Aliso: A Journal of Systematic and Floristic Botany

Volume 16 | Issue 2 Article 5

1998

Conserving Plants as Evolutionary Entities: Successes and Unanswered Questions from New Zealand and Elsewhere

Ian A. E. Atkinson
Ecological Research Associates of New Zealand, Inc.

Aliso, 16(2), pp. 103–112

CONSERVING PLANTS AS EVOLUTIONARY ENTITIES: SUCCESSES AND UNANSWERED QUESTIONS FROM NEW ZEALAND AND ELSEWHERE

IAN A. E. ATKINSON[1]

Ecological Research Associates of New Zealand, Inc.
P.O. Box 48-147
Silverstream 6430, New Zealand

ABSTRACT

Saving a species from extinction may not insure that its future will continue as before, even when the surviving population is in a wild habitat. Former selection forces may be missing or replaced by others so that the species develops along a different evolutionary pathway. Such disruption of evolutionary direction may be particularly important for island taxa given that modification by humans and their introduced organisms is making many islands more similar to continental habitats. In restoring habitats for island species, special attention should therefore be given to identifying the major selective forces likely to have been operating during the evolution of those species. It will not always be practical to reinstate all these selective forces. However, there are sometimes opportunities to restore, or reconstruct by species substitution, the biotic selection formerly brought about by herbivores, predators, competitors, pollinators and seed dispersers. Systems restored in this way will not be authentic replicas but may function more like systems of the past than those operating at present. Data from New Zealand, where restorative action has been taken on more than 40 islands, are used to examine these general principles. The ongoing restoration of Round Island, Mauritius, is used to illustrate the kinds of questions that this approach generates: should species thought likely to have once been present on Round Island be re-established?; should a giant tortoise be introduced to the island to substitute for the extinct species of tortoise that was lost last century?

Key words: herbivory, islands, restoration, conservation.

INTRODUCTION

"The patterns of evolution on islands usually dictate that insular organisms be overtaken . . . . They are part of the entire pattern of life on earth, and without them, the entire pattern would be incomplete, even meaningless." Sherwin Carlquist, 1965.

The significance of islands as centers for plant and animal evolution is well recognized as is their importance as refuges for the taxa that have resulted. But the question arises as to whether islands will continue to be centers for population divergence in the face of the continuously extending and all-pervading influence of humans on island environments. If not, is there anything we can or should do about it? I will examine these questions using examples from islands in New Zealand and elsewhere and, where possible, identify options we may have for influencing the course of events.

GEOLOGICAL AND RECENT HISTORY OF NEW ZEALAND ISLANDS

New Zealand consists of three main islands: North Island, South Island, and Stewart Island. The land is a continental fragment that separated from the southern continent of Gondwana some 85 million years ago (Stevens 1994). However, because of long isolation, the New Zealand biota is more characteristic of an oceanic island than of a continental island. The indigenous vascular flora, for example, comprises only about 2400 species and nearly 80% of these are endemic. In common with the floras of many other isolated islands, some groups of plants are quite unusual, and adaptive radiation into a variety of habitats is apparent within some families and individual genera.

Surrounding the main islands are smaller islands on the continental shelf, commonly referred to as offshore islands and all within 50 km of the main islands. Most of these islands are concentrated in four areas: northeastern North Island, Cook Strait, around Stewart Island, and Fiordland in southwestern South Island. Their geology is varied: volcanic, sedimentary, and metamorphic rocks are all represented (Fig. 1).

Contrasting with the continental-shelf islands are eight groups of oceanic islands, all 50 km or more from the mainland, mostly volcanic, and commonly referred to as outlying islands. They lie at considerable distances from the main islands, varying from the ca. 50 km of the Three Kings Islands north of the country, to the 900 km that separates the southernmost island of the Kermadec group from New Zealand (Fig. 1). The Chatham Islands, unlike the other outlying island groups, originated as a fragment of Gondwana at the

[1] Presented as the annual Nakashima Lecture in Island Biology, sponsored by the Santa Barbara Botanic Garden.

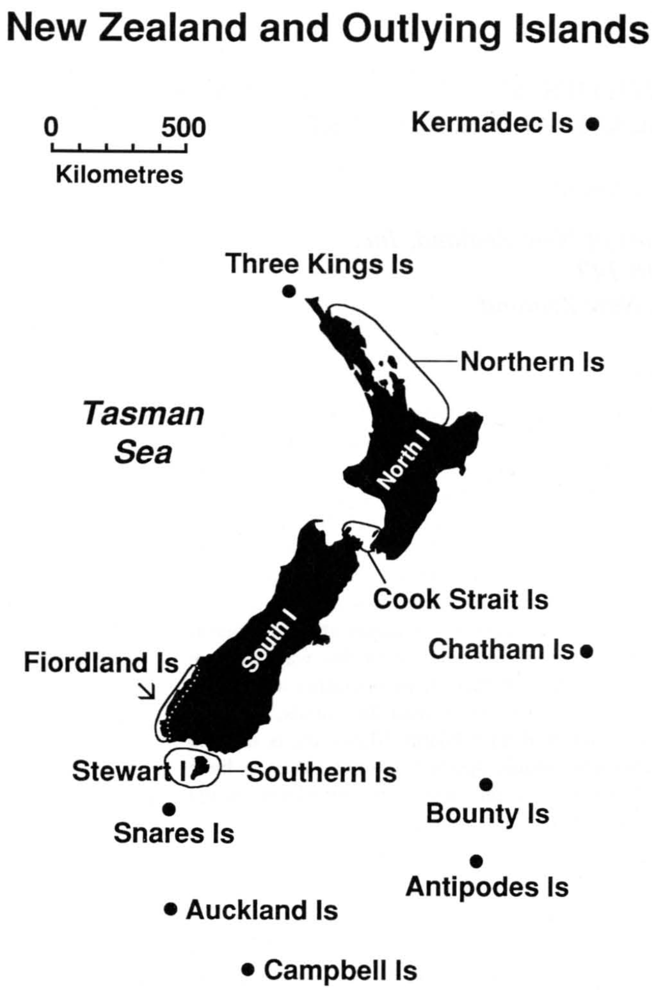

Fig. 1. Islands of New Zealand showing the four main areas of continental-shelf islands (encircled) and the distant oceanic islands north, east and south of the main islands.

same time as New Zealand became separated. They have remained extremely isolated ever since as well as being extensively if not completely submerged during the early Pleistocene period (Hay et al. 1970).

The most significant historical event that distinguishes the evolutionary history of plants and animals on the offshore islands from that of the outlying islands concerns their past connections with the main islands. During the last glacial period, sea level sank some 100 m below its present level, thus connecting the offshore islands to the mainland. As a result, the indigenous plants and animals of these islands are, or were, shared with the main islands and endemism is extremely low. The only exception is the Poor Knights Islands group, 20 km east of the North Auckland mainland. These islands stand on the edge of the continental shelf and were apparently not connected during the most recent period of low sea level, 10–25 thousand yr ago. Some taxon differences are apparent among the indigenous plants and animals of the Poor Knights islands but they have not been quantified.

Because of shallow depths to the sea bottom, some offshore islands remained connected to the mainland as late as 7000 yr BP (Towns and Ballantine 1993) and even then the majority of these islands were not completely isolated from the main islands. Most offshore islands lie immediately east of New Zealand and are thus leeward of the mainland relative to the prevailing westerly winds. Thus for many wind- or bird-dispersed plants, gene flow has continued from the mainland to offshore islands for much of the past 7–10 thousand yr.

Table 1. Comparison of offshore with outlying islands in New Zealand. General differences are summarized with respect to distance (isolation) from three main islands in km, age in years, numbers of islands ≥5 ha, level of endemism, relative species diversity, and the level of human disturbance.

	Offshore	Outlying
Isolation (km):	<50	≥50
Age (yr):	ca. 7–10 thousand	2–75 million
No. of islands:	290	50
Endemism:	very low	high
Species diversity:	relatively high	low
Human disturbance:	major	minor

The outlying islands have never been connected to the New Zealand mainland and, excepting the Bounty Islands, which lack a vascular flora, all show a degree of endemism among their plants and animals (Table 1). However, many plant endemics of the islands in the subantarctic zone (i.e., Auckland, Campbell, and Antipodes Islands) are shared among them or with Macquarie Island (Australian territory) further south (Atkinson and Bell 1973).

The biotic communities of the outlying islands are often dominated by endemic species, particularly in the Chatham group. Another characteristic feature is the presence of large colonies of surface-nesting seabirds such as albatrosses, mollymawks, penguins, and shags (cormorants). Some offshore and many outlying islands support dense colonies of burrow-nesting seabirds (e.g., petrels, shearwaters, and prions) which continually bring nutrients to these islands from vast stretches of ocean.

Both outlying and offshore islands have been substantially modified by humans and their introduced animals. Many offshore islands were burnt or otherwise cleared during pre-European times when inhabited or visited by Maori settlers. Of the outlying islands, only the Three Kings and Chatham Islands were permanently occupied during pre-European times. For both island groups, the European period has brought increased modification of some islands and effective conservation of others.

CONSERVING PLANTS AS EVOLUTIONARY ENTITIES

Evolution is an inexorable process that will continue in some way no matter what humans may do to the

planet. So far as individual taxa are concerned, however, if changed conditions result in their populations declining to extinction, further evolution is terminated. Our concern about these losses has generated the effort now expended in preventing extinctions. We must also be concerned about the nature of what it is that we apparently save from extinction. Is it a group of self-maintaining populations with variability within or between populations sufficient to give the particular taxon the capacity to respond to natural environmental changes, including local catastrophes? Or do we have a collection of individuals so protected in an artificial environment, or so exposed to new and extreme selection pressures that, in either case, the evolutionary potential of the taxon has been lost?

In addition to the question of how best to maintain the evolutionary potential of taxa surviving in greatly-altered environments, there is a second question: that of knowing the true evolutionary relationships of isolated populations that are treated as belonging to the same taxon (Woodruff 1989, Rojas 1992). In a majority of cases we presently know little of the variability below species level and a number of species presently regarded as single entities will prove to be distinct, even if cryptic, species.

For these reasons it appears that, in addition to paying attention to the sizes and genetic structure of populations we protect, we must also consider the changes in selection forces that are now acting on those populations as a result of their altered environment. I will concentrate on the second question, the nature of the selection regime in which any plant we try to conserve must live.

MAINTAINING OR RESTORING SELECTION REGIMES

We must first identify the major selection forces that act on all plants although the list given in Table 2 is unlikely to be complete. These forces or factors can be of two kinds: nonspecific or species-specific. Climatic and edaphic conditions or catastrophes such as cyclones and landslides, are nonspecific selection forces in that all plants can be affected though not all species respond in the same way. Selection factors such as herbivores, competitors, pollinators, pathogens, and parasites involve other organisms in the plant's environment. With these biotic selection factors, unlike the physical factors, there is the possibility that two-way selection between the interacting species, may result in coevolutionary responses.

