

Review

Conservation and restoration of plant–animal mutualisms on oceanic islands

Christopher N. Kaiser-Bunbury^{a,*}, Anna Traveset^b, Dennis M. Hansen^c^a Ecosystem Management, Institute of Terrestrial Ecosystems, Swiss Federal Institute of Technology (ETH) Zurich, 8092 Zurich, Switzerland^b Institut Mediterrani d'Estudis Avançats (CSIC-UIB), C/Miquel Marqués 21, 07190-Esporles, Mallorca, Illes Balears, Spain^c Department of Biology, Stanford University, 371 Serra Mall, Stanford, CA 94305, USA

ARTICLE INFO

Article history:

Received 13 February 2009

Received in revised form

9 October 2009

Accepted 9 October 2009

Keywords:

Monitoring of interactions

Mutualistic networks

Pollination

Rewilding

Seed dispersal

ABSTRACT

Islands harbour much of the world's threatened biodiversity. Recent work has highlighted how it is not species diversity *per se* but rather the interactions between organisms that breathes life into ecosystems. Thus, the real challenge to preserving and restoring biodiversity on islands is not to only focus on species themselves, but more importantly on maintaining and restoring the integrity of interactions between the species. Here we argue that mutualistic plant–animal interactions play a pivotal role with regards to conservation and restoration on islands. Furthermore, these interactions are ideally suited for inter-island comparisons due to ecological and evolutionary similarities across geographical and taxonomical boundaries. The similarities include highly generalised mutualistic systems, the evolution and readjustment of plant reproductive traits, and a disharmony in taxonomic groups of mutualists, compared to continental ecosystems. We highlight past and present threats to island plant–animal mutualisms, as well as the challenges and opportunities inherent to these interactions. In particular, we (1) argue that mutualistic networks provide an ideal approach to collect information and advance our knowledge on the systems, (2) suggest the use of interactions as biodiversity monitoring and assessment tools, (3) highlight the differences and similarities between pollination and seed dispersal interactions in the context of restoration, and (4) briefly discuss the ambiguous role of alien invasive species in the management of mutualistic interactions. Finally, we highlight how a recently proposed but controversial restoration strategy, rewilding, can be gainfully applied to and further advanced in island settings.

© 2009 Rübel Foundation, ETH Zürich. Published by Elsevier GmbH. All rights reserved.

Contents

Introduction	132
Evolutionary and ecological similarities of insular plant–animal mutualisms	132
Generalised interactions	132
Readjustment of plant reproductive traits	133
Strong disharmony in taxonomical groups of mutualists	134
Past and present threats	134
Species extinctions	134
Species introductions	134
Fragmentation	135
Opportunities and challenges in conservation and restoration of mutualistic interactions	136
The network approach: basis for restoration and conservation of mutualistic interactions	136
Mutualistic interactions as biodiversity monitoring tools	137
Pollination or seed dispersal: setting priorities	138
Alien invasive species and mutualistic interactions	138
Rewilding, a current controversial issue in conservation biology: islands at the forefront again?	139
Conclusion	140
Acknowledgements	140
References	140

* Corresponding author. Tel.: +41 44 632 89 45; fax: +41 44 632 15 75.

E-mail address: ch.kaiser@env.ethz.ch (C.N. Kaiser-Bunbury).

Introduction

Islands harbour much of the world's threatened biodiversity, most of which is endangered by habitat degradation and loss (Bolger et al., 1991; Kier et al., 2009), exploitation of natural resources (Rainbird, 2002) and the intentional or accidental introduction of alien invasive species (Moulton and Pimm, 1986; Vitousek et al., 1997; Mack et al., 2000; Sax et al., 2002; Berglund et al., 2009). The Holocene extinction of island endemics has resulted in some of the most severe losses to global species richness (Simberloff and Boecklen, 1991; Steadman, 1995; Whittaker and Fernández-Palacios, 2007), and since about 1600 CE, 80% of the recorded extinctions have been island species (Groombridge, 1992).

However, increasing evidence has confirmed that it is not the decline of species diversity *per se* that scientists, conservationists, and restoration managers should be most concerned about, but rather the interactions between organisms that breathe life into ecosystems (e.g. Janzen, 1974; Bond, 1994; Buchmann and Nabhan, 1996; Kearns et al., 1998; Traveset and Richardson, 2006). Despite the fact that the connection between species extinction and ