ISLANDS: WHERE Novelty is the norm

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4.1 INTRODUCTION

Islands have much to offer our understanding of novel ecosystems and many of the concepts presented in the previous chapter (Chapter 3), for it is there that novel assemblages of species have developed most rapidly and dramatically. Start with a depauperate biota, wait millennia and add people (with their unique capacity to break down biogeographic barriers), and novelty is the inevitable outcome. Islands lack the biological buffering capacity of continents, with their vast areas and rich biota. That is not to say that all island ecosystems are novel assemblages; many islands, including some that are densely populated, still harbor ecosystems composed almost exclusively of native species growing on land unchanged by human activity. But the vulnerability of island ecosystems to change has long been recognized, and it is a well-documented generality.

In Section 4.2 we briefly discuss the three main factors that influence island ecosystem novelty: physical geography, biogeography and human ecology. There is a massive literature on each of these themes, and we make no attempt to review it here. Instead, our objective is to provide some context for development of the main topic of interest in keeping with the principal subject matter of this book: when and how to intervene in novel ecosystems. Intervention is covered in Section 4.3, where it is discussed in relation to need, barriers and feasibility.

A chapter on islands could include all manner of bounded, isolated environments, from ponds to mountain peaks. We restrict our purview to non-continental land masses currently surrounded by ocean, whether that has been true throughout their geological history or not.

Where we make comparative statements our reference is always the continental land masses, but to be

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concise we do not always state this explicitly. The geographic expertise of the authors is concentrated primarily in the tropics and subtropics, and this is reflected in most of the examples cited. Why include a separate chapter that deals specifically with islands? In our view, what we see on islands today may indicate what can be expected on continents tomorrow. In many ways, islands are the window to the future.

4.2 INSULAR TRAITS THAT FOSTER NOVELTY

A number of island traits influence ecosystem novelty. Some of those described here are unique to islands while others pertain equally well to continents; inevitably, there are many exceptions to statements cast here as generalizations. Nevertheless, most traits described fit most islands and, more importantly, their influence in determining when and how to intervene in novel ecosystems has broad applicability.

4.2.1 Physical geography

The relatively small area of islands facilitates change in the wake of outside forces. Small land areas mean short internal distances, which in turn mean rapid expansion of outside agents. For example, an agriculturebased human society quickly exploits suitable land (Rolett and Diamond 2004) or an introduced species is soon dispersed into all suitable habitats (Whittaker and Fernández-Palacios 2007).

Given similar latitudes and physiography, an island and continent would be expected to have similar numbers of bioclimatic zones and be subject to similar kinds and frequencies of disturbance. An important difference arises because continents typically have some habitats that cover huge areas, portions of which are likely to escape agents of change through vastness alone, whereas each habitat type on an island is relatively small and susceptible to change in its entirety. Consequently, population sizes and areas of occupancy of many island species, especially habitat specialists, are naturally small which makes them particularly vulnerable to extinction (Caujapé-Castells et al. 2010).

A second way that islands and continents frequently differ is in uniformity of parent material. On many islands the entire land mass derives from a single, relatively uniform substrate, whether from continental fragments, uplift, volcanism or biotic activity (in the case of atolls). Continents, in comparison, typically contain a greater variety of parent materials, so a single climate regime is likely to cover soils that differ in their developmental history. This observation does not ignore the great environmental heterogeneity of some (particularly large) islands often caused by steep climate gradients. Even on islands possessing such heterogeneity however, the sameness of parent material may yet be observed. This can contribute to the feeling of sameness in ecological communities, even when moving across steep climatic gradients (e.g. Vitousek 2004).

4.2.2 Biogeography

Isolation by water confers islands with famously unique biogeographic attributes. Natural colonization rates decline with distance from donor continents and diminishing island size, such that the smallest, most remote islands tend to have fewest species. As a result, entire functional groups and life forms may be missing; large mammals, a life form limited by both oversea dispersal ability and area of habitat available on islands, are the most conspicuous absentees. Other functional groups become bottled as anachronistic 'Lazarus' taxa now extirpated from continents. Plants occasionally become relicts, thriving in the absence of competitors that long ago vanquished them on the continents. As these filters alternatively limit or enhance the relative abundances of various groups, they yield disharmonic flora and fauna, not reflecting the diversity at higher levels of taxonomic classification that characterize their donor continents (Carlquist 1966). A spider might raft to a remote island on an airborne strand of web, but a frog is unlikely to survive the swim; a coconut might tolerate the float, while an orange would not. Disharmony and this loss of functional groups decrease with proximity to continents, and these in turn confer islands with uniquely high rates of human-mediated species invasion and subsequent species replacement.

Landscape age, like island size and distance from donor continents, leads to biogeographic differences among islands (e.g. Parent et al. 2008). Time and genetic isolation in an environment without finely divided niche foster evolutionary radiation of endemics, a process that has been recognized since Bates and Darwin and is now well documented in many groups of plants and animals (Whittaker and Fernández-Palacios 2007). Evolution of defenses against enemies that would be present on larger continental landscapes is relaxed in endemics that evolve in enemy-free habitats. We therefore find the textbook examples: flightless birds, thornless raspberries and scent-free mints. When enemies do arrive, the defenseless endemics are faced with challenges for which they are ill-equipped, and extinction often follows.

Sometimes, however, evolving in isolation and in small habitats provides survival benefits. The small populations that typify island endemics have likely survived genetic bottlenecks, conferring them with an attribute of great value when outside changes reduce population sizes below those that might not be tolerated by continental species (Adsersen 1989). Furthermore, a high degree of plasticity in island biota may bode well for adaptation to climate change. One recent analysis of 150 datasets encompassing both continents and islands indicated that organisms that evolved with opportunity to expand into a broad range of habitats that were not previously saturated with habitat specialists may be pre-adapted to change (Laurence et al. 2011).

An impoverished, disharmonic biota is almost certain to assemble into a community having a less complex structure than one with a full complement of functional groups. In forests at latitudes where the biogeographer might expect to find trees of many height classes, a few species sometimes dominate structure; these are often shorter than typical of the same climatic zone on continental land masses. In tropical and subtropical latitudes, the shorter stature may be due to wind storm frequency or it may simply reflect the genetic potential for height growth of the species that colonized. Furthermore, with relatively few competing species of similar stature, selection pressure for increased height is likely to be low even if the genetic potential is present. This was the case in the Galapagos for example, where a Miconia shrubland was readily invaded by the Cinchona tree (Jäger et al. 2007; Fig. 4.1).

Broad realized niches are typical on remote islands, where relatively few species occupy many environments and perform many roles. Plant-animal interactions, for instance, are often highly generalized (Kaiser-Bunbury et al. 2010). Likewise, the few species present might fill many roles in stand development from primary succession colonist to undisturbed ecosystem dominant (Mueller-Dombois 2008). A prime



Figure 4.1 Trees in a formerly treeless ecosystem. *Cinchona pubescens* forest in what was previously *Miconia robinsoniana* shrubland, Santa Cruz, Galápagos. One outcome of this invasion is increased substrate for epiphytes. Photograph courtesy of Mandy Trueman.

example is *Metrosideros polymorpha*, a Hawaiian endemic that previously dominated nearly all forests in the archipelago, thriving under rainfall regimes from 200 to more than 11,000 mm per year, substrates 0–4.6 million years old and from sea level to the tree line (Vitousek 2004). Today, its niche space is collapsing as introduced species permeate its range. It is out-competed at the onset of primary succession by nitrogen-fixing trees (Hughes and Denslow 2005), after fires fueled by grasses (Hughes et al. 1991), under high light by gap-filling pioneer trees (Mascaro et al. 2012) and in dense shade by a clonal understory tree (Zimmerman et al. 2008).

Islands are also famous for adaptive radiations, which can yield high species diversity and rather small realized niches. In these cases, however, the resulting species diversity may have the same vulnerability (as a group) to introduced organisms as a single wideranging species. For example, the lobeliad radiation in Hawai'i resulted in spectacular endemic diversity, but the resulting species have similar reproductive and morphological traits. Most Hawaiian lobeliads depend on native honeycreepers (another famous radiation) for pollination (Givnish et al. 2009), and in this way the whole group became vulnerable to a single event: the colonization of Hawai'i by avian malaria, which decimated honeycreeper populations. Similarly, the spread of feral ungulates throughout Hawaiian forests threatens all lobeliads, whose stems are notoriously weak and easily crushed.

4.2.3 Human ecology

People are the agents of change that lead to novelty everywhere. Recognition of the unique aspects of insular human ecology is useful when attempting to understand the ubiquitous and rapid development of novel ecosystems on islands. The history of some islands has been one of human population turnover, sometimes motivated by resource scarcity, sometimes by cultural clashes and sometimes by shifts in global power. The resulting cultural changes have typically led to more marked change than on islands colonized and utilized by a single cultural group over a long period of time. Each time the culture changes, the new culture brings with it new species and new approaches to land use, both of which facilitate novelty.

Even where cultural continuity is sustained, the sea is the inescapable boundary, and limits to agricultural expansion – fertile soil and fresh water – are quickly reached. It becomes expensive to further intensify agriculture, requiring labor or fossil energy to provide the requisite water and nutrients. At this stage, some combination of three pathways is likely: sustain the status quo through labor-intensive agriculture and fisheries (rarely a stand-alone outcome); degrade land, potentially followed by population collapse (e.g. Rapa Nui); or substitute imports for indigenous resources (nowadays, most islands). Imports track the ever-extending reach of global trade and it is that switch – from resource autonomy to import dependence – that has led to widespread novelty of island ecosystems.

It is no surprise that the physical and biogeographic features of islands, coupled with human behavior, lead to uniquely high rates of species invasion and subsequent species replacement. Islands are notorious for their high abundance and diversity of introduced species (Lonsdale 1999), and it is those newcomers growing together that form the novel ecological communities so widespread on islands today. Furthermore, in some places much of the resident non-native flora has not yet naturalized suggesting that further expansion of novel ecosystems is in the offing (e.g. Galápagos; Trueman et al. 2010).

Species introductions often begin with those that provide goods and services not available from the local flora and fauna. At one time the human-mediated flow

of species around the world was largely intentional with ship captains, horticulturists, bird fanciers and forage scientists ranking high among the vectors. With increased sensitivity to movement of non-native species, intentional introductions are now secondary sources and stowaways have taken the lead. Because islands are so import-dependent, they receive a significant share of unintentional introductions, especially in cargo containing imported foodstuffs. For example, a recent study in Galápagos found that two cargo ships bringing produce from mainland Ecuador unintentionally carried an incredible 179 invertebrate taxa that were not native to the islands (Herrera 2011). Further exacerbating the risk of unwanted entry, few islands have adequate staff to thoroughly screen cargo (e.g. Zapata 2007).

Not infrequently, an island society that becomes import-dependent relaxes pressure on the land. In Puerto Rico, for example, forest cover increased from the 1960s to the present as a result of rural-to-urban migration (Lugo 2004). But what of the composition of those new forests? The abundance of non-native species characteristic of islands typically leads to novel ecosystems. In the absence of pressure on the land for agriculture, these mature to their logical conclusion: ecosystems that differ substantially in composition from those that dominated historically. These novel ecosystems sometimes harbor native species as subordinate members of the community (Lugo and Brandeis 2005; Kueffer et al. 2007; Mascaro 2011). Nevertheless, successful invasion elsewhere is a strong predictor of invasion in a new locale, resulting in a familiar sameness in species composition among novel ecosystems on islands of comparable latitude and climate (Mueller-Dombois and Fosberg 1998; Castro et al. 2010).

4.3 INTERVENTION

In keeping with sound ecosystem management, intervention in novel ecosystems is called for only after clear goals have been set, the resources needed to accomplish the objectives are available and there is a reasonable expectation of success. Managers often focus first on the scarcity of resources with which to do the job, but defining the goals and objectives (while not always easy) must be the first priority. Conservation value is a key and obvious goal, but intervention to accomplish it might have unpredictable implications for other goods and services; these must also be considered before attempting intervention. For example, the removal of introduced mangrove trees may satisfy a conservation objective but have a negative effect on productivity of native fish (Fig. 4.2). Sometimes enhancement of those non-conservation goods and services is the objective itself: increase water yield, augment the rate of carbon sequestration or enhance images in the viewshed. Goal-setting for intervention efforts is complicated by the fact that it is not uncommon for transformations (or the species that lead to them) to be valued as positive by some sectors of society and negative by others. Should a minority value judgment ever override that of the majority? Where unique products of evolution are threatened and where intervention might sustain them, the morally responsible answer is 'ves'.