Table 2. Major selection factors that operate on islands.

Nonspecific regimes	Species-specific regimes
Climate	Herbivores, predators
Edaphic conditions	Competitors
Periodic catastrophes	Pollinators and dispersers
	Pathogens and parasites

Individual selection forces together make up a regime that determines the evolutionary pathway of an island's plants (and animals). Human influence may alter or modify many of these forces. Whether or not we try to intervene to reduce this influence is a value judgement for which there is unlikely to be general agreement. However, on some islands at least, there are reasons why it is worth doing. First, it can prevent us from losing some species altogether. Second, as scientists we can acknowledge that it will help retain opportunities for further study of evolutionary processes. Third, but not least, maintaining or restoring selection regimes for a few species is likely to have flow-on effects beneficial for the whole island system. In this respect we will be sustaining part of the world's fast-diminishing biodiversity in the broader sense of what that word means.

How do current methods for conserving plant species relate to this need to maintain their evolutionary potential? Preservation in a germplasm bank removes the plant from normal selective forces but buys time for taking more comprehensive action. Protection in a botanical garden exposes the plant to a selection regime very different from that in which it evolved but again buys time for more comprehensive action.

In situ protection of the plant in its original habitat is a preferred option; but on larger land masses, particularly those inhabited by people, it is sometimes difficult if not impossible to remove human influences. On islands, however, more options are available for maintaining or restoring selection regimes comparable to those operating in the past.

RESTORING SELECTION REGIMES ON ISLANDS IN NEW ZEALAND

Options for maintaining or restoring selection regimes on New Zealand islands can be examined in relation to individual selection forces.

Climate

Gradual climatic change, whether human-induced or not, is not something we can do much about. Few offshore islands have a large altitudinal range but they span more than 12 degrees of latitude. Given that most plant species of these islands are shared with the main islands, it would be possible to translocate a species that was considered endangered by climatic change. Such action could not be justified on outlying islands because of the need to protect their endemic populations from genetic mixing with related taxa. More rapid climatic fluctuations or sudden climatic events can be treated as periodic catastrophes (see below).

Edaphic Conditions

In general, edaphic conditions of moisture storage, nutrient availability and aeration on islands have not been substantially altered by human activity. If, however, overfishing or pollutants reduce the food supply of some of the seabirds that nest on islands, one could expect a large decrease in nutrient input with consequent changes in the island's vegetation. Intervention should be directed primarily at restoring the health of the seabird populations.

Periodic Catastrophes

This selection force is also largely out of human control. Protected areas large enough to provide a variety of sites for cyclical recovery processes are important in this context. Our best insurance against complete loss of species or communities is to protect many different islands and to include among them large islands. In this way some islands or parts of islands are more likely to escape the effects of a particular catastrophic event.

Herbivores

The major vertebrate herbivores in New Zealand were originally 11 species of large ratite birds, moa, in the genera *Dinornis, Pachyornis, Euryapteryx, Emeus, Anomalopteryx* and *Megalapteryx.* Adult weights of these birds ranged from 15 to 200 kg, but in one species to over 250 kg. From what can be inferred of their numbers, particularly at moa-hunter butchery sites, they were a major selection force influencing plants in forest, scrub, shrubland, and sometimes more open communities from the coast to above treeline (Greenwood and Atkinson 1977; Anderson 1984; Atkinson and Greenwood 1989; Cooper et al. 1993). However, the outlying islands and all but three or four of the largest offshore islands were apparently without moa so that we are not faced with trying to substitute a vertebrate herbivore for these extinct birds to restore this part of the selection regime. A few species of much smaller native birds, either wholly or partly herbivorous, have declined or been lost from many islands although, being still extant, they can be restored to an island. By far the most significant change to herbivore selection pressure on islands has been the introduction of mammals such as goats, pigs, sheep, cattle, and occasionally Australian brushtail possums. The eradication of these animals from islands of increasing size is a success story (Fig. 2). Most notable are the eradications of pigs from Aorangi Island (110 ha), Poor Knights group in 1936, goats from Great Island (408 ha), Three Kings group in 1946, and from Raoul Island (2938 ha), Kermadec group in 1984, and possums from Kapiti Island (1965

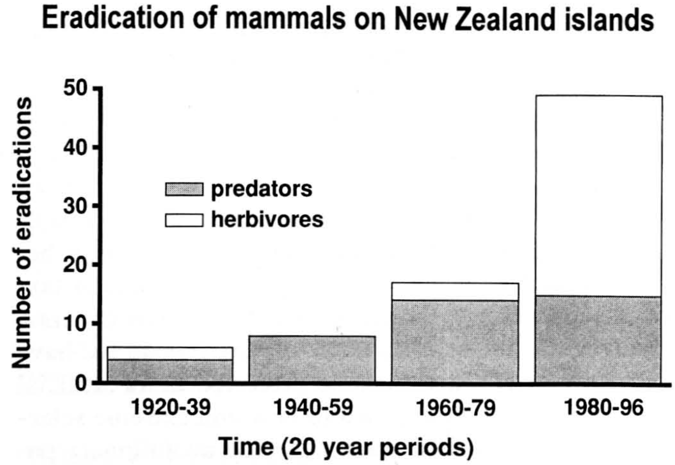

Fig. 2. Eradications of mammalian predators and herbivores from New Zealand islands summarized in 20-yr periods.

ha) in 1985. Since 1980 many introduced mammalian predators, particularly rats, have also been eradicated from islands. Although this has greatest significance for the island's indigenous fauna, eradication of animals such as rats can remove unwanted selection pressures on native plants. For example, Pacific rats, *Rattus exulans,* are known to eat flowers, fruit, seeds, shoot apices, leaves, petioles, twigs, and bark of some woody species as well as seedlings and root bases of their juveniles (Campbell et al. 1984). It is probable that these effects translate into reduced recruitment for at least a few species of native tree but more work is needed to confirm this.

Competitors

Significant contact by Europeans with the New Zealand region began in 1793. In the succeeding 200 years new vascular plants have established at an average rate of eight species per year (Atkinson and Cameron 1993). More than 90 species of introduced weeds are now seen as significant competitors of native plants on offshore or outlying islands and are therefore classified as problems (I. Atkinson, unpub.). The incidence of problem weeds is greatest among the northern islands. Here the climate is favorable for a wide variety of adventive plants and the relatively high density of the human population has promoted a high rate of naturalization on the adjacent mainland. Esler and Astridge (1987), in their study of weeds in the greater Auckland region, have shown that new species are becoming naturalized at a rate of about four species per year. The problem on islands decreases as one moves south and is least on the outlying islands excluding those with a history of human settlement (Fig. 3).

What to do about the weed problem on islands is very much an unanswered question. In more extreme cases, such as islands invaded by Argentine pampas [*Cortaderia selloana* (Schultes) Asch. & Graebn.,

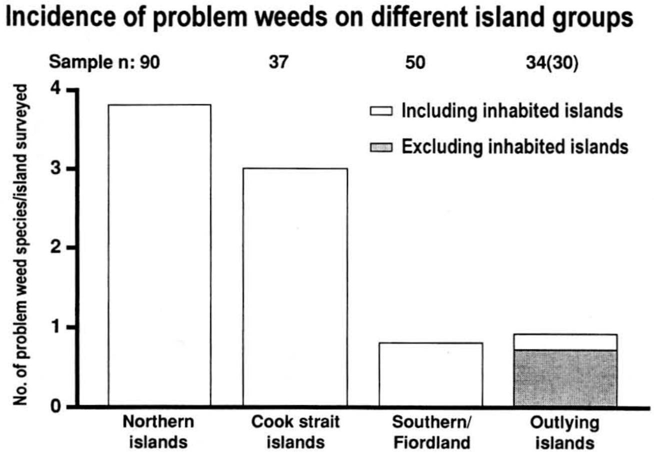

Fig. 3. Incidence of problem weeds, considered as competitors of indigenous plants, on four groups of New Zealand islands.

Cortaderia jubata (Lemoine) Stapf], some communities have been completely changed in structure and composition. Limited control is carried out on some islands using herbicides or mechanical methods but there are few islands where we can say with certainty that a particular weed species has been eradicated. Biological control may be a solution in the long term but the testing necessary to insure that nontarget species will not be affected is so expensive that application of this method has concentrated on weeds of economic significance.

Pollinators and Dispersers

The kind of pollination mechanism is understood for many indigenous plants in New Zealand but with respect to insect- and bird-pollinated flowers we are often ignorant of which species are the key pollinators. Until these are identified we cannot judge the extent to which this part of the selection regime may have been altered. With respect to seed dispersal, plants that are dispersed by wind or water may not have suffered any reduced gene flow compared with prehuman conditions. But for bird-dispersed species, the indigenous pigeon (*Hemiphaga novaeseelandiae*), which is a strong flier and considered a key disperser of tree species with large fleshy fruits (Clout and Hay 1989), is steadily decreasing on the mainland. Thus, gene flow from this source to islands in now much reduced especially from areas where forest has been almost completely replaced by farmland. In this respect the northern group of offshore islands is becoming more like outlying islands in its degree of isolation.

Pathogens and Parasites

Restoration projects to date have not perceived any need to maintain or restore these selection factors, probably because other problems have seemed more important.

RESTORING ISLAND SYSTEMS

One of the difficulties we have had with ecological restoration in New Zealand has been that of getting universal scientific support for the way in which we define restoration goals. We have usually defined goals in terms of the composition of a particular kind of community at a particular period in time.

The identified time period is certainly essential to include in a goal statement because without it we do not know where we are going. For example, there have been such large changes in selection pressures related to browsing effects in New Zealand between prehuman, pre-European and post-European periods, that we must first decide which of these broad time periods is the one of interest. It is sometimes necessary to subdivide the post-European period because the combination of introduced mammalian predators and herbivores has changed frequently as more and more alien species have established. These changes alone have so altered the selection regime operating at particular times in New Zealand's history that to ignore them is to deny that introduced organisms have any effects on the functioning of soil-plant-animal systems.

A difficulty with defining restoration goals in terms of community composition is that it appears to contradict the dynamic nature of communities especially if time periods as short as 20 years are specified. Furthermore, the composition of most biotic communities of the past is only known in broad terms.

For these reasons I suggest that an alternative way of defining restoration goals, that emphasizes selection regimes, may be more useful. In the context of islands this would be management aimed at reinstating the major selection forces that formerly acted on the island's plants and animals during a specified historic or prehistoric period.

