenses were either absent or weakly expressed among the native plants. For example, although a few living specimens of the native wiliwili (*Erythrina sandwicensis*) may now be found growing on steep-sided ravines, this tree was probably much more common in the past. Although it does produce some thorns on its trunk, wiliwili does not have the same degree of thorny protection from ungulates that has helped the alien kiawe (*Prosopis pallida*) become the dominant tree species in all but the almost barren hardpan desert on the summit plateau. "Tree tobacco" (*Nicotiana glauca*), now found in severely eroded areas, is also resistant to ungulates (Fig. 4). Toxic substances produced by this tree generally discourage feral goat browsing.



Figure 4. The central plateau of Kaho'olawe has been stripped of both vegetation and soil under the impact of almost two centuries of large domestic and feral ungulate populations. The alien "tree tobacco" (*Nicotiana glauca*) has survived the intense browse pressure by virtue of its unpalatable (toxic) leaves, a defense mechanism generally lacking in native Hawaiian plants. (Photo: M. Merlin.)

Hatuta'a and Eiao

The old volcanic island of Hatuta'a (referred to as Hatutu on several charts) is located 335 mi (102 km) northwest of Nukuhiva in the northwestern group of the Marquesas Archipelago (Figs. 1, 5). Its surface area is about 6.2 mi² (16 km²), and it has a maximum elevation of 1,395 ft (425 m) (Decker 1970). The Island projects prominently from the sea but does not have sufficient height or size to induce much orographic rainfall; thus, the climate of Hatuta'a is similar to that of the surrounding ocean, resulting in markedly xeric conditions.

Domesticated or wild ungulates have not been introduced on Hatuta'a because of difficult access and insufficient fresh water (Decker 1973). Hatuta'a is an important rookery for many species of seabirds, including boobies, sooty terns, white terns, and frigate birds (*Sula* sp., *Sterna fuscata*, *Gygis alba*, and *Fregata minor*); it also provides a final refuge for the small Marquesan ground dove (*Gallicolumba rubescens*). A number of endemic invertebrate species can still be found on this remote Marquesan island (Perrault 1978). The largely undisturbed xerotropical vegetation of Hatuta'a is dominated by clumps of native scrub and tussock grass (*Eragrostis xerophila*). The flora includes 30 known species, with six endemic to the Marquesas Islands (Fig. 6).

Prehistoric Polynesians used Hatuta'a, as evidenced by a number of stone platforms along the central crest of the Island beneath groves of *Pisonia grandis*, the only tree on Hatuta'a. The Island is occupied by some alien species, including a rat and a number of pantropical weeds (e.g., coffee senna, hairy spurge, wild water lemon, and pigweed (*Senna occidentalis*, *Chamaesyce hirta*, *Passiflora foetida*, *Portulaca oleracea*); yet Hatuta'a can be described as "a pristine terrestrial ecosystem -- the only sizeable one left undisturbed in the central Pacific dry zone" (Decker 1973).

The brief, but insightful, ecological observations on Hatuta'a made by Decker over 30 years ago (April 1960) were generally confirmed more recently by Montgomery *et al.* (1980). These authors described the "thick, green mantle of grasses with clumps of *Pisonia* trees" that covered the Island. Although they noted the presence of "curious and bold rats (probably *Rattus exulans*)," they also observed many seabirds still nesting on Hatuta'a. Furthermore, they reported that the native Marquesan ground dove was still common and appeared to be unalarmed by the presence of humans until approached at close range.

Eiao is located 1.5 mi (2.5 km) northeast of Hatuta'a (Fig. 5). It is volcanic in origin but is much larger (20 mi² or 52 km²) and higher (1,890 ft or 575 m) than Hatuta'a. Eiao has accessible landing spots and a number of freshwater springs. The history of human land use and impact on Eiao has differed greatly from that on Hatuta'a, especially after the arrival of Europeans. For example, livestock released on Eiao have had a devastating effect on the native vegetation and soil conditions on Eiao in the past hundred years. When Decker visited Eiao in February 1960, he reported that the Island was "a barren gullied desert of rock and orange clay" (Decker 1973). He pointed out that the small amount of native

forest that still remained on the Island was limited to topographic refugia that persisted because they were "inaccessible to the feral sheep that run freely over the island, starving and preyed upon by feral swine" (Fig. 7). The sheep were so enfeebled that they "could be run down and captured by hand" (Decker 1973).

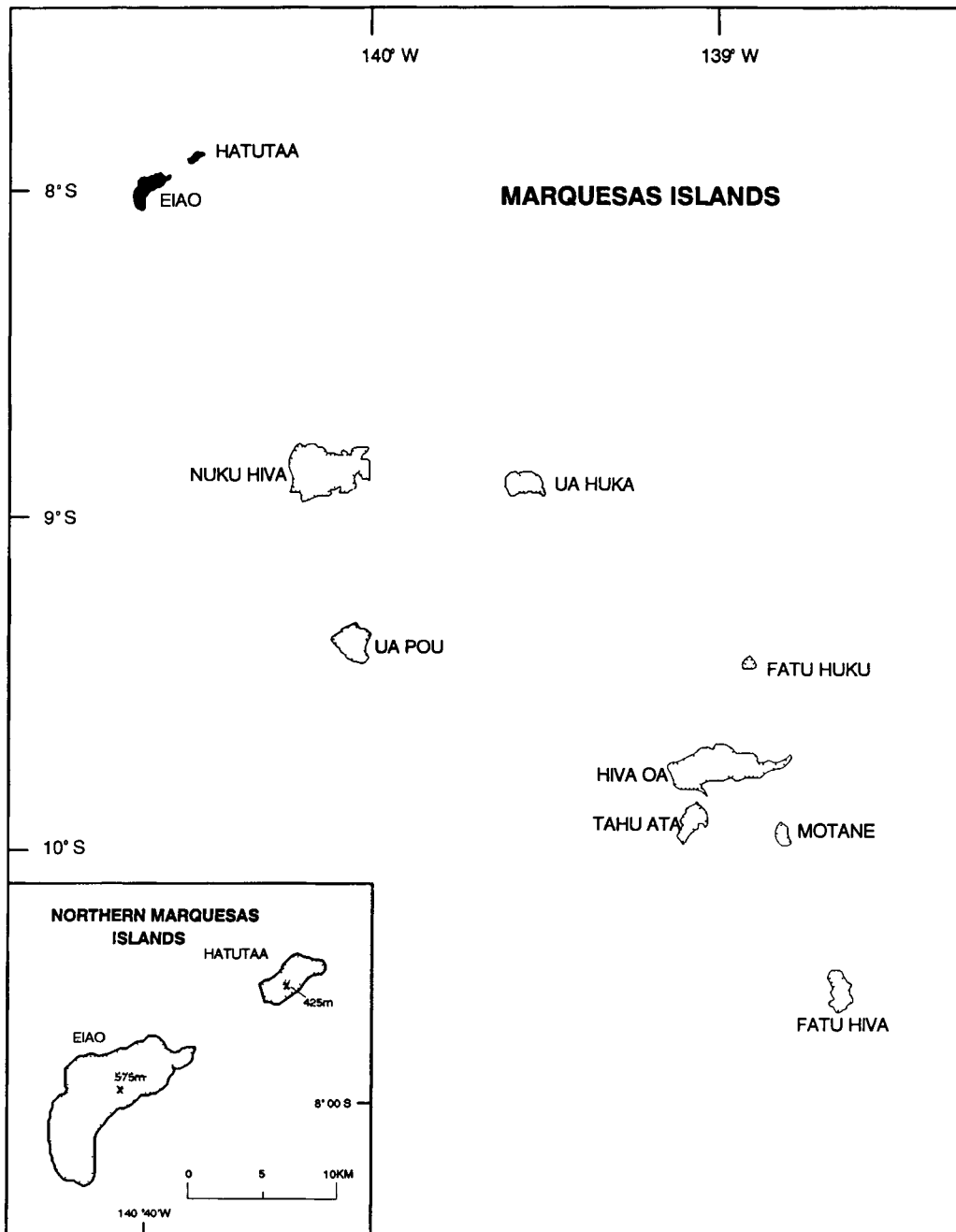


Figure 5. Map of Marquesas Archipelago, showing Hatuta'a and Eiao.



Figure 6. The Marquesan island of Hatuta'a with nearby Eiao in the background. Ungulate-free Hatuta'a supports a native dryland ecosystem dominated by tussocks of *Eragrostis xerophila* and the shrubs *Waltheria lophanthus* and *Cordia lutea*. Windswept trees in background are *Pisonia grandis*. (Photo: B. Decker.)

Observations made during a more recent expedition to Eiao in 1978, (W.C. Gagné, pers. comm. 1986) indicated that many native species may still be found on steep cliffs out of reach of feral sheep and pigs. These refugia would likely be greatly diminished if goats were introduced to the Island. Presently the area covered by "primitive forest" on the extensive plateau above 1,475 ft (450 m) is extremely reduced (Perrault 1978). The extreme habitat deterioration on Eiao is indicated by the condition of feral sheep, which were even observed consuming poisonous plants such as coffee senna, a tropical American shrub that is rare on Hatuta'a but relatively common on Eiao. Although normally toxic to livestock, parts of the plant were found in the stomach of a sheep caught and killed on Eiao in 1960 (Decker, pers. comm. 1986).

The relatively remote, adjacent islands of Hatuta'a and Eiao in the semiarid northern Marquesas provide dramatic illustration of the persistence of native ecosystems with and without feral ungulates. Feral sheep and pigs have devastated much of Eiao, and the native flora has been largely supplanted by alien species. On nearby Hatuta'a the lack of permanent water sources frustrated human settlement and the successful establishment of feral ungulates. The native vegetation on Hatuta'a has



Figure 7. The island of Eiao has been ravaged by feral sheep, leading to native ecosystem destruction and massive soil erosion. (Photo: B. Decker.)

not been significantly modified, although some of the same alien plant species that have become common in the ungulate-disturbed ecosystem of nearby Eiao are present in small numbers as casual adventives on Hatuta'a (e.g., coffee senna and pigweed). We hypothesize that the lack of early successional habitats on undisturbed Hatuta'a has limited the successful spread of adventives.

Kermadec Islands

The Kermadecs are a chain of small, basaltic islands lying northeast of New Zealand (Figs. 1, 8). The northern group includes volcanically active Raoul (by far the largest island in the chain, with an area of 7,270 a (2,943 ha) and eight small outliers comprising the Meyer and Herald islets (combined area 100 a or 40 ha). The southern Kermadecs include Macauley (800 a or 324 ha), volcanically active Curtis (130 a or 53 ha), and the smaller islets of Cheeseman and L'Esperance (20 and 12 a, or 8 and 5 ha).

Although these islands were uninhabited at the time of European discovery (1788), direct archaeological and indirect botanical evidence indicate prehistoric Polynesian presence on Raoul, where adzes of a type common in the southern Cook Islands have been found (Duff 1968); several plant species of probable Polynesian introduction occur (e.g., candlenut, *Aleurites moluccana*, and ti, *Cordyline fruticosa*).

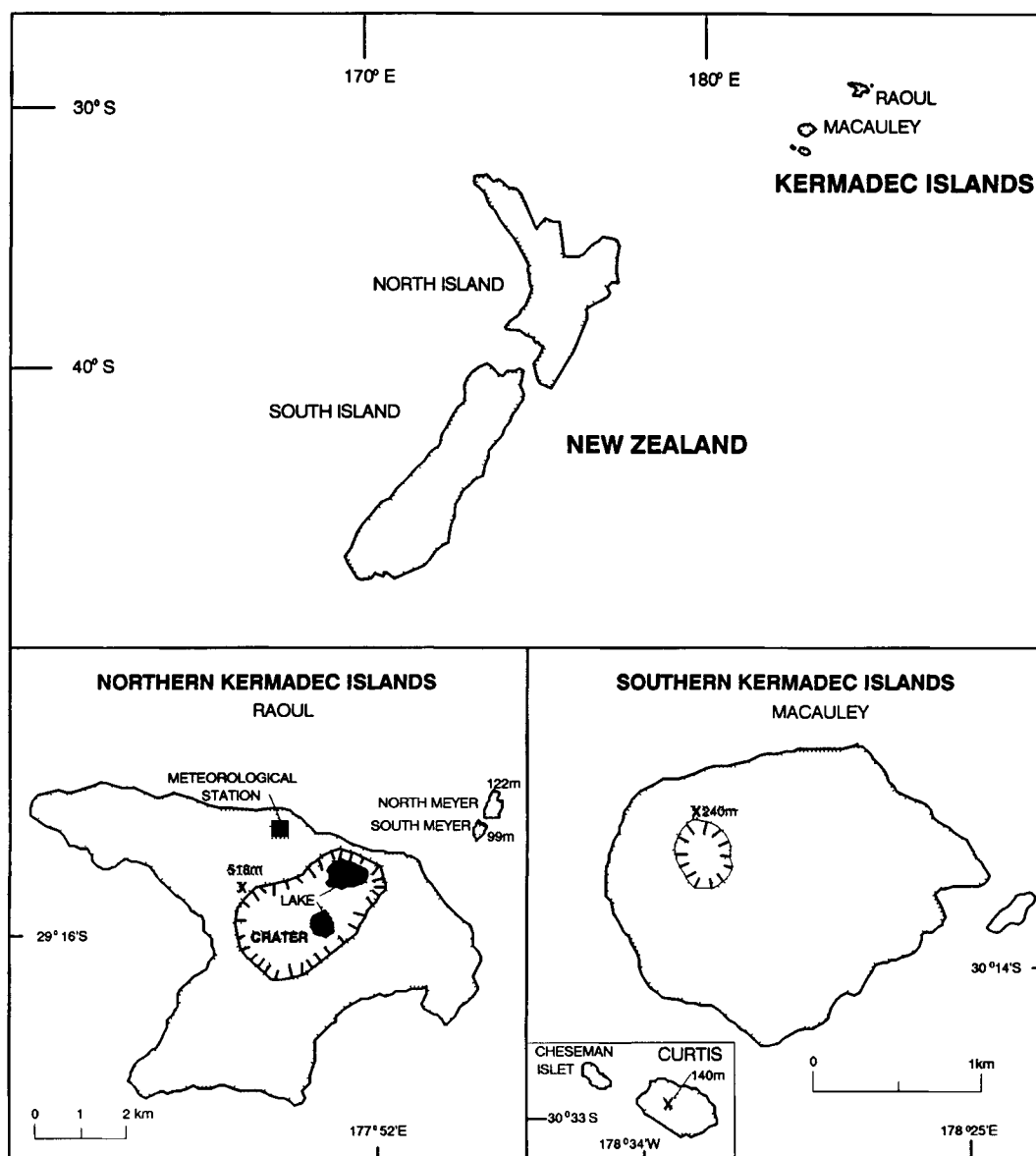


Figure 8. Map of Kermadecs showing Raoul and other islands discussed.

Periodic European settlement and farming attempts occurred on Raoul beginning in 1836 (Morton 1964). A permanently manned meteorological station has been in operation since 1937. All other islands in the Kermadecs have remained uninhabited.

Feral ungulate populations became established in the Kermadecs early in the 19th century but were restricted to Raoul and Macauley, where both goats and pigs were feral by 1836 (Straubel 1954). Pigs disappeared from Macauley by 1840 and only occurred in limited numbers on Raoul until their final eradication in 1966 (Sykes 1969). Feral goats have remained the only

significant alien ungulate to impact native ecosystems on Raoul and Macauley over the past 150 years.

The interactions among native and alien plants on goat-ravaged Raoul and Macauley may be compared with the situation on the nearby outliers of North and South Meyer (1.2 mi or 2 km from Raoul) and Curtis (2 mi or 3.5 km from Macauley). The outliers have never supported ungulate populations but do share a number of alien plant species with their larger neighbor islands. Numerical comparisons of alien and indigenous plants in the Kermadecs are drawn from Sykes' (1977) definitive flora of the Islands.

The native vascular flora of the Kermadecs includes 133 species, of which 23 taxa (20.3%) are considered endemic. Although there are a few tropical Pacific elements, the overwhelming affinities of the native flora are with temperate New Zealand. A detailed comparison of native and alien elements in the flora of Raoul and the nearby Meyers is presented in Table 1. The total vascular flora of Raoul is 237 species, with 133 aliens accounting for 56% of this total. On the ungulate-free Meyer islets, there are 59 species, of which 25 (42%) are aliens.

At first glance, the percentage of aliens on the Meyers may seem high given lack of human disturbance and absence of feral ungulates; however, large colonies of nesting seabirds provide substantial natural ground disturbance (and probable dispersal mechanisms) favoring early successional aliens. The impacts of the seabird colonies in the Meyers may be compared with similar conditions of natural disturbance and plant dispersal created by relatively large seabird colonies on Nihoa in the Northwestern Hawaiian Islands and Hatuta'a in the northern Marquesas (see discussion of these islands above).

Comparative analysis of 21 alien species occurring on both Raoul and the Meyers (Table 1) shows that on Raoul 15 (71%) of the shared species can be described as "common or widespread" (qualitative assessment in Sykes 1977), whereas on the Meyers, only 7 (33%) of the shared species were described as common. The remaining 14 species on the Meyers exist only as rare or casual adventives. From these data it would appear that alien plants are twice as likely to establish widespread populations where goats had been present (Raoul), as where absent (Meyers).