The two attributes of novel ecological communities that typically motivate intervention on islands are species composition and ecosystem functioning. By definition, novelty derives from species composition and the effects of this composition on the abiotic environment (see Chapter 6); the high endemism, small populations and species loss that characterize many islands combine to lower the threshold for conversion to a novel condition (see Chapter 3). Species-focused preservation or restoration is therefore a common objective of intervention on islands, as it is on continents. Where intervention is aimed at species composition, the target is reasonably well defined (even though the pre-human-contact flora and fauna may not be completely known) and success or failure is readily measured.

In the case of ecosystem functioning, there is unlikely to be a reference point so the target is much more diffuse. Nevertheless, there is considerable overlap between intervention to change composition and intervention to achieve changes in processes; intervention in a novel ecosystem to change functioning invariably involves manipulation of species composition. Typically, this means reducing the abundance of one or more introduced species that affect particular ecosystem processes. In the absence of historical ecosystems where processes are known however, success or failure of intervention aimed at ecosystem functioning must be measured against the performance of the novel ecosystem not subjected to management.

The high degree of endemism commonly encountered on islands, coupled with small population sizes of those endemics and the consequent high risk of species loss, can motivate a strong desire to restore an ecosystem to its historical analogue if it is even theoretically possible. The desire to save endemic plant and animal species often becomes a matter of local pride and, when coupled with popular recognition of high vulnerability to invasions of non-native species, makes intervention a prominent component of resource management on many islands. Those experiences may offer insights to those who work on larger land masses and are faced with decisions on assessment of the *need* to intervene, recognition of potential *barriers* to intervention and assessing the *feasibility* of intervention.

4.3.1 Need

Under what circumstances is intervention in novel ecosystems on islands essential or even warranted? The need for intervention ranges across a gradient from conserving or restoring a nearly intact original system to managing a novel system that provides valued goods or services. The combination of need and opportunity to restore nearly intact ecosystems to their historical state often occurs at upper elevations, especially on tropical and subtropical islands. There are two reasons for this: (1) lowland ecosystems were typically (but not inevitably; e.g. Galápagos) the first to be obliterated following human settlement of islands; and (2) the richness of introduced species diminishes with elevation (Fig. 4.3). Hence, the ecosystems that retain native species as well as a reasonable semblance of pre-colonization structure are typically at higher elevation, and these tend to be the sites where intervention is focused on species composition. Classic historical restorations in lowland ecosystems often prove impossible or limited to educational exercises, except where species traits and treatment effects are well known.

Although species-driven intervention is typically done on behalf of one or more highly valued species, the opposite is often true as well: the need for intervention arises when one component, and not the entire ecosystem, is characterized as a bad actor. Sometimes the undesirable element is a thorn-covered plant or a toxic herp, but more often than not it is a species that poses a threat outside the novel ecosystem. It might be a potentially invasive weedy species that would have an economic impact on agriculture, a predator that would pose a threat to potential prey elsewhere or an arthropod that is a potential vector of pathogenic organisms. The key element in this kind of intervention



Figure 4.2 Stand of non-native mangrove, *Rhizophora mangle*, Hawai'i Island (a) before and (b) after chemical control using herbicide. The structure is a fyke net, used to trap fish during an ebbing tide. There were higher densities of native than non-native fish in the mangroves, and the killing of the mangroves did not reduce densities of non-native fish. Photographs and findings by Richard A. MacKenzie.



Figure 4.3 Changes in non-native plant species richness with altitude from three islands: Tenerife, Hawaii and La Réunion. Continental data from Switzerland and Australia are included for comparison. The relative richness of non-native species diminishes at high elevation, whether peak richness occurs at low or mid-elevation. Republished with permission of Ecological Society of America, from Pauchard et al (2009); permission conveyed through © Clearance Center, Inc.

is protection of something valued outside of the novel ecosystem housing the problematic species. The novel ecosystem itself might be tolerable, or even highly valued, but a particular component might merit efforts at containment or (rarely) eradication.

Deviations from historical functioning can be especially marked when new functional groups become part of the mix. If the resulting changes have undesirable and broad scale effects the need to intervene is typically perceived to be high, despite the limited prospects of success. There are many examples of such process-changing naturalizations covering a broad range of functional groups: nitrogen-fixing trees in Hawai'i (Vitousek and Walker 1989; Hughes and Denslow 2005); ants on Christmas Island (O'Dowd et al. 2003; see also Chapter 14); foxes on the Aleutian Islands (Croll et al. 2005); rabbits on sub-Antarctic islands (Bergstrom et al. 2009); tree snakes (now sustained by non-native lizards) on Guam (Fritts and Rodda 1998); a parasitic fly causing high mortality of Darwin's finches in Galápagos and thereby affecting seed dispersal and pollination (Koop et al. 2011); and fire-prone grasses in many places (D'Antonio and Vitousek 1992). However, enhanced richness of an existing functional group is not typically regarded as disruptive. In Puerto Rico, for example, African grasses in pastures and unmown urban lots have influenced the composition of the bird community. From a forested island having two native, granivorous bird species, the island now has 18 granivores (the two natives plus 16 non-natives) all associated with novel grass communities (Raffaele 1989).

Water is a resource in short supply on many islands, and the need to intervene in a novel ecosystem might be motivated by a desire to augment water yield. Nevertheless, it is difficult to know whether or not intervention (manipulation of plant species or life form composition, for example) will have the desired effect. Transpiration is driven by a combination of physical processes, plant morphology and anatomy and phenology and when these change, water relations change. There is some evidence that those introduced plant species that tend to dominate novel ecosystems have greater leaf area per unit ground area, and therefore potentially higher rates of transpiration, than their predecessors (van Kleunen et al. 2010). Although the difference in water use between historical and novel might be only a few percent, this can be a crucial amount in dry climates (e.g. Thaxton et al. 2011). Evapotranspiration from tree plantations is sometimes high enough to reduce water yield (e.g. pines in Fiji; Waterloo et al. 1999), and this might also be the case from watersheds covered with novel ecosystems. Nevertheless, there are no published examples of water flows from paired watersheds (historical and novel) with which to substantiate or refute this possibility. Those who would intervene in a novel ecosystem with the expectation of increasing water yield are therefore advised to proceed only when data indicate a reasonable likelihood of success.