The extent to which this aim is met will depend, in the first instance, on how much information can be obtained about the biota and environmental conditions formerly present in the particular habitat and time period of interest. An advantage of this kind of goal definition is that it emphasizes evolutionary as well as ecological processes because it prompts us to inquire more fully into what selective forces would have been operating during the time period of interest.

A second advantage is that although the kind of community would have to be identified with respect to its major plant and animal components (in order to characterize this part of the selection regime), this would not imply that particular proportions of these components have to be achieved; the dynamic nature of communities is accommodated.

I do not wish to pretend that this approach to restoring biotic communities of the past will produce authentic replicas of these communities. We have little

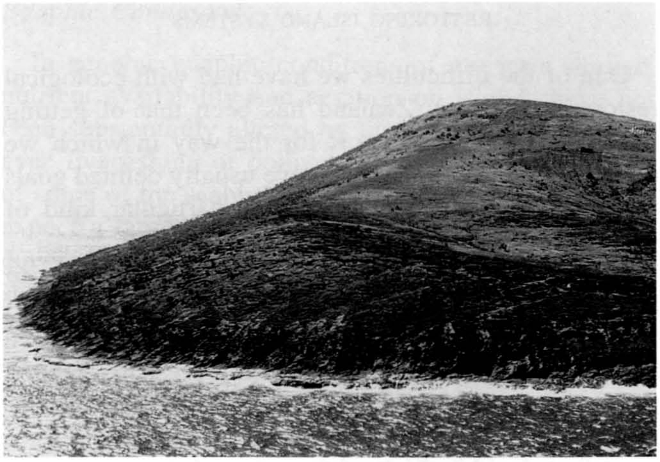

Fig. 4. Round Island viewed from the south showing the gullied slopes supporting a partial cover of the vines *Ipomoea pes-caprae* and *Tylophora coriacea* with scattered palms of *Latania loddigesii.*

chance of quantifying past selection pressures in a meaningful way and our best restoration efforts will sometimes be rather poor imitations. But describing a past environment in terms of the major selection forces likely to have been operating, may help to make our ecological reconstructions much closer to historic communities in a functional sense than are present-day systems. And whatever their shortcomings, we need to remember some of the primary reasons why we attempt ecological restorations on islands: to provide habitats for species that can no longer survive in present-day conditions, to insure that species will continue along evolutionary pathways in which disruption by human activity is minimized, and, by providing a greater variety of community systems, compensate to a limited degree for losses of biodiversity now taking place in so much of the world.

AN EXAMPLE: ROUND ISLAND, MAURITIUS

Round Island (57° 47′ E; 19° 51′ S) lies 22.5 km NE of mainland Mauritius, the central member of the Mascarene Islands (Réunion, Mauritius, and Rodrigues) in the southern Indian Ocean. It is an eroded basaltic volcano of late Pleistocene age, having an area of 151 ha and height of 280m (Fig. 4). Its steep slopes, mostly 10–25° but steeper within its breached crater, are composed of layer upon layer of welded scoriaceous tuff deposited as subaerial ash beds (Montaggioni and Nativel 1988). The island is channeled by numerous ravines and shallower valleys cut during the intense rainfalls of cyclonic storms, and weathering has sculptured slopes into strangely shaped steps, pedestals, and precarious overhangs.

The conservation value of Round Island came to international attention as a result of the survival there of several endemic gecko, skink, and snake species that had disappeared from mainland Mauritius as a result of introduced rats, cats, shrews, mongooses, snakes, lizards, and geckos. The island is also an important breeding site for several species of seabird, notably the only population known from the Indian Ocean of the Herald petrel (*Pterodroma arminjoniana*) and the largest breeding colony of wedge-tailed shearwaters (*Puffinus puffinus*) in the Mascarene Islands.

Effects of Rabbits and Goats

The earliest description of the island (Lloyd 1846) showed that the lower and middle slopes were covered by a palm savannah community dominated by three species of palm: latania (*Latania loddigesii* Mart.), bottle palm (*Hyophorbe lagenicaulis* Bailey), and hurricane palm (*Dictyosperma album* var. *conjugatum* (Bory) Balf f.). The structure of this community has greatly altered since Lloyd's time and only a few stands and many scattered trees of latania are left with a ground vegetation infiltrated by weedy aliens. Upper slopes of the island were covered by a stunted hardwood forest that included, among other plants, three species of ebony (*Diospyros* spp.). This forest has disappeared completely. In terms of species present or likely to have been present originally, all that is left on the island (only at a lower altitude) are a few individuals of two hardwood species, *Gagnebina pterocarpa* (Lam.) Baill. (Leguminosae) and *Fernelia buxifolia* Lam. (Rubiaceae).

This catastrophic depletion of Round Island's vegetation was brought about by the introduction of rabbits at some time before 1810, followed by the introduction of goats between 1846 and 1868 (Merton et al. 1989). Thus, in the succeeding 100 years the island's plants were exposed to vertebrate herbivory of a kind and intensity entirely unknown in their earlier evolutionary history. Previously, the only large vertebrate herbivore present was one species of giant tortoise (*Geochelone*), which apparently was still surviving on the island at the time of Lloyd's visit in 1844 (Cheke 1987). This tortoise, together with a second species, was also present on Mauritius but all tortoises indigenous to these islands are now extinct.