On Raoul, the feral goat population increased to several thousand from the initial liberation of a few individuals in the early 19th century. Efforts to rid Raoul of goats began in 1937, and since then, about 15,000 animals have been killed (Parkes 1984a). After 1971, annual organized hunting expeditions steadily accelerated the decline in numbers of feral goats. Parkes (1984a) reported that feral goats were close to eradication, and Sykes (pers. comm. 1986) noted that the last goat was exterminated in 1984. The evidence from Raoul indicates that native species are now more common, especially those that were most palatable and previously quite rare due to severe ungulate foraging pressure. For example, since the significant decline in the number of goats on Raoul, the woody endemic *Coprosma acutifolia* has become a dominant understory species again in some local forests on the Island. Furthermore, rare species such as

Table 1. Composition of Raoul and North and South Meyer islands in the northern Kermadecs, with special reference to shared alien species.

	Raoul Island	North & South Meyer
Island area (ha)	2,943	12
Maximum elevation (m)	518	122
No. indigenous vascular plant species	104	34
No. alien plant species	133	25
Total flora (species)	237	59
Percent aliens in total flora	56	42
No. shared alien species on Raoul and Meyers	21	21
Rare or casual shared aliens	6	14
Common or widespread shared aliens*	15	7
Percent common and widespread species in shared alien flora	71	33

*Common and widespread shared aliens: *Cassia floribunda*, *Polycarpon tetraphyllum*, *Conyza bonariensis*, *Sonchus oleraceus*, *Sida rhombifolia*, *Oxalis corniculata*, *Rumex brownii*, *Portulaca oleracea*, *Alocasia macrorrhiza*, *Cyperus brevifolia*, *Bromus catharticus*, *Eleusine indica*, *Paspalum dilatatum*, *Sporobolus africanus*, *Stenotaphrum secundatum*. (Extracted from Sykes 1977.)

Homalanthus polyandrus, *Hebe breviracemosa*, and *Boehm australis* var. *dealbata* are now seen more often than before the goat removal program (Parkes 1984b). Goat browsing had reduced *H. breviracemosa* from its relatively common status in 1854 to a very rare species by 1908. The species was not observed again until a single young individual was seen in 1983.

A generally similar picture prevails in the comparison of Macauley (with goats) and Curtis (goat-free) in the southern Kermadecs. Macauley has a total vascular flora of 53 species, of which 14 (36%) are aliens. (Seven of the aliens are common or widespread.) Curtis Island, lying 22 mi (35 km) to the south of Macauley (Fig. 8), supports a vascular flora of 19 species, which includes only three aliens (15.8%). These aliens (*Oxalis corniculata* var. *repens*, *Solanum nigrum*, and *Conyza bonariensis*) are shared with Macauley. Only the composite herb *Conyza bonariensis* is common on both islands, associated with the disturbed ground of seabird colonies and pioneering on cinder substrates in the active volcanic crater on Curtis. *Oxalis corniculata* is common on Macauley but rare on Curtis, while *Solanum nigrum* is abundant on the recent volcanic substrates of Curtis but largely replaced on Macauley by the native *Solanum nodiflorum*. In spite of significant differences in outlier distance from the main islands of Raoul and Macauley, the proportions of widespread adventives in the total flora of the Meyers (7/59 or 11.8%) and Curtis (2/19 or 10.5%) are strikingly similar.

Goats were finally eradicated from Macauley in 1970, although all except two had been killed by 1966 (W.R. Sykes, pers. comm. 1986). Further vegetation change on Macauley and potential re-equilibration among alien and native elements should provide valuable information on the persistence and resilience of insular flora and vegetation. Woody plants were almost completely eliminated on Macauley through browsing by goats, with only a few *Myoporum* left growing on the inaccessible cliffs of the Island. However, regeneration of native herbaceous plants such as *Mariscus*, *Scirpus*, *Solanum*, and *Conyza* was already under way by 1970 (W.R. Sykes, pers. comm. 1986).

Now that ungulates have been removed from Raoul, the chances are good that a number of endemic species, such as those mentioned above, may once again extend their distributions and develop larger populations. What is still lacking from the Kermadecs are quantitative, long-term, micro-distributional studies of plant species interactions that could be used to test the generally subjective conclusions discussed above. The Kermadecs provide an exceptional opportunity for studies of competition between alien and native elements.

Henderson and Nauru

Although not in close proximity, both Henderson and Nauru islands, in the tropical Pacific (Fig. 1), are elevated limestone islands known as makatea. Henderson has been uninhabited and only rarely visited during recent centuries, but Nauru has supported a human population for over a millenium. During the 20th century, Nauru has experienced the radical environmental effect of phosphate mining.

The great majority of the approximately 24 or more of these known raised coral or makatea islands in the world's tropical oceans has been severely modified by long-term human settlement, including the mining of phosphate deposits in the 20th century. Aldabra in the western Indian Ocean and Henderson in the South Pacific are the only islands of this raised limestone type that are still largely unaltered. Henderson has been called one of the most scientifically fascinating of all coral islands (Fosberg *et al.* 1983).

Henderson Island, like Hatuta'a in the northern Marquesas and Nihoa in the Hawaiian Islands, is a small tropical Pacific landfall where relatively inaccessible and dry conditions have precluded establishment of domestic livestock or feral ungulate populations. More remote than either Hatuta'a or Nihoa, Henderson (Figs. 1, 9) is a raised atoll located 125 mi (200 km) east-northeast of Pitcairn, the closest inhabited island. It covers about 14 mi² (37 km²) in land area and reaches a maximum elevation of 110 ft (33 m). Like other elevated atolls, Henderson has surfaces that are extraordinarily eroded. Due largely to solution of its limestone substrate, the surface is commonly pitted, often presenting deep holes and jagged pinnacles, which, with isolation, location, and almost complete lack of freshwater resources, have limited human use of this island.