There is a perception among some members of the conservation community that ecosystem novelty is 'bad'. Nevertheless, novel ecosystems characterize much of today's world (see Chapters 8 and 9). They often provide goods and services valued by society, and many provide habitat for native and even endemic species (e.g. Lugo 2004). But even when those novel ecosystems do not harbor native plant and animal species in need of protection, there is no reason they should not be managed to optimize ecosystem services. Novel ecosystems afford unbridled opportunities for intervention: species re-introductions for conservation, sequestration of carbon, watershed protection, recreation, timber and non-timber forest products, and more. To perceive a need to intervene only for purposes of species preservation is to miss opportunities.

4.3.2 Barriers

Just as determining when intervention is needed, knowing when intervention may not be called for is important. With their histories of ecosystem change and close relationships between people and environment, islands offer some lessons in making that determination. Some barriers to intervention are obstacles to be overcome before management actions can proceed; other barriers are counter-indications, which signal a need to carefully assess the full range of consequences before moving forward (see Chapter 18).

One barrier to intervention – landscape size – is more formidable on islands, where it is an insurmountable physical obstacle, than on continents. The limited area of island landscapes effectively reduces the options available for response to allochthonous agents of change such as climate and sea level. On a continental landscape, there is potential for developing corridors that provide opportunities for species redistribution in response to environmental change; in the smaller landscapes that characterize islands however, long-distance corridors are seldom possible.

The first potentially surmountable barrier encountered by almost every ecosystem manager who proposes to intervene in a novel ecosystem is that of public opinion. Just like natural systems, novel assemblages have their proponents. Proposed interventions that do not adequately address the concerns of public opinion supportive of the status quo are unlikely to be implemented. The necessity to engage public opinion early in the process of setting goals and objectives is essential (see Chapter 30), and the process requires the use of three tools that tend to be minor (or missing) components of the biologist's toolkit: education, mediation and conflict resolution. Gaining public buy-in is often the most difficult part of intervention.

Intervention is counter-indicated where it is likely to reduce habitat suitability for a threatened species that uses the novel ecosystem. Sometimes the role of novelty in supporting a threatened species is subtle. For example, it is not uncommon for native species to become at least partially dependent upon non-natives that provide food, pollinate flowers or disperse seeds. Management actions that disrupt those inter-specific linkages, even when inadvertent, would be ill-advised; avoiding them requires knowledge of the interactions within the novel system.

The risk of unintended consequences may be greater on islands than on continents. This may be because the comparatively low species-richness of island communities is only modestly buffered against change, such that a shift in environmental conditions resulting from management can lead to conditions that favor potentially explosive growth of non-target species. For example, six of the nine endemic ant species in Mauritius are restricted to less than one hectare occupied by a dark, cool, dense thicket of native and invasive plants near the summit of Le Pouce mountain (Alonso 2010; Fig. 4.4). Removal of the non-native invasive plants would likely change the abiotic conditions and would almost certainly facilitate invasion by the ant *Pheidole megacephala*, which has probably played a role in the extirpation of native ants at lower altitudes in Mauritius and already occurs on the border of this patch (L. Lach, unpublished data, 2011).

The consequences of intervention for species composition are not the only barriers to action: sometimes an abiotic service is the key. Water yield on high islands is a good example of the value of novelty, and intervention in novel systems that augment water yield is risky. Cloud-water interception by tall vegetation in the wet montane tropics, for example, typically augments rainfall by at least 5–20%. During the dry season, canopy drip can exceed rainfall in drier climates (Bruijnzeel 2004). Mountainous islands in the trade wind latitudes almost invariably exhibit this phenomenon and, on islands where the historical vegetation was scant or short stature (e.g. Ascension Island; Lanai in the



Figure 4.4 Dense patch of native and non-native plants that is the last remaining habitat of six endemic ants species, Le Pouce, Mauritius. Intervention would likely lead to invasion by *Pheidole megacephala* which occurs on the edges of the patch and has been implicated in the local extirpation of native ants elsewhere. Photograph: Lori Lach.

Hawaiian Islands), novel ecosystems containing tall trees were intentionally created to augment the capture of dry-season water.

Even more striking than the differences in water yield due to changes in species composition or vegetation stature are those between green and brown ecosystems: de-vegetated landscapes may not transpire, but they do not store much water either and they are subject to high rates of soil erosion. Re-vegetation, even by a novel assemblage, is invariably a more desirable watershed management alternative than bare soil. Unless there are compelling reasons to do so, drastic intervention in successfully revegetated watersheds (novel or not) is seldom warranted. Those beautiful, green mountains on many islands are blanketed with novel ecosystems, established to protect watersheds against erosion and now valued for their aesthetic value by tourists and locals alike. Intervention without substantial assurance of successful restoration to historical conditions is unlikely to be warranted.

Sometimes there is a tendency to intervene in a novel system by attacking species based solely on their identity and reputations elsewhere. This is a common mistake and one that might result in expenditure of resources that would be better deployed on other management actions. For example, rats and mongooses have been part of Puerto Rico's wet forests for so long that they constitute a small part of the local food web (Willig and Gannon 1996) and no longer pose a threat to those native species that have survived thus far. Given their relatively low abundance and wide distribution, attempts to eradicate these small mammals would likely be futile. Another example is that the goats introduced five centuries ago onto nearby Mona Island continue to feed on rare and endangered plants as part of their diet that comprises 20% of the flora (Meléndez Ackerman et al. 2008); there are no records of goatdriven extinctions, however. Predictions of no success, or no impact if successful, are money-saving counterindicators of intervention.

4.3.3 Feasibility

Intervention is not to be undertaken lightly anywhere, but islands – heavily modified by people and of modest geographic complexity – are often excellent candidates for active management. Furthermore, the high endemism and small population sizes of native biota discussed earlier are strong motivations for intervention.