The 1989 Restoration Plan

The last goat on Round Island was shot by Daniel Pellicier about 1979 and rabbits were eradicated by a New Zealand Wildlife Service party led by Don Merton in 1986 (Merton 1987). The island thus became completely free of introduced mammals after more than 175 years. This made it possible to begin planning an ecological restoration for the island. I was fortunate to be included in the planning team which worked on the island for three weeks in June-July 1988. The project was instigated and sponsored by the Jersey Wildlife Preservation Trust in collaboration with the Mauritian

Table 3. Options for restoring Round Island, Mauritius. Five major options and their acceptance in a multidisciplinary management plan (Merton et al. 1989) are summarized.

Option	Response in plan
1. Do nothing.	Rejected.
2. Maintain precautions against invasions by alien animals and plants.	Accepted as essential for successful restoration.
3. Eradicate or control problem weeds.	Accepted as essential for successful restoration.
4. Reestablish plants and animals formerly present.	Accepted while acknowledging that the species lists of last century are very incomplete.
5. Establish selected plants and animals of Mauritius not certainly known to have been originally present.	Accepted with proviso that selected species are ecologically appropriate and will either facilitate restoration or are threatened with extinction on the Mauritius mainland.
6. Establish threatened species from dry lowland zones of other Mascarene islands.	Rejected because other Mascarene species should be protected as close as possible to the islands where they originated.

Ministry of Agriculture, Fisheries and Natural Resources with further major financial support from Wildlife Preservation Trust International (Merton et al. 1989).

When I arrived on the island it was immediately apparent that two plants at least were very effective as pioneers on the steep tuff slopes which are largely bare of soil: the latania palm and the Mauritian screwpine (*Pandanus vandermeerschii* Balf.). Although much less common than the latania, like latania the screwpine has leaf margins edged with a row of short sharp spines. These mechanical deterrents may explain why some regeneration of both species took place in the presence of goats and rabbits. In contrast, the bottle palm was reduced to about 20 individuals with only eight remaining full-grown adults, and the hurricane palm was reduced to two adults, one upright and the other stunted and semiprostrate. Young bottle palms lack leaf margins with spines and I presume (without having seen plants) that juvenile hurricane palms are also without spines. Bottle palms began to regenerate close to remaining adults almost immediately after the rabbits were eradicated. However, even though the hurricane palm has flowered several times and set seed, no seedlings have established on the island. Seedlings have been raised from this plant on Mauritius but at present none have been returned to the island.

Options for Restoration

Options that were considered in the 1989 plan for restoring Round Island are listed in Table 3 together with reasons for rejection or adoption. The difficulties of landing on the island from the sea make it easier to inforce stringent precautions against introductions of alien animals and plants (Option 2). All boxes, crates, camping equipment, and foodstuffs to be taken to the island must be sealed against the entry of rodents, young snakes, lizards, and invertebrates such as giant land snails. Careful inspection is necessary during unpacking on the island. Further precautions against invasion of vulnerable islands by alien animals are given by Moors et al. (1992). All visitors to the island must also insure that their footwear, socks, and other clothing are completely free of seeds. Alien plants can still reach the island if wind- or bird-dispersed so that constant vigilance for newly established immigrants must be maintained.

With respect to Option 3, at least 28 species of alien plants have already established on the island (W. Strahm, pers. comm.) but weeding has been concentrated on the two species seen as the most serious threats: the shrubby tree, *Desmanthus virgatus* (L.) Willd. (Mimosaceae), and the perennial herb, *Desmodium incanum* DC. (Leguminosae).

Re-establishment of plants and animals formerly present on the island (Option 4) has so far been restricted to the sowing of bottle palms in suitable microsites over a much larger area than that which the species presently occupies. Lloyd's (1846) description clearly shows that all three of the island's palm species were very abundant in 1844 so that considerable work will be needed to increase the distribution of bottle palm and re-establish the hurricane palm in numbers more comparable to those of the latania. Establishment on open sites of these three palms, together with the Mauritius screwpine, was identified in the 1989 plan as the mainstay of the effort to restore a native plant cover to the island.

The fifth option of establishing selected plants and animals of Mauritius not known to have been certainly present in the past was accepted by the study team but provoked some controversy. Seven plant species were recommended as ecologically suitable and likely to have once inhabited Round Island (Merton et al 1989). *Scaevola taccada* Roxb. (Goodeniaceae) for example, is a widespread strand species and *Dracaena concinna* Kunth (Liliaceae), *Gastonia mauritiana* Marais (Araliaceae), and *Tarenna borbonica* (E.G. & A. Henderson) Verde. (Rubiaceae) are all present in coastal areas

of Mauritius or its smaller islands. Three of the seven recommended species are considered to be currently vulnerable or endangered based on guidelines established by the International Union for Conservation of Nature (IUCN). To date, only *D. concinna* has been established on the island.

North et al. (1994) were uneasy with this fifth option because they consider that the pioneer characteristics of these recommended species "may also have unpredictable and undesirable impacts on species known to be native to Round Island." Their view was that such action should not be taken, at least in the short term.

