



## The biology of insularity: an introduction

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### Summary of special issue

Insular environments, ranging from oceanic islands to fragments of once-contiguous natural systems, have long been used by biologists to test basic principles of ecology, evolution and biogeography. More recently, insular environments have figured prominently in conservation ecology, where the aim has usually been to conserve species or assemblages unique to isolated habitats. Improving the level of communication among the evolutionary biologists, theoretical ecologists and conservation biologists who study insular biotas will work to the benefit of all. This volume was inspired by a recent conference on the ecology of insular biotas, in which participants from a wide range of disciplines came together to compare ecological processes across a variety of taxonomic groups inhabiting a wide range of isolated environments. In this introduction, we point out the themes underlying these very diverse contributions. First we elaborate on the value of islands for elucidating processes underlying ecosystem functioning, population dynamics of reintroduced species, and restoration of disturbed habitats, and emphasize those areas where the use of islands could be expanded. The second section focuses on the link between ecology and evolutionary processes in insular systems and includes examples from oceanic islands, naturally patchy habitats and recently fragmented habitats. The third section illustrates some of the ways that invasive alien species on oceanic islands affect plant–animal mutualisms, particularly seed dispersal and pollination. The final section, on consequences of habitat fragmentation, focuses mainly on studies that describe the consequences that fragmentation has for plants and animals as they are forced into artificially insular environments. We close with a study that points out the differences among types of insular systems and identifies gaps in our knowledge of insular biotas, particularly the importance of explicitly incorporating patch type, age and patch–matrix contrasts in research. Finally, we recommend a greater emphasis on linking ecological theory and applied research, and improving communication between those who ask basic ecological questions and those who use insular systems for conservation.

### Keywords

Biodiversity, conservation, evolution, habitat fragmentation, insular ecosystems, invasive alien species, islands, island biogeography, plant–animal interactions, restoration.

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### INTRODUCTION

Biogeography is the study of the geographical patterns of species distribution (Quammen, 1996). These patterns are influenced by two features. First, environmental conditions change predictably along spatial gradients, and second,

organisms vary in their response to this environmental change (Lomolino, 2000).

The study of insular systems, especially islands, has provided fundamental insights into the relationships between geographical patterns and biological processes for at least 150 years, by inspiring scientists such as Darwin, Wallace, Mayr, Wilson and Diamond. In turn, many island systems both small, such as Mauritius, Krakatau, Hawai'i and the Galápagos, and large, such as Madagascar, New

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Zealand and Australia, have become icons for biologists. Also inspirational, if less well known, have been other patches of habitat surrounded by a contrasting environmental matrix – such as Lake Baikal, Mt Kilimanjaro and deep sea hydrothermal vents. Recently, anthropogenic habitat islands created through fragmentation of formerly contiguous habitats have received increasing attention as the ecological scope and consequences of fragmentation have expanded.

Although islands in the sea, other habitat islands, and fragments are all insular by virtue of their geographical and/or ecological isolation from similar environments, they are nonetheless quite diverse. For example, they vary in accessibility, size, age, permanence, habitat complexity and degree of contrast with the surrounding matrix (MacArthur & Wilson, 1967; Whittaker, 1998; Ricketts, 2001; Watson, 2002). Yet researchers have sometimes been tempted to treat all insular systems as functionally similar, for example by uncritically applying island biogeography theory to the design of nature reserves (Simberloff & Abele, 1982). These attempts have revealed that we must examine the phenomenon of insularity in greater detail if we wish to make generalizations about how it structures biological diversity (Lomolino, 2000; Watson, 2002). As a step towards understanding the effects of insularity, we convened a conference on the 'Ecology of Insular Biotas' in 2001 (Denslow, 2001), attended by 170 scientists from a broad range of disciplines. This special issue contains selected contributions from these conference participants. The papers are grouped into four overlapping categories that reflect contemporary influences on the interplay between process and pattern in insular systems: ecological processes, evolutionary processes, invasive alien species and habitat fragmentation.