Not infrequently, the proper course of intervention calls for attempts to contain or, where possible, eradicate one or more non-native species whose effects are deemed harmful (Figs 4.2, 4.5). This is particularly pertinent on islands because of their highly simplified food webs dominated by few, often non-native, species (e.g. Bergstrom et al. 2009). Dealing with such species on continents is very difficult, especially when the target species is well established and widespread. The likelihood of successful eradication is greater on islands however because the area, number of habitats and number of individuals to be covered by the effort are land-limited. Furthermore, efficacy of control is more easily assessed when area is limited and refugia are few.

There is a substantial record of successful eradications from islands, and the procedures are becoming more successful with experience and the availability of better tools (see many examples in Veitch and Clout 2002; Veitch et al. 2011). Goats, for example, have been eliminated from more than 120 islands (Campbell and Donlan 2005). A particularly ambitious example was Project Isabela in the Galápagos archipelago, which removed more than 140,000 goats from 500,000 ha. The main factors that led to success were sufficient resources, technical know-how, mitigation of nontarget impacts and support from the local community (Carrion et al. 2011). Substantial success has also been achieved with other mammals including rats, cats, pigs and sheep. Plants often prove more difficult however, especially if populations cover sizable areas. Managers considering eradication of non-native plant species would do well to note the words of Mack and Lonsdale (2002): "The record of eradicating invasive plants . . . consists of few clear victories, some stalemates, and many defeats." Likewise, attempts to eradicate ants, even on islands, almost always fail.

In addition to simplifying eradications, the comparatively small and isolated land area of islands facilitates species introductions and re-introductions. A small area can however be a two-edged sword with respect to species introductions, for undesired species invasions can cover all suitable habitats in a very short time. A stunning example is that of the galling wasp (*Quadrasticus erythrinae*) which was detected in early 2005 on native Hawaiian Wiliwili trees (*Erythrina sandwicensis*) as well as introduced congeners; within six weeks it had spread across all of the high islands (Rubinoff et al. 2010).

Social acceptability sometimes makes intervention more feasible on islands than on continents. On islands, the degree of novelty already present opens the door to tinkering with introduced-species composition to achieve specific objectives. Members of the conservation community who would be very skeptical of any proposal to modify the composition of an ecosystem composed of native species are often neutral, or even welcoming, toward active management that affects structure and composition of novel ecosystems. Nevertheless, even on islands with their relatively small and accessible human populations, insufficient involvement of the community can compromise long-term success (Gardener et al. 2010).

Sometimes the novel ecosystem itself can provide the matrix into which endangered species can be reintroduced and thereby saved. This is the case when endangerment was caused by over-exploitation or by land-cover conversion to agriculture. An example from Puerto Rico is typical: more than a century ago, sugarcane supplanted floodplain forests believed to have been dominated by a variety of native tree species including Manilkara bidentata and Pterocarpus officinalis (Abelleira-Martínez and Lugo 2008). Although both of these tree species were almost extirpated from the coastal plain, they can still be found on remnant alluvial sites. After the abandonment of sugarcane cultivation in the 1970s, forests dominated by the introduced tree Spathodea campanulata developed on the floodplains and continue to occupy them 40 years later. More than half of the species in these novel forests are indigenous (including two endemics), but Manilkara and Pterocarpus are absent. The extirpation of a forest type and its eventual replacement by a novel forest that does not include the former dominants, even where soil fertility and hydrology are intact, raises questions about the reversibility of novel forests. Will Pterocarpus (which is wind-dispersed) or Manilkara (animal-dispersed



Figure 4.5 Intervention targeting plant species capable of transforming ecosystem structure or functioning. (a) Girdling the N-fixing tree, *Falcataria moluccana*, using bark spuds. National Park of American Samoa. Photograph courtesy of Tavita Togia. (b) Precision application of purple-dyed herbicide to individual *Miconia calvescens* growing in remote native-dominated vegetation. Orange hose connects herbicide reservoir on helicopter to pilot-controlled spray ball. Photograph courtesy of Maui Invasive Species Committee. (c) The killed trees are *Castilla elastica*, originally introduced to Samoa as a source of raw material for cricket balls. Cricket is all but gone; *Castilla* remains. This ecosystem grades from actively managed agroforest on the lower slope to nearly native forest on the upper slope. Tutuila, American Samoa. Photograph courtesy of Katie Friday.

and requiring specific microsites; O'Farrill et al. 2011) ever re-colonize? Deliberate seed introductions and seedling transplants might speed the process provided that these two species prove competitive in the new biotic milieu. A comparable situation has been analyzed in Seychelles, where novel *Cinnamonum verum* dominated forests are managed as habitat for rare native plants and animals (Kueffer et al. 2010; Seychelles case study in Chapter 27).

Propagule availability is not the only factor that leads to rarity of former dominants in novel ecosystems. In many instances a species' absence is due to change in competitive balances among species; introduced diseases, herbivores or predators; sustained exploitation; or changes in abiotic conditions that make it impossible for the endangered species to thrive (Caujapé-Castells et al. 2010). In those situations the agents of change must be dealt with directly, or reintroduction will fail for the same reasons that led to the original decline of the species.

Extinction rates on islands can be high, thus increasing the likelihood the novel ecosystem may be missing some of its structural/functional 'parts'. One logical approach is reconstruction or intervention that chooses species for inclusion or elimination based on the traits of species in the historical community. This approach has been used as a basis for designing sustainable agroecosystems, and it is likely to serve equally well when selecting species for design of less-utilitarian ecological systems, especially where invasion resistance is a criterion for restoration (Funk et al. 2008). What better place to experiment with, and eventually implement, designer ecosystems than on islands that have already suffered species losses and undergone human-mediated invasions?

Some of the most innovative and boldest efforts at restoring functionality involve rewilding on islands. Rewilding with non-native taxon substitutes – replacing recently extinct species with extant analogues from other geographic areas to resurrect lost ecosystem functioning – is controversial, primarily because the focus has been on replacing continental megafauna species that went extinct in the late Pleistocene (Donlan et al. 2006). In contrast, rewilding on islands offers much less controversial restoration scenarios. Insular mega-vertebrates weighed hundreds rather than thousands of kilograms, and many of them went extinct only a few hundred years ago compared with 12,000– 40,000 years ago for continental Pleistocene megafauna. Consequently, practitioners working on degraded islands around the world are spearheading the use of taxon substitutes involving birds, fruit bats, lizards and other taxonomic groups (Hansen 2010). The Mascarene Islands in the Western Indian Ocean offer an excellent example. By replacing recently extinct endemic giant tortoises with extant tortoises from other islands in the region, herbivory and seed dispersal likely to benefit native plants and control invasive non-native plants have been reinstated (Hansen 2010; Griffiths et al. 2011; Fig. 4.6).



Figure 4.6 Aldabra giant tortoise, *Aldabrachelys gigantea*, introduced on Rodrigues as herbivores and seed dispersers to replace two endemic *Cylindraspis* giant tortoise species, both recently extinct. Many endemic plant species have anti-tortoise-herbivory traits so the introduced tortoises, here and in Mauritius, seem to prefer invasive species such as this non-native *Leucaena leucocephala*. Photograph and text courtesy of Dennis Hansen.

4.4 WINDOW TO THE FUTURE?

At first glance, it may seem counter-intuitive to itemize the differences between islands and continents while also arguing that islands are a window into a future of novelty for all of Earth's ecosystems. If novelty arises on islands due to a lack of biogeographic buffering capacity, for instance, why should we predict the same outcome on continents? Buffering capacity is not the only factor determining the amount of change in an ecosystem, however: the strength of the *driver* is also paramount. While islands appear far more vulnerable to the biotic and abiotic forces that cause novel ecosystems to emerge, novel ecosystems are the likely results as these forces grow stronger and more widespread on continents.

Consider anthropogenic climate change. Although affecting all ecosystems on Earth, climate change is already altering island ecosystems. Limited area, lack of corridors and lower habitat heterogeneity (in many cases) imply high vulnerability of islands to climate change, and recent evidence confirms this. Coastline erosion due to sea-level rise is shrinking the land area of some Pacific Island nations made vulnerable by their small size and may literally wipe them off the map. Warming also allows the spread of disease vectors that directly cause avian extinctions (Benning et al. 2002). On continents, ecosystems may have higher buffering capacity, but this will mean little when climate change leads to wholesale biome shifts as predicted within one century by most global circulation models (Bergengren et al. 2011). High species diversity and a range of parent materials in an African savanna will not halt desertification, nor will the vast range of black spruce (Picea mariana) in North America shield it from thawing permafrost.

The global human footprint is also tracking what has already occurred on islands (see Chapters 8 and 9). For instance, islands have been referred to as 'paradise' for introduced species (Denslow 2003); indeed, their contribution to novelty is most apparent there. But comparative studies suggest that the fundamental ecological controls underlying species introductions are part of a global pattern of pervasive and widespread changes in ecological communities that are mechanistically consistent between islands and continents. For example, Sax and Gaines (2003) found that plant species richness at the regional scale is increasing on both islands and continents because species introductions far exceed extinctions. Similarly, novel ecosystems completely dominated by introduced species emerge on islands and continents alike when the introduced species in question add functional diversity not present in the historical ecosystem.

Novel ecosystems are so ubiquitous on islands that it is not surprising that there have been many attempts to manipulate them to achieve particular ends. Some of those interventions have been successful and some have failed, but we can learn from all of them. Most of them are applicable to continents. Five lessons from islands and elsewhere have particularly widespread applicability.

1. Recognize and embrace the need for social success. Ecologists, land managers and conservation biologists tend to be strong in the biological and physical sciences, but weak in the social sciences. It is not unheard of for intervention to begin and be halted soon after because a broad range of community members objected. Lack of social acceptance usually leads to no long-term biological or physical success. It is essential to identify stakeholders and involve them in planning from the start.

2. Assess the odds of success or failure prior to intervening. Funds are scarce for resource managers everywhere, so it is astonishing that investments are made that have little chance of success. Value judgments are inevitably involved, and some circumstances call for desperate measures. Futile expenditures are not in the best interest of resource managers, however.

3. *Evaluate the full range of values involved.* Intervention motivated by a single factor without considering ancillary impacts is ill advised. It is better to assess the full range of values provided by a novel ecosystem than to act based exclusively on one value, only to learn belatedly that intervention was the wrong course of action.

4. *Guard against unintended consequences.* These occur within and outside of novel ecosystems subjected to intervention. It is a general tenet of system science that to understand any unit, one must understand the next largest system of which it is a part as well as the next smallest unit that is a part of the system of interest. Avoid those unintended outcomes by understanding the target system and its parts as well as the larger landscape in which the intervention is to occur.

5. *Recognize local constraints and capitalize on local opportunities.* Resource managers would do well to act cautiously, paying due attention to unique local conditions. Nevertheless, intervention is hampered when each situation is regarded as so completely unique that

it must be fully understood before any action whatsoever can be taken. Balanced judgment is called for.

Adhering to those five guidelines does not guarantee success, but not paying attention to any one of them greatly increases the likelihood of failure. Resource managers on islands have demonstrated that they can sometimes do it well. They have learned from their mistakes and others are now in a good position to benefit from their experiences.

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REFERENCES

- Abelleira-Martínez, O. and Lugo, A.E. (2008) Post sugar cane succession in moist alluvial sites in Puerto Rico, in *Post-agricultural succession in the Neotropics* (ed. R.W. Myster), Springer, New York, 73–92.
- Adsersen, H. (1989) The rare plants of the Galápagos islands and their conservation. *Biological Conservation*, **47**, 49– 77.
- Alonso, L. (2010) Ant conservation: Current status and a call to action, in *Ant Ecology* (eds L. Lach, C.L. Parr and K.L. Abbott), Oxford University Press, Oxford UK, 59–74.
- Benning, T.L., LaPointe, D., Atkinson, C.T. and Vitousek, P.M. (2002) Interactions of climate change with biological invasions and land use in the Hawaiian Islands: Modeling the fate of endemic birds using a geographic information system. PNAS, **99**, 14246–14249.
- Bergengren, J.C., Waliser, D.E. and Yung, Y.L. (2011) Ecological sensitivity: a biospheric view of climate change. *Climatic Change*, doi: 10.1007/s10584-10011-10065-10581.
- Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K. and Chown, S.L. (2009) Indirect effects of invasive species removal devastate World Heritage Island. *Journal of Applied Ecology*, **46**, 73–81.
- Bruijnzeel, L.A. (2004) Hydrological functions of tropical forests: not seeing the soil for the trees? *Agriculture*, *Ecosystems and Environment*, **104**, 185–228.