Preliminary archaeological research on Henderson in 1971 revealed traces of prehistoric Polynesian occupation that may have lasted 300 years (Sinoto

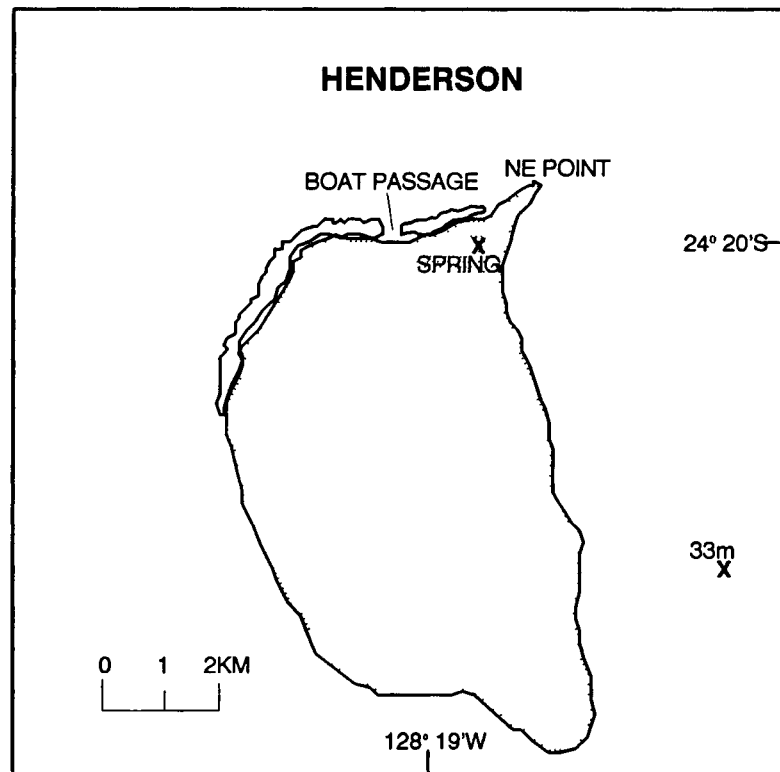


Figure 9. Map of Henderson Island, a raised atoll 125 mi east-northeast of Pitcairn, the closest inhabited island.

1983), ending prior to the European discovery of the island in 1606. Quiros described the island as uninhabited at that time (Fosberg *et al.* 1983). Prehistoric human impact on the Henderson Island flora appears to have been minimal. For example, the records from Quiros's expedition indicate that the only plant producing edible fruit was a native species of hala (*Pandanus tectorius*). If the early Polynesians brought in and cultivated any of their traditionally important cultigens, or inadvertently introduced any alien weeds, only two of these species, ti and candlenut, have ever been recorded from Henderson, and it is possible that both were brought in by Pitcairn islanders in the 19th century. Ti was collected only during the Mangarevan Expedition in 1934, when Fosberg recorded just six plants, and candlenut was collected only during the Whitney Expedition in 1922 (Fosberg *et al.* 1983).

Although Henderson has its share of native birds (including four extant endemic taxa of land birds) (Bourne and David 1983), herpetofauna, insects, and land snails (18 species, according to Cooke and Kondo 1960), no native terrestrial mammals are found on the Island. The Polynesian rat (*Rattus exulans*), first recorded from Henderson in 1819 (King 1820), was probably brought to the Island by prehistoric Polynesians. At least three species of birds, a storm-petrel (*Nesofregatta fuliginosa*) and two pigeons (*Ducula* spp.), no longer are found on Henderson. They have been

identified in archaeological sites and are thought to have been extirpated by prehistoric Polynesians (Steadman and Olson 1985).

If pigs were brought to Henderson by prehistoric Polynesians, they almost certainly disappeared long before the first European contact. D.R. Tait released some pigs in 1912, but no record of them exists on Henderson after this date (Fosberg *et al.* 1983). Brodie (1851) reported that Pitcairn islanders brought several goats with them on their first visit to Henderson in 1843 but failed to release them. The only report of an actual release of goats on Henderson indicated that three individuals were put on the Island in 1923 (Beck 1923). However, they reportedly had vanished by the time of the Mangarevan Expedition in 1934 (Fosberg *et al.* 1983). Perhaps the very dense vegetation and treacherous terrain precluded the establishment of feral goat or pig populations on Henderson.

In 1982 a wealthy American citizen proposed to the British Government to build a "holiday home with an airstrip" on Henderson in exchange for development assistance on Pitcairn (Bourne and David 1983). At that time there were no formal conservation measures that applied to Henderson or the other islands in the Pitcairn group. However, strong concern was expressed within the scientific community. Noting the advantages of its small size, isolated position, and "simple enough biota that its relationships, processes and functioning may possibly be understood with adequate investigation," Fosberg *et al.* (1983) argued that the proposed settlement of Henderson should not be approved since it would undoubtedly "permit the destruction of the only remaining intact example of one of the most important classes of islands." A resolution to this effect was adopted at the XV Pacific Science Congress, February 1-11, 1983, in Dunedin, New Zealand (Pacific Science Association Information Bulletin 1983). The Government of the United Kingdom later rejected the lease and development proposal in mid-December of 1983 (Pacific Science Association 1984).

Most of Henderson Island is today covered by a thickly vegetated tangled scrub and scrub-forest, with emergent *Pandanus* trees rising above the general canopy. In the interior of the depression that once was a former lagoon site, as well as parts of the makatea, the vegetation is more sparsely distributed (Fosberg *et al.* 1983). Except for some of the taller parts of the scrub-forest where the canopy is more complete, it is extremely difficult for humans, (or presumably, hoofed mammals) to move about freely because of very dense vegetation and the dissected limestone substrate.

The flora of Henderson (St. John and Philipson 1962) includes 8 ferns and 55 angiosperms. Fosberg *et al.* (1983) recorded two additional species of flowering plants and listed six species and five varieties of angiosperms as endemic to Henderson. The alien plant species that were listed included coconut, *Cocos nucifera* (Pitcairn islanders are reported to have started planting this species on Henderson as early as 1843; see Brodie 1851), ti, candlenut, and *Achyranthes aspera*. Fosberg *et al.* (1983) suggested that *A. aspera*, collected just once (1912), was "the only one of the four [adventives that was] not a deliberate

introduction." However, it is possible that *A. aspera* is a relatively rare indigenous species on Henderson, since its fruits become attached to birds that could have dispersed it to this remote island.