The danger of adopting this view is that it neglects the continuing extreme vulnerability of Round Island to weed invasion. In Mauritius itself, excepting those small areas that are regularly hand-weeded, there are no stands of native forest remaining without woody weeds, such as *Psidium cattleianum* Sabine (Myrtaceae), *Ligustrum robustum* Bl. (Oleaceae), *Rubus molucanus* L. (Rosaceae), *Flacourtia indica* (Burm. fil.) Merrill (Flacourtiaceae), *Tabebuia pallida* (Lindl.) Miers (Bignoniaceae), *Wikstroemia indica* (L.) C. A. Meyer, *Lantana camara* L. (Verbenaceae), and *Leucaena leucocephala* (Lam.) de Wit. (Leguminosae). With the ever-increasing build-up of an alien seed source on Mauritius, even though not all these species are dispersed by wind or birds, the risk of further problem weeds invading Round Island is high. Photographic evidence gathered on the island in 1988 indicates that at least 40% of the island was bare of vegetation at that time and individual slopes, such as those of the crater, were showing more than 90% bare ground. The ease with which a new invader can spread is shown by *Cenchrus echinatus* L. (Poaceae), discovered in 1987, represented by very few plants in 1988, and now reported by B.D. Bell (pers. comm. 1996) as present in all sectors of the island. The zone nearest the shoreline, where *Argusia argentea* (L. fil.) Heine (recorded from the island during the last century) and *Scaevola taccada* are likely to have been important, is particularly vulnerable. This zone is virtually devoid of vegetation at present.

To reduce the risk of weed invasion it is essential to accelerate the early stages of vegetation recovery on Round Island. If the recovery of a plant species extant on the island became threatened by the spread of any native plant, either already present or introduced to the island, this can be anticipated by regular monitoring with appropriate protective action. An introduced species unsuited for the currently difficult environmental conditions prevailing on the island will soon disappear. If a native species of Mauritius spreads rapidly through some open communities and colonizes bare ground, this appears preferable to a tangle of weeds from other countries. The latter scenario could easily terminate all restoration options for the island. In any case a pioneer native species is unlikely to persist at high density during later stages of succession.

Restoring Selective Forces

There is little we can or need do to restore nonspecific selection forces. The climatic regime may not have altered in any fundamental way from that of a century or two ago. Vegetation destruction and death of root systems following browsing and grazing by goats and rabbits have resulted in an incalculable loss of soil. Much of this loss will have resulted from the high-intensity rainfalls of particular cyclonic storms. Cyclones will continue to bring about further losses of vegetation through erosion, but it can be expected that as vegetation cover strengthens, adverse effects will become more localized. At present many slopes have lost whatever soil cover they had originally.

Restoring species-specific selection regimes will pose some interesting questions. Minimizing weed invasion and restoring plant species that were probably once present on the island, as discussed above, is likely to restore plant competition in the palm savanna and a future hardwood forest to a functioning condition more like that of the past. With invertebrates we can hope that a significant part of the original fauna has survived in small pockets of less depleted vegetation and soil but apparently no studies have been made. With the reptiles it is clear that a very significant part of the original fauna has survived even if in numbers and proportions that are greatly changed. Populations of some seabird species that previously bred on the island may now have been greatly reduced, but, as with invertebrates and reptiles, their populations can rebuild with the developing soil and vegetation.

In contrast to these groups, the land bird and land mammal faunas of the island have disappeared and it can be presumed that some plant-pollinator and -disperser relationships have ceased. Bones examined by Cheke and Dahl (1981) show that the Rodrigues fruit bat, *Pteropus rodricensis,* was once present, a species that is now extremely rare on Rodrigues Island. Some of the island's land birds, however, are probably extinct throughout the region. Of land birds that have survived on mainland Mauritius, would Round Island have once supported the echo parakeet (*Psittacula echo*), pink pigeon (*Columba mayeri*) and the Mauritius kestrel (*Falco punctatus*), all of which may be either threatened or endangered? Those who have studied these birds consider it likely that they were present (Dr D. V .Merton, pers. comm.) but if this view is correct, Round Island's vegetation would have to be more developed and more diverse to support the parakeet, pigeon, or the fruit bat. The kestrel might

easily survive on the island now but, given that this species would become the top predator, it would not be wise to establish it until more plant cover is available for species such as Guenther's gecko, *Phelsuma guentheri* (Merton et al. 1989).

Restoring the selection forces formerly exerted on Round Island plants by vertebrate herbivores implies restoring a giant tortoise. The only giant tortoise that has survived in the Indian Ocean region is the Aldabra tortoise, *Geochelone gigantica.* Its skull morphology appears to be somewhat different from either of the two extinct tortoises of Mauritius (Arnold 1979) which may suggest a slightly different kind of feeding behavior. Fundamentally, however, it is a tortoise and like most reptiles, the restricted movement of the mandible lacks the feeding efficiency associated with the transverse grinding action of the mammalian jaw system when feeding on plants (Norman and Weishampel 1985). For this and other reasons, by far the most ecologically equivalent animal that can be substituted for the extinct giant tortoise of Round Island, is the Aldabra tortoise. Now is not the time to introduce the tortoise while so many plants on the island are still recovering, but, in my view, such action should be seriously considered at an appropriate time in the future.

Reinstatement of part of the selection regime that formerly operated on Round Island will not result in an authentic replica of some earlier Round Island system. It may however allow development of a system that, in a functional sense, approximates a past system much more closely than can be achieved by leaving the island to recover at its own rate with minimal intervention (weed control and re-establishment of a few plant species). The more comprehensive approach to restoring Round Island advocated here, can provide an environment in which indigenous plants and animals of the Mauritius region can not only survive, but also interact in the manner they did prior to the impact of humans.

ACKNOWLEDGMENTS

I am grateful to John Campbell and John Flux for comments on the manuscript and to Ruth Kiel and Alan Barkus for preparing the figures. My thanks go to staff of the Santa Barbara Botanic Garden for personal assistance during the period of my visit and I thank the Botanic Garden for their financial support enabling me to present this paper during the "Plant Evolution and Conservation on Islands" symposium of May 4th, 1996.