- Campbell, K. and Donlan, C.J. (2005) Goat eradications on islands. *Conservation Biology*, **19**, 1362–1374.
- Carlquist, S. (1966) The biota of long-distance dispersal. I. Principles of dispersal and evolution. *The Quarterly Review* of Biology, **41**, 241–270.
- Carrion, V., Donlan, C.J., Campbell, K.J., Lavoie, C. and Cruz, F. (2011) Archipelago-wide island restoration in the Galapagos Islands: reducing costs of invasive mammal eradication programs and reinvasion risk. *PLoS ONE* 6:e18835. doi: 18810.11371/journal.pone.0018835.
- Castro, S.A., Daehler, C.C., Silva, L., Torres-Santana, C.W., Reyes-Betancort, J.A., Atkinson, R., Jaramillo, P., Guezou, A. and Jaksic, F.M. (2010) Floristic homogenization as a teleconnected trend in oceanic islands. *Diversity and Distributions*, **16**, 902–910.
- Caujapé-Castells, J., Tye, A., Crawford, D.J., Santos-Guerra, A., Sakai, A., Beaver, K., Lobin, W., Florens, F.B.V., Moura, M., Jardim, R., Gómes, I. and Kueffer, C. (2010) Conservation of oceanic island floras: present and future global challenges. *Perspectives in Plant Ecology, Evolution and Systematics*, **12**, 107–130.
- Croll, D.A., Maron, J.L., Estes, J.A., Danner, E.M. and Byrd, G.V. (2005) Introduced predators transform subarctic islands from grassland to tundra. *Science*, **307**, 1959–1961.
- D'Antonio, C.M. and Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.
- Denslow, J.S. (2003) Weeds in paradise: thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden*, **90**, 119–127.
- Donlan, C.J., Berger, J., Bock, C.E., Bock, J.H., Burney, D.A., Estes, J.A., Foreman, D., Martin, P.S., Roemer, G.W., Smith, F.A., Soule, M.E. and Greene, H.W. (2006) Pleistocene rewilding: An optimistic agenda for twenty-first century conservation. *American Naturalist*, **168**, 660–681.
- Fritts, T.H. and Rodda, G.H. (1998) The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annual Review of Ecology and Systematics*, 29, 113–140.
- Funk, J.L., Cleland, E.E., Suding, K.N. and Zavaleta, E.S. (2008) Restoration through reassembly: plant traits and invasion resistance. *Trends in Ecology and Evolution*, **23**, 695–703.
- Gardener, M.R., Atkinson, R. and Renteria, J.L. (2010) Eradications and people: lessons from the plant eradication program in Galapagos. *Restoration Ecology*, **18**, 20–29.
- Givnish, T.J., Millam, K.C., Mast, A.R., Paterson, T.B., Theim, T.J., Hipp, A.L., Henss, J.M., Smith, J.F., Wood, K.R. and Sytsma, K.J. (2009) Origin, adaptive radiation and diversification of the Hawaiian lobeliads (Asterales: Campanulaceae). *Proceedings of the Royal Society B*, **276**, 407–416.
- Griffiths, C.J., Hansen, D.M., Zuël, N., Jones, C.G. and Harris, S. (2011) Resurrecting extinct interactions with extant substitutes. *Current Biology*, **21**, 762–765.

- Hansen, D.M. (2010) On the use of taxon substitutes in rewilding projects on islands, in *Islands and Evolution* (eds V. Pérez-Mellado and C. Ramon), Institut Menorquí d'Estudis, Maó, Menorca, Spain, 111–146.
- Herrera, H.W. (2011) Monitoreo de invertebrados terrestres en barcos de carga desde Guayaquil a Galápagos. Report for the Ecuadorian Ministry of Environment, Puerto Ayora, Galápagos.
- Hughes, F., Vitousek, P.M. and Tunison, T. (1991) Alien grass invasion and fire in the seasonal submontane zone of Hawaii. *Ecology*, **72**, 743–746.
- Hughes, R.F. and Denslow, J.S. (2005) Invasion by a N₂-fixing tree alters function and structure in wet lowland forests of Hawai'i. *Ecological Applications*, **15**, 1615–1628.
- Jäger, H., Tye, A. and Kowarik, I. (2007) Tree invasion in naturally treeless environments: Impacts of quinine (*Cinchona pubescens*) trees on native vegetation in Galápagos. *Biological Conservation*, **140**, 297–307.
- Kaiser-Bunbury, C.N., Traveset, A. and Hansen, D.M. (2010) Conservation and restoration of plant-animal mutualisms on oceanic islands. *Perspectives in Plant Ecology Evolution and Systematics*, **12**, 131–143.
- van Kleunen, M., Webber, E. and Fischer, M. (2010) A metaanalysis of trait differences between invasive and noninvasive plant species. *Ecology Letters*, **13**, 235–245.
- Koop, J., Huber, S., Laverty, S. and Clayton, D. (2011) Experimental demonstration of the fitness consequences of an introduced parasite of Darwin's finches. *PLoS ONE* 6:e19706. doi: 19710.11371/journal.pone.0019706.
- Kueffer, C., Schumacher, E., Fleischmann, K., Edwards, P.J. and Dietz, H. (2007) Strong belowground competition shapes tree regeneration in invasive *Cinnamomum verum* forests. *Journal of Ecology*, **95**, 273–282.
- Kueffer, C., Schumacher, E., Dietz, H., Fleischmann, K. and Edwards, P.J. (2010) Managing successional trajectories in alien-dominated, novel ecosystems by facilitating seedling regeneration: a case study. *Biological Conservation*, **143**, 1792–1802.
- Laurence, W.F., Useche, D.C., Shoo, L.P., Herzog, S.K., Kessler, M. and 48 others. (2011) Global warming, elevational ranges and the vulnerability of tropical biota. *Biological Conservation*, 144, 548–557.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- Lugo, A.E. (2004) The outcome of alien tree invasions in Puerto Rico. Frontiers in Ecology and the Environment, **2**, 265–273.
- Lugo, A.E. and Brandeis, T.J. (2005) New mix of alien and native species coexists in Puerto Rico's landscapes, in: *Biotic Interactions in the Tropics: Their Role in the Maintenance of Species Diversity* (eds D.E.R.P. Bursalem, M.A. Pinard and S.E. Hartley), Cambridge University Press, Cambridge.
- Mack, R.M. and Lonsdale, W.R. (2002) Eradicating invasive plants: Hard-won lessons for islands, in *Turning the Tide: Eradication of Invasive Species* (eds C.R. Veitch and M.N.