## ECOLOGICAL PROCESSES IN INSULAR SYSTEMS

Islands have been treated as 'model systems' through which to understand ecological and evolutionary processes since Darwin landed on the Galápagos and Wallace explored the Malay archipelago (see reviews in Vitousek *et al.*, 1995; Quammen, 1996). In the opening paper of this section, Vitousek (2002) compares the use of islands in ecology to that of model organisms in other fields of biology, and reviews recent contributions of island studies to our understanding of ecosystem processes. His emphasis is on a long series of studies of the islands of Hawai'i that evaluated the roles of temperature, precipitation and long-distance dust transfer in nutrient cycling and decomposition. Vitousek points out that although oceanic islands have been used very effectively to answer questions in evolution and speciation as well as ecosystem ecology, they are greatly underutilized in the fields of conservation biology and cultural evolution.

The use of islands as 'true replicates' in ecological studies where the spatial and temporal scales are too large for experimentation (as opposed to the study of islands for their own properties) is a theme repeated in the paper by Wardle

(2002). He reviews island studies that have given insight into the roles of trophic interactions and the role of biodiversity, including results of an excellent example of this approach using small islands in a lake in northern Sweden (Wardle *et al.*, 1997). On these islands there is a strong correlation between island size and successional stage of the vegetation simply because of the greater probability of lightning striking the larger islands and inducing wildfires. This resulted in strong relationships, mediated through differences in successional stage, between island size and ecosystem variables such as carbon sequestration, decomposition rates and nitrogen acquisition.

Towns' (2002) study illustrates the potential for using islands to guide restoration efforts. He evaluates the anticipated restoration trajectory of New Zealand's Korapuki Island, which has been heavily disturbed by introduced rats and rabbits, using as 'benchmarks' two nearby islands that are very similar in climate and vegetation but lack rats and rabbits. He presents several potential restoration scenarios and emphasizes the importance of considering the life-spans of affected plant and animal species in predicting recovery rates. Comparisons with adjacent islands allow for a focused evaluation of whether restoration is successful, and whether the results can then be applied to other areas, including mainland habitats.

The value of islands to understanding population dynamics is demonstrated by Armstrong *et al.* (2002) in their study of three bird species reintroduced to New Zealand islands. They compare island manipulations to microcosm experiments: starting conditions are known, the entire system can be monitored, and the population is essentially closed to immigration and emigration. This allows them to distinguish factors controlling population size in a manner not possible at most mainland sites. These factors differ among species and islands, and may include food limitation and disease. These results reinforce the importance of species-specific and site-specific variables in determining the success of restoration efforts.

Islands are not only useful tools for evaluating restoration attempts, but they may also have a high intrinsic conservation value: they often contain unique species assemblages because of species impoverishment, and they may harbour remnant populations of species that have been eliminated from mainland areas by introduced predators (Daugherty *et al.*, 1990). Rodda & Dean-Bradley (2002) combine a thorough literature review with results from their own studies to examine the hypothesis that herpetofaunal assemblages on islands demonstrate 'excess density compensation' (greater aggregate biomass per area) compared with mainland areas. They find clear support for excess density compensation on small islands, including the example provided by Nelson *et al.* (2002), who found extraordinarily high densities of tuatara (*Sphenodon guntheri* Buller) on a small (4 ha) island off the coast of New Zealand. This high aggregated biomass was associated primarily with degree of species impoverishment, but available data were insufficient to test whether reduced suites of predators were responsible.