LITERATURE CITED

ANDERSON, A. 1984. The extinction of moa in southern New Zealand, pp. 728–740. *In* P. S. Martin and R. G. Klein [eds.], Quaternary extinctions. A prehistoric revolution. University of Arizona Press, Tucson.

ARNOLD, E. N. 1979. Indian Ocean giant tortoises: their systematics and island adaptations. *Philos. Trans.*, Ser. B. **286**: 127–145.

ATKINSON, I. A. E., AND B. D. BELL. 1973. Offshore and outlying islands, pp. 372–392. *In* G. R. Williams [ed.], The natural history of New Zealand. A.H. and A.W. Reed, Wellington, New Zealand.

———, AND E. K. CAMERON. 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. *Trends Ecol. Evol.* **8**: 447–451.

———, AND R. M. GREENWOOD. 1989. Relationships between moas and plants, pp. 67–96. *In* M. R. Rudge [ed.], Moas, mammals and climate in the ecological history of New Zealand. *New Zealand J. Ecol.* **12** (Supplement).

CAMPBELL, D. J., H. MOLLER, G. W. RAMSAY, AND J. C. WATT. 1984. Observations on foods of kiore (*Rattus exulans*) found in husking stations on northern offshore islands of New Zealand. *New Zealand J. Ecol.* **7**: 131–138.

CARLQUIST, S. 1965. Island life. A natural history of the islands of the world. American Museum of Natural History, The Natural History Press, Garden City, New York.

CHEKE, A. S. 1987. An ecological history of the Mascarene Islands, with particular reference to extinctions and introductions of land vertebrates, pp. 57–59. *In* A.W. Diamond [ed.], Studies of Mascarene island birds. Cambridge University Press, Cambridge.

———, AND J. F. DAHL. 1981. The status of bats on western Indian Ocean islands, with special reference to Pteropus. *Mammalia* **45**: 205–238.

CLOUT, M. N., AND J. R. HAY. 1989. The importance of birds as browsers, pollinators and seed dispersers in New Zealand forests, pp. 27–33. *In* M. R. Rudge [ed.], Moas, mammals and climate in the ecological history of New Zealand. *New Zealand J. Ecol.* **12** (Supplement).

COOPER, A., I. A .E. ATKINSON, W. G. LEE, AND T. H. WORTHY. 1993. Evolution of the moa and their effect on the New Zealand flora. *Trends Ecol. Evol.* **8**: 433–437.

ESLER, A. E., AND S. J. ASTRIDGE. 1987. The naturalization of plants in urban Auckland, New Zealand. 2. Records of introduction and naturalization. *New Zealand J. Bot.* **25**: 523–537.

GREENWOOD, R. M., AND I. A. E. ATKINSON. 1977. Evolution of divaricating plants in New Zealand in relation to moa browsing. *Proc. New Zealand Ecol. Soc.* **24**: 21–33.

HAY, R. F., A. R. MUTCH, AND W. A. WATTERS. 1970. Geology of the Chatham Islands. New Zealand Geological Survey Bulletin n.s. 83. New Zealand Department of Scientific and Industrial Research, Wellington.

LLOYD, J. A. 1846. Account of a voyage to Round Island and Serpent Island in December 1844. *Proc. Soc. Hist. Nat. Ile. Maurice*: 154–162.

MERTON, D. V. 1987. Eradication of rabbits from Round Island, Mauritius: a conservation success story. Dodo. *J. Jersey Wildlife Preserv. Trust* **24**: 19–44.

———, I. A. E. ATKINSON, W. STRAHM, C. JONES, R. A. EMPSON, Y. MUNGROO, E. DULLOO, AND R. LEWIS. 1989. A management plan for the restoration of Round Island, Mauritius. Jersey Wildlife Preservation Trust, Jersey, Channel Islands.

MONTAGGIONI, L., AND P. NATIVEL. 1988. La Reunion Ile Maurice Gerlogie et apercus biologigues. Masson, Paris. 192 p.

MOORS, P. J., I. A. E. ATKINSON, AND G. H. SHERLEY. 1992. Reducing the rat threat to island birds. *Bird Conservation Int.* **2**: 93–114.

NORMAN, D. B., AND D. B. WEISHAMPEL. 1985. Ornithopod feeding mechanisms: their bearing on the evolution of herbivory. *Amer. Naturalist* **126**: 151–164.

NORTH, S. G., D. J. BULLOCK, AND M. E. DULLOO. 1994. Changes in the vegetation and reptile populations on Round Island, Mauritius, following eradication of rabbits. *Biol. Conservation* **67**: 21–28.

ROJAS, M. 1992. The species problem and conservation: what are we protecting? *Conservation Biol.* **6**: 170–177.

STEVENS, G. R. 1994. Developing trends in south western Pacific biogeography in Late Mesozoic and Cenozoic times. Palaeopelagos Special Publication **1**: 397–420.

TOWNS, D. R., AND W. J. BALLANTINE. 1993. Conservation and restoration of New Zealand island ecosystems. *Trends Ecol. Evol.* **8**: 452–457.

WOODRUFF, D. S. 1989. The problems of conserving genes and species, pp. 76–88. *In* D. Western and M. C. Pearl [eds], Conservation for the twenty-first century. Oxford University Press, New York.