In any case, it is safe to say that Henderson Island today probably contains one of the least disturbed ecosystems of any tropical oceanic island in the Pacific. Except for a very small number of species, the alien plants and mammals that have been consciously or inadvertently brought to Henderson have not become naturalized. The rugged terrain has probably played a major part in suppressing the establishment of feral animal populations and consequently has allowed the native vegetation to remain largely intact.

Nauru is a small (8.5 mi² or 22 km²) makatea island in the Central Pacific 26 mi or 42 km south of the equator (Figs. 1, 10). The highest spot on the Island is no more than 100 ft (30 m) above sea level. Although the Island is normally wet (average rainfall is 80 in. or 2,030 mm/yr), annual precipitation exhibits great variation from 41 to 180 in. (1041-4,572 mm) per year (Carter 1981). The discovery of high-quality tricalcic phosphate rock in the central plateau of Nauru in 1906 led to the initiation of surface strip mining, which has continued to the present. Phosphate extraction involves complete removal of surface vegetation and soil, exposing new coralline substrate. Manner *et al.* (1985) recently investigated both the composition of remaining undisturbed plateau forest

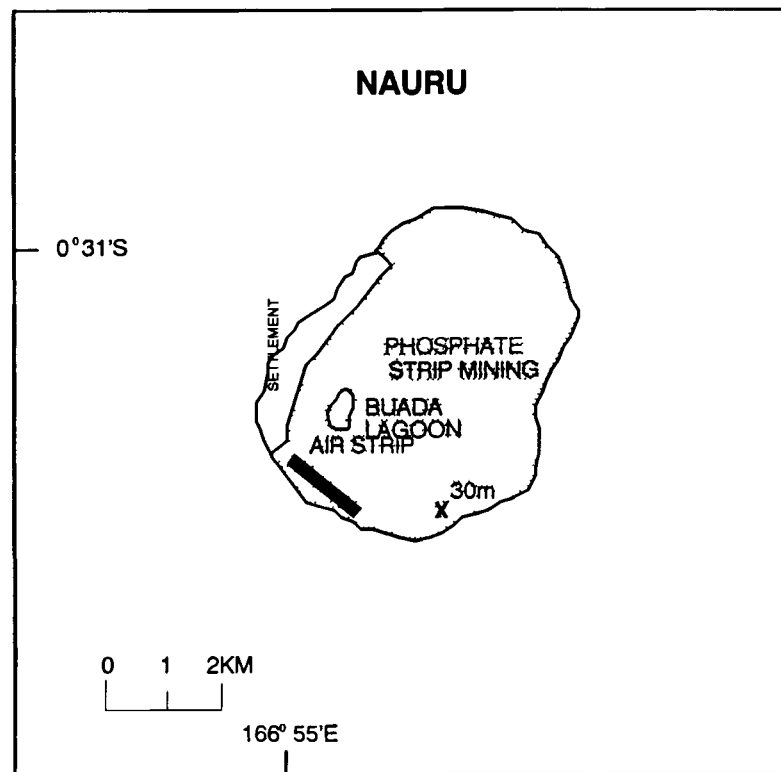


Figure 10. Map of Nauru, a small makatea island 26 mi south of the equator.

on Nauru and post-mining successional sequences that have developed over the past 75 years (Fig. 11).



Figure 11. Open-face mining of phosphate rock on Nauru involves removal of all vegetation, soil, and mineral deposits, leaving newly exposed barren coralline rock with "pit and pinnacle" micro-topography (bottom photo). Vegetation succession on these mined surfaces, although initially involving some aliens, returns after 20-40 years to native species-dominated shrub and tree communities (e.g., *Dodonaea viscosa*, *Ficus prolixa*) (top photo). (Photos: H. Manner.)

Although the Nauru flora includes 467 species, of which more than 90% are aliens of prehistoric Polynesian or recent introduction, the majority of these species (261) are introduced ornamentals that have not become naturalized and are restricted to home gardens and cultivation (Manner *et al.* 1985). A total of 126 species, including 81 adventive aliens and the native flora of 45 species, constitutes the potential pool of successional colonizers on disturbed areas of the central plateau. The natural forest vegetation of the central plateau is dominated by *Calophyllum inophyllum* (canopy height to 52 ft or 16 m), and in the most severe limestone areas by *Ficus prolixa* (canopy height to 65 ft or 20 m). Manner *et al.* (1985) found that in areas mined within the past 20 years, alien species such as *Tridax procumbens*, *Vernonia cinerea*, *Eragrostis tenella*, and *Phyllanthus amarus* were dominant. The native ferns *Microsorium (Polypodium) scolopendria* and *Nephrolepis biserrata* were also abundant in this early successional stage. At sites mined 20 to 40 years ago, native shrubs and sedges (*Scaevola taccada*, *Dodonaea viscosa*, and *Fimbristylis cymosa*) have substantially replaced pioneer aliens. At sites mined over 40 years ago, native trees and shrubs, including *Ficus prolixa* and noni or Indian mulberry (*Morinda citrifolia*), become dominant. Alien tree species such as *Casuarina littoralis* and common guava (*Psidium guajava*) do not figure significantly in intermediate successional stages. These results from Nauru suggest a resilience in the native flora and a clear competitive advantage where human disturbance is not continual and where feral ungulates are absent.

Southern Cook Islands

The islands of Atiu (10 mi² or 27 km²), Mitiaro (8.5 mi² or 22 km²), Mauke (7 mi² or 18 km²), and Mangaia (20 mi² or 52 km²) are all located in the southern region of the Cook Islands (Figs. 1, 12). The first three islands lie relatively close together and are collectively known as the Ngapotoru group. This group and Mangaia (110 mi or 180 km to the south) are not nearly as isolated as Henderson Island. They also differ from Henderson in that they all have central volcanic areas and a continuity of human occupation extending back at least a thousand years. On the other hand, like Henderson, these four southern Cook Islands have relatively wide areas of makatea, which circumscribe the central volcanic regions (Fig. 12).