Clout), IUCN SSC Invasive Species Specialist Group, Gland, Switzerland and Cambridge, UK, 164–172.

- Mascaro, J. (2011) Eighty years of succession in a noncommercial plantation on Hawai'i Island: Are native species returning? *Pacific Science*, 65, 1–15.
- Mascaro, J., Hughes, F.R. and Schnitzer, S.A. (2012) Novel forests maintain ecosystem processes after the decline of native tree species. *Ecological Monographs*, doi: 10.1890/ 11-1014.1.
- Meléndez Ackerman, E.J., Cortés, C., Sustache, J., Aragón, S., Morales Vargas, M., García Bermúdez, M. and Fernández, D.S. (2008) Diet of feral goats in Mona Island Reserve, Puerto Rico. *Caribbean Journal of Science*, **44**, 199–205.
- Mueller-Dombois, D. (2008) Pacific island forests: successionally impoverished and now threatened to be overgrown by aliens? *Pacific Science*, **62**, 303–308.
- Mueller-Dombois, D. and Fosberg, F.R. (1998) Vegetation of the Tropical Pacific Islands. Springer, NY.
- O'Dowd, D.J., Green, P.T. and Lake, P.S. (2003) Invasion 'meltdown' on an oceanic island. *Ecology Letters*, 6, 812–817.
- O'Farrill, G., Chapman, C.A. and Gonzalez, A. (2011) Origin and deposition sites influence seed germination and seedling survival of *Manilkara zapota*: implications for longdistance, animal-mediated seed dispersal. *Seed Science Research*, doi:10.1017.
- Parent, C.E., Caccone, A. and Petren, K. (2008) Colonization and diversification of Galápagos terrestrial fauna: a phylogenetic and biogeographical synthesis. *Philosophical Transactions of the Royal Society B*, **363**, 3347–3361.
- Pauchard, A., Kueffer, C., Dietz, H., Daehler, C.C., Alexander, J., Edwards, P.J., Arévalo, J.R., Cavieres, L., Guisan, A., Haider, S., Jakobs, G., McDougall, K., Millar, C.I., Naylor, B.J., Parks, C.G., Rew, L.J. and Seipel, T. (2009) Ain't no mountain high enough: Plant invasions reaching new elevations. *Frontiers in Ecology and the Environment*, 7, 479–486.
- Raffaele, A.H. (1989) The ecology of native and introduced granivorous birds in Puerto Rico, in *Biogeography in the West Indies: Past, Present, and Future* (ed. C.A. Woods), Sandhill Crane Press, Gainesville, FL, 541–566.
- Rolett, B. and Diamond, J. (2004) Environmental predictors of pre-European deforestation on Pacific islands. *Nature*, 431, 443–446.
- Rubinoff, D., Holland, B.S., Shibata, A., Messing, R.H. and Wright, M.G. (2010) Rapid invasion despite lack of genetic variation in the erythrina gall wasp (*Quadrastichus erythrinae* Kim). *Pacific Science*, **64**, 23–31.
- Sax, D.F. and Gaines, S.D. (2003) Species diversity: from global decreases to local increases. *Trends in Ecology and Evolution*, 18, 561–566.
- Thaxton, J.M., Cordell, S., Cabin, R.J. and Sandquist, D.R. (2011) Non-native grass removal and shade increase soil moisture and seedling performance during Hawaiian dry forest restoration. *Restoration Ecology*, doi: 10.1111/j. 1526-1100X.2011.00793.x.

- Trueman, M., Atkinson, R., Guézou, A.P. and Wurm, P. (2010) Residence time and human-induced propagule pressure at work in the alien flora of Galapagos. *Biological Invasions*, **12**, 3949–3960.
- Veitch, C.R. and Clout, M.N. (eds) (2002) Turning the tide: the eradication of invasive species. Proceedings of the International Conference on the Eradication of Island Invasives. Gland, Switzerland, IUCN.
- Veitch, C.R., Clout, M.N. and Towns, D.R. (eds) (2011) Island invasives: eradication and management. *Proceedings* of the International Conference on Island Invasives. Gland, Switzerland: IUCN and Auckland, New Zealand.
- Vitousek, P.M. (2004) Nutrient Cycling and Limitation: Hawai'i as a Model System. Princeton University Press, Princeton, NJ.
- Vitousek, P.M. and Walker, L.R. (1989) Biological invasion by Myrica faya in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. Ecological Monographs, 59, 247–265.
- Waterloo, M.J., Bruijnzeel, L.A., Vugts, H.F. and Rawaqa, T.T. (1999) Evaporation from *Pinus caribea* plantations on

former grassland soils under maritime tropical conditions. *Water Resources Research*, **35**, 2133–2144.

- Whittaker, R.J. and Fernández-Palacios, J.M. (2007) Island Biogeography: Ecology, Evolution, and Conservation. 2nd edition. Oxford University Press, Oxford, UK.
- Willig, M.R. and Gannon, M.R. (1996) Mammals, in *The Food Web of a Tropical Rain Forest* (eds D.P. Reagan and R.B. Waide), The University of Chicago Press, Chicago, IL, 399–431.
- Zapata, C.E. (2007) Evaluation of the quarantine and inspection system for Galapagos (SICGAL) after seven years, in *Galapagos Report 2006–2007*. Puerto Ayora, Galapagos, Ecuador: Charles Darwin Foundation, Galapagos National Park & INGALA.
- Zimmerman, N., Hughes, R.F., Cordell, S., Hart, P., Chang, H.K., Perez, D., Like, R.K. and Ostertag, R. (2008) Patterns of primary succession of native and introduced plants in lowland wet forests in Eastern Hawai'i. *Biotropica*, **40**, 277–284.