Several of these island studies assume or demonstrate the existence of a 'keystone' species (e.g. Nelson *et al.*, 2002; Towns, 2002); one whose removal results in large changes in community composition despite a relatively low biomass (Paine, 1966, 1969; Mills *et al.*, 1993; Power *et al.*, 1996). For islands, these are generally herbivores (e.g. Allen *et al.*, 1994; Green *et al.*, 1997), predators (e.g. Cushman, 1995; Schoener & Spiller, 1997; Towns, 2002) or burrowing seabirds (e.g. Anderson & Polis, 1998; Mulder & Keall, 2001; Towns, 2002). Scarff & Bradley (2002) directly address the question of how to determine the proportion of species whose removal will have large consequences for ecosystem functioning. They present results from aquatic microcosms simulating oxidation ponds from which different eukaryotes were deleted in turn. A drawback of most microcosm studies is that they are usually artificial with respect to species identities and composition and are often conducted over relatively short time periods (Vitousek, 2002). Scarff and Bradley reduce these problems by seeding communities with mixtures of species from existing ponds, and by using species with very short life spans. Despite low species richness, their results point to very high redundancy within the eukaryote community in their microcosms. This contrasts with results from other systems such as experimental grassland studies (Symstad *et al.*, 1998; Hector *et al.*, 1999) and the assumptions underlying island restoration programmes. The extent to which species loss from insular communities affects community composition and ecosystem function requires much more investigation.

## EVOLUTIONARY PROCESSES IN INSULAR SYSTEMS

The world's insular environments have long been recognized as ideal natural laboratories for the study of evolution. The following contributions demonstrate how studies of insular evolution can provide insights into organisms' ecology and guidelines for their conservation.

Gillespie (2002) used ecological and molecular data to analyse adaptive radiation within the spider genus *Tetragnatha* in three Polynesian archipelagoes. She found that each archipelago was colonized independently by continental ancestors rather than by island-hopping spiders from nearby islands. After colonization, each spider lineage radiated into multiple habitats, with the selection pressures of similar habitats resulting in convergent evolution among lineages on different islands. This study illustrates the role that radiation and local adaptation can play in structuring communities.

Holzappel *et al.* (2002) studied the geographical distribution of genetic variation in *Dactylanthus taylorii* Hook. f., an endangered root-holoparasitic plant endemic to New Zealand. They found evidence for long isolation and restricted gene flow among populations, and for two regional clusters which are likely the result of repeated volcanic events causing large-scale disturbance of the vegetation along the region dividing the clusters. However, within a region, geographical distance was not a good predictor of genetic similarity between populations. This

study raises questions regarding the management of rare species that represent the remnants of a large population vs. management of species that naturally occur in small, isolated populations.

Clarke's (2002) contribution focuses on a naturally patchy terrestrial environment – relatively fire-resistant rocky patches embedded in a matrix of fire-prone eucalypt forest. Here, the rocky habitat was dominated by plants that are killed by fire and then regenerate from seed, whereas the matrix was dominated by species that survive fire and resprout. Clarke suggests that the different life-history strategies may have resulted from evolutionary responses to differences in fire frequency and intensity in the two environments.

Blumstein (2002) used populations of Tammar wallabies (*Macropus eugenii*, Desmarest) that had been exposed to different suites of predators to test the extent to which antipredator behaviour is evolutionarily labile. He hypothesized that natural selection would redirect resources away from antipredator behaviour in wallaby populations that occupied isolated environments that had lost their predators. Some defences, such as visual recognition of predators, were retained even after 9500 years of relaxed selection, while others, such as olfactory and acoustic recognition, were lost and may require experience to be maintained. Blumstein suggests that the possible loss of antipredator behaviour should be assessed before managers use animals from predator-free patches to restore populations in environments that contain predators.

## EFFECTS OF ALIEN SPECIES ON PLANT–ANIMAL MUTUALISMS IN INSULAR SYSTEMS

On islands world-wide, waves of extinctions of endemic animals have followed the arrival of humans, the animals they have introduced and the changes that both have wrought on island environments (Vitousek, 1988; Paulay, 1994; Steadman, 1995; McConkey & Drake, 2002). The surviving endemic animals have often had their ranges or population sizes severely reduced. As the native fauna becomes depleted, mutualistic plant–animal interactions, such as pollination and seed dispersal, can be caught in positive feedback loops in which native plants and animals decline in tandem (Atkinson, 1989; Bond, 1995; Towns *et al.*, 1997). For the surviving species, changes in the suite of available pollinators, dispersers and plants may eventually drive evolutionary changes in floral traits, seed size, bill shape and niche breadth (Bond, 1995; Lord *et al.*, 2002; Riera *et al.*, 2002).

Meehan *et al.* (2002) estimate the potential for vertebrate-mediated seed dispersal in Tonga's rain forests to have been compromised by the extinction of its two largest frugivorous pigeon species. Data from fossil bones suggest Tonga's extinct endemic pigeons were capable of dispersing several plant species that have diaspores too large to be dispersed by the birds present today. Species whose dispersal has been compromised face many potential threats, especially as

Tonga's remaining forests become increasingly fragmented (cf. Wiser *et al.*, 2002).

Riera *et al.* (2002) illustrate the role that invasive alien animals may play in at least partially replacing extirpated native species in mutualistic plant–animal interactions. In the Balearic Islands, an endemic, frugivorous lizard has been driven locally extinct by introduced mammalian predators. One of these omnivorous mammals has extended the range of at least one endemic plant species by dispersing it into higher elevation zones than the lizard formerly achieved. This study highlights a potentially common, but under-reported phenomenon: invasive alien animals that increase the abundance of a native species.

Hansen *et al.* (2002) examine the potential for alien and endemic animals to compete for floral resources on endemic trees in Mauritius. Here, introduced bees (*Apis mellifera* L.) may limit nectar availability for endemic bird species. A further feature of this interaction is that the bees are less efficient pollinators than are the birds. Thus, although bees transfer pollen, they may be still be negatively impacting the trees as well as the birds.

### CONSEQUENCES OF FRAGMENTATION – IMPOSED INSULARITY

Many environments that were once extensive and contiguous have become fragmented; insularity has been imposed upon them. This has occurred at spatial scales ranging from the continental, such as North America's prairie and India's forests, to the already small and insular, such as forests on most of the world's inhabited, oceanic islands.

In an ambitious undertaking, Laurance *et al.* (2002) employ Geographic Information System analysis to examine the relationships among ten biophysical and anthropogenic predictor variables and deforestation across the entire Brazilian Amazon. They find that deforestation is most strongly associated with sites that have a high population density, highway access and/or a pronounced dry season. One valuable outcome of this approach is the power it may give to allow the pattern of future fragmentation to be predicted.

Ross *et al.* (2002) present evidence that plant species richness in eucalypt forest fragments of eastern Australia is determined by a complex interaction among patch size, age and disturbance history. Here, the nature of the disturbance plays a key role in determining native species richness, which may increase following a natural disturbance, such as fire, but decrease following anthropogenic disturbance.

Wiser *et al.* (2002) document severe forest fragmentation on a densely populated Polynesian island. Only 3% of Tongatapu supports developed forest, and this is mainly restricted to small (mean size 15 ha), disjunct and degraded forest fragments. Nevertheless, the fragments still show signs that they may continue to harbour significant components of native biodiversity, especially in environments that experience a strong marine influence and are never cleared for shifting agriculture.

Banko *et al.* (2002) present a comprehensive account of an endangered Hawaiian honey-creep whose range has been reduced as the habitat it can occupy has contracted through forest fragmentation and the spread of alien species. The endangered birds are now unable to exploit the full elevational range over which they once foraged for seeds and insects. Because the seasonal availability of these food resources is determined at least partly by elevational differences in climate, they have become more concentrated in both space and time, possibly increasing the birds' vulnerability to extinction.

Lens & Van Dongen (2002) examined fragmented populations of an endangered thrush in Kenya to ask whether developmental instability, estimated from fluctuating asymmetry, can be used to monitor stress in bird populations. They found that while some estimate of stress can be gained from fluctuating asymmetry, a better estimation is achieved when additional data, e.g. from body condition, are incorporated in the assessment. They suggest that this approach can provide valuable information for managers making population translocations.