In spite of the fact that ungulates have long been present on Atiu, Mitiaro, Mauke, and Mangaia, the topographically rugged, raised reef regions of these four islands, like that on Henderson, remain largely dominated by native species (Sykes 1980; Merlin 1991). One has only to look at the central volcanic regions of these islands, now largely (in some areas completely) devoid of native plant species (Fig. 13), to see what centuries of cultivation and animal husbandry have done (Sykes 1980). Although a large number of weedy plants have become naturalized in the central volcanic interiors of Atiu, Mitiaro, Mauke, and Mangaia, aliens have generally not been able to spread into the makatea areas. The native species on raised reefs appear to be more than adequate competitors when faced with aliens in the absence of hooved mammals or other sustained human disturbances that might create early successional conditions.

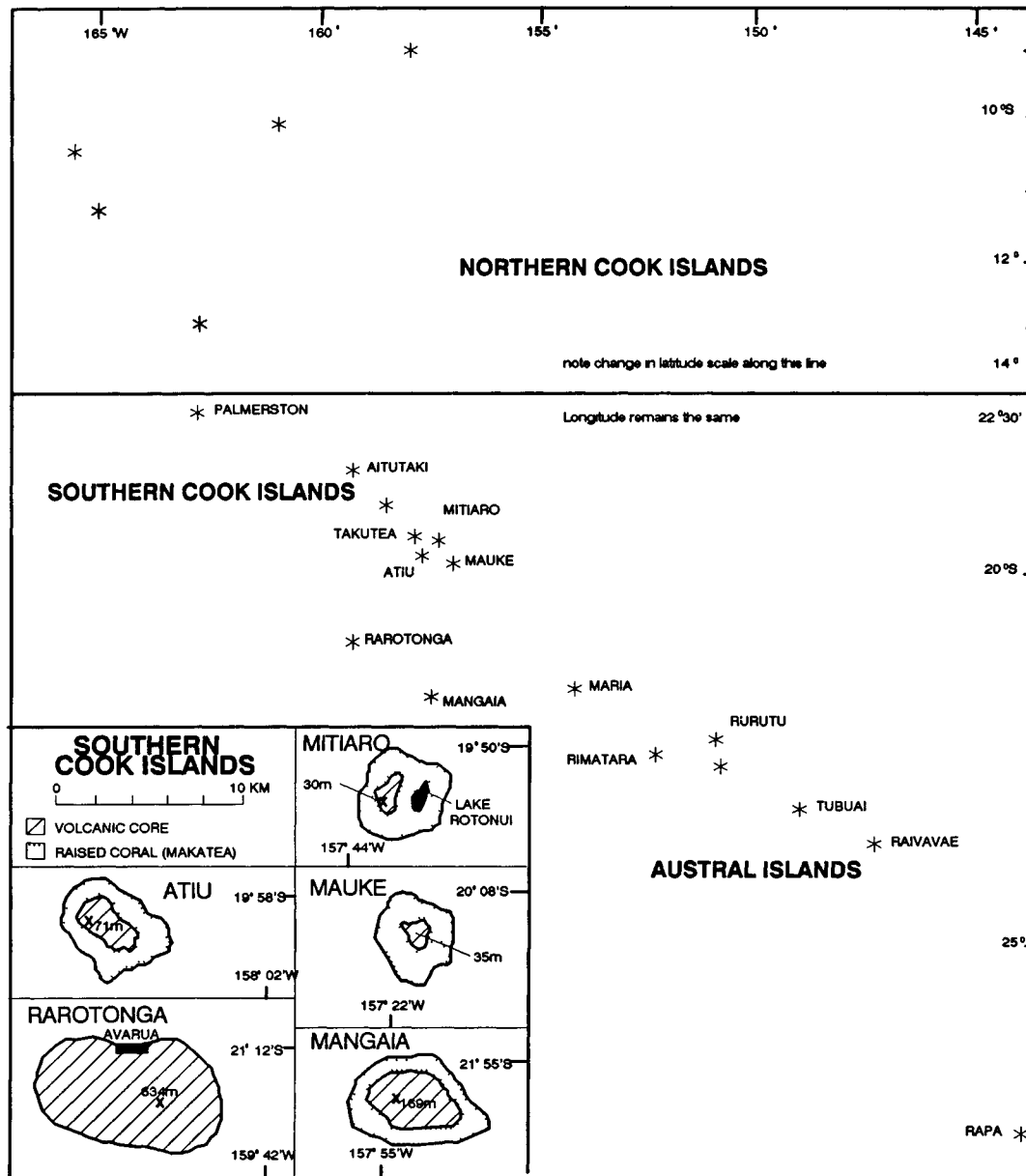


Figure 12. Map of the southern Cook Islands.

Rarotonga (Fig. 12), the largest (25 mi² or 64 km²), highest (2,140 ft or 652 m), and most populated of the Cook Islands (approximately 10,000 people), has only a very small area of coastal makatea. Most of the coastal lowlands are composed of alluvial and colluvial deposits from the eroded basaltic interior of the Island. Although the restricted area of raised coral on Rarotonga is still dominated by native species, the vegetation in the coastal and lowland zones of the Island today is dominated by alien species, including a host of cultivated crops, ornamentals, and a wide range of weedy adventives (Sykes 1980). The



Figure 13. Atiu in the Southern Cook Islands retains an intact native makatea forest on coastal limestone, while the more hospitable (with respect to soils and topography) central volcanic core of the island (at right) has been largely transformed by centuries of agricultural use. (Photo: M. Merlin.)

anthropogenic vegetation that nearly covers the entire extent of the low-lying areas inland of the coastal strand (and often deep into the interior of the Island along the valley bottoms) is very much like the severely altered vegetation one finds on the much-weathered volcanic interiors of Atiu, Mauke, Mitiaro and Mangaia islands.

A number of introduced woody species have become naturalized in parts of the uplands of Rarotonga. These include candlenut, found in some areas up to about 1,310 ft (400 m); ti, usually seen on shady slopes up to about 1,475 ft (450 m); and hau (*Hibiscus tiliaceus*), which is quite common along the many streams in the interior of the Island. In addition to these three plants (probably introduced during the pre-European period), some alien woody species have become naturalized in the montane areas of Rarotonga. These include common guava, *Syzygium* sp., *Solanum mauritianum*, lantana (*Lantana camara*), and *Ardisia humilis* in the lower elevations; and African tulip (*Spathodea campanulata*), strawberry guava (*Psidium cattleianum*), and *Cecropia palmata* in the lower and upper areas of the uplands. A number of introduced herbaceous weeds also in the uplands of Rarotonga include *Elephantopus mollis*, *Mikania micrantha*, and *Paspalum conjugatum* (Hilo grass).

Recent research in the upland region of Rarotonga provides quantitative evidence that native species continue to dominate the vegetation of the rugged interior (Merlin 1985). For example, over 92% of all the woody plants (dbh 1.0 in. or ≥ 2.5 cm) sampled along upland forest transects were either indigenous or endemic to Rarotonga. In addition, native plants accounted for 95.6% of the basal area covered by the arborescent vegetation in the montane study area. On the highest parts of the Island (above 1,475 ft or 450 m), native species accounted for more than 99% of the woody vegetation. Casual observations in the uplands as a whole also indicated that herbaceous vegetation is heavily dominated by native species (Merlin 1985).

Alien plants in the upland regions of Rarotonga are almost exclusively found in environments intentionally or accidentally disturbed by humans. Undoubtedly the lack of easy access, steepness of slope, and high rainfall in the montane areas of Rarotonga has greatly reduced the degree of human interference there. Native vegetation in the uplands has also probably not been significantly replaced by alien species because of the general absence of ungulates. In all likelihood, truly feral populations of pigs, goats, cattle, or other potentially disruptive hoofed animals have never been present in the montane region of Rarotonga. "The native vegetation in the rugged interior of the island therefore has not suffered from the deleterious effects of mammalian grazing, trampling, scarification, or seed dispersal of exotic weeds" (Merlin 1985). The evidence from the uplands of Rarotonga thus tends to support the hypothesis that in conditions of competition between alien and native plants without associated disturbance (on volcanic soils), native plant species are also able to hold their own against a diverse assemblage of alien species.

CONCLUSIONS

Generalizations drawn from the above qualitative examples of competitive interactions among native and alien flora must be evaluated cautiously in light of the many unconsidered variables and unique environmental histories associated with each of the islands discussed. It would appear however, that the competitive ability of insular floras (at least against early successional adventives), in the absence of severe or persistent feral ungulates, is probably sufficient to resist displacement by many alien plant species. One of the best examples of this can be found in the uplands of Rarotonga. Moreover, there is evidence from a number of oceanic islands, including Nauru in the Pacific and Barbados (Watts 1970) in the Caribbean, indicating that if native plants are displaced due to direct or indirect human impact, they may regain their dominant positions when human-induced disturbance (such as phosphate mining on uplifted coral-limestone islands or browsing, grazing and rooting by introduced ungulates on volcanic islands) ceases. A general conclusion drawn from island comparisons herein is that alien plant communities (early successional) evidence no specific pattern of competitive advantage in situations where alien ungulates or other forms of human disturbance are absent.

Questions of competitive interactions involving "climax" or late successional aliens are less clearly understood. For example, can native

insular plant communities dominated by endemic species that have undergone radical adaptive shifts (such as those found in the native *Scalesia* forests of the Galapagos Archipelago) ultimately compete against introduced "real" trees? The introduction of common guava to the Galapagos appears to have severely altered the present distribution of native vegetation (including the woody species of *Scalesia* and *Croton*) on at least three islands, San Cristobal, Floreana, and Isabela. Common guava "has grown out of control and covers vast areas of the humid highlands" (Eckhardt 1972). It has also been reported that the rank growth of alien elephant grass (*Pennisetum purpureum*) in some areas has prevented regeneration of native tree species such as *Scalesia* and *Eugenia* (Stone *et al.* 1988).

The role of feral ungulates in the relationships between native and alien plants in the Galapagos is quite instructive. Removal of feral cattle from anthropogenic grasslands in the highlands of San Cristobal about 50 years ago allowed previously cropped guava shoots to quickly develop into mature trees that dominate "the dense tangled and dwarf forests prevalent today" (Eckhardt 1972). It is possible that guava trees may now have a seed bank and other reproductive advantages (*e.g.*, allelopathy) that preclude the regeneration of native woody species. Although less radically affected than San Cristobal, parts of the highlands of Floreana and Isabela also appear to have experienced subsequent conversion of the native forests to grassland and then to guava-dominated scrub forest, through the initial presence and later removal of cattle (especially feral cattle).

The present paper suggests specific areas for further research to clarify the nature of competition between native and alien island plants with and without associated disturbance. Additional long-term studies of population dynamics in mixed native/alien ecosystems are needed. All the island groups described above offer opportunities for comparative studies under different disturbance regimes. For example, although common guava became a severe pest in significant areas of three of the four inhabited islands in the Galapagos, on the fourth of these islands, Santa Cruz, the species still formed only a minor part of the woody vegetation approximately 35 years after its introduction. In the 1980s, however, the tree apparently became more abundant. "What influences, man-made or natural, may induce its proliferation are still unknown" (Eckhardt 1972).

In summary, the comparisons made herein and studies cited from elsewhere suggest that competition of alien and native plants on islands with and without past and current disturbance by humans and livestock is a very complicated subject. Although severity and periodicity of natural and unnatural disturbances (including seabird colonies), proximity and kind of alien and native plant propagules, and site specificity can influence outcomes, it is likely that competitive advantages of native species are less important in early succession than late succession. In many cases, removal of disturbance caused by ungulates or humans results in dominance of native rather than alien species, particularly if enduring changes such as loss of pollinators, shading, allelopathy, or altered nutrient cycles have not been effected.

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