### DISCUSSION

In recent years, many excellent books have addressed phenomena associated with insularity, including: evolution (Wagner & Funk, 1995; Grant, 1998), metapopulation ecology (Hanski, 1999), island biogeography (Whittaker, 1998), island ecosystem function (Vitousek *et al.*, 1995), forest fragmentation (Laurance & Bierregaard, 1997), inselbergs (Porembski & Barthlott, 2000) and invasive species (Mooney & Hobbs, 2000). However, none of these has attempted to cover the full range of biological phenomena associated with insularity, perhaps because such an undertaking may be beyond the scope of a single publication. Indeed, we do not yet even know to what extent different insular systems can be directly compared. In the final paper in this collection, Watson (2002) addresses this important question by providing a framework into which the diverse array of studies on insular biotas can be placed. His classification scheme categorizes insular systems based on three factors: whether the patch is an island (always isolated) or a fragment (remnant of a larger patch), the age of the patch, and the level of contrast between the patch and the surrounding matrix. Watson points out that of the eight resulting categories, only two are well-represented in the literature: old islands with high patch–matrix contrast and young fragments with low contrast. Furthermore, the goals of the studies differ, with fragmentation studies generally being driven by site-specific, application-orientated goals and studies of older islands or fragments driven by broader, more theoretical questions. That bias is reflected in this volume: papers in Section I (*Ecological Processes*) are concerned primarily with general ecological principles on oceanic islands, while sections III (*Effects of Alien Species*) and IV (*Consequences of Fragmentation*) are dominated by papers concerning short-term responses in young habitat fragments. Only in Section II (*Evolutionary Processes*) are a

range of patch types represented, perhaps reflecting the explicit focus in this discipline on effects of time and level of connectivity. Until the types of questions asked and the approaches used in answering them become more similar for different patch types, the role of patch age is incorporated more explicitly in all studies, and patch–matrix contrast is accounted for, it is unlikely that we will be able to apply information gained from one insular system to another.

The importance of understanding insularity from a theoretical standpoint so that this knowledge can be applied to conservation is becoming increasingly urgent given the rate at which insular habitats are being created through fragmentation and the rate at which these fragments and other insular environments are being assailed by invasive alien species. Human-induced insularity can, at the very least, lead to landscape-level changes through modification of vegetation cover; at worst, it can lead to spirals of extinction. While there is no antidote to extinction, it is possible to reverse range declines by removing alien species and restoring damaged ecosystems (e.g. Towns, 2002). The progressive restoration of species assemblages and re-establishment of lost linkages between populations provides a powerful means for testing hypotheses about species distributions and interactions (e.g. Gilpin, 1987), and community assembly (e.g. Diamond, 1975; Roughgarden, 1989; Morin, 1999). In addition, using islands as replicates in large-scale comparative approaches to ecological and conservation questions can help untangle potentially confounding effects that hamper many single-site studies (Simberloff & Wilson, 1969; McConkey & Drake, 2002; Wardle, 2002).

It is therefore vital that we continue our attempts to close the gap between those who work on conservation of species using islands as a convenient conservation tool, and those asking basic ecological questions about insularity. Communication between these two groups will enhance what island studies can teach us about conservation. For example, in order to know whether restoration methods used successfully on offshore islands should be applied to habitat patches on mainlands, we need to be able to distinguish among those properties that are unique to true islands, those unique to habitat patches and those common to insular systems in general. The site-specific approach used in most conservation and restoration projects does not allow this to be tested.

In summary, in order to understand insularity, it is imperative that ecologists, evolutionary biologists, biogeographers and conservationists continue to communicate and seek new frameworks and paradigms (e.g. Lomolino, 2000; Whittaker, 2000; Watson, 2002) so that we may someday confidently make generalizations about insular systems and then apply them to conservation problems. In order to develop robust generalizations, it is also important that under-represented taxa and environments be exploited for the insights they can offer. Across the planet, the increase in patchiness through habitat fragmentation and the loss of isolation through introduction of invasive alien species combine to make insularity an increasingly important phenomenon. It is encouraging that so many imaginative scientists are contributing to its study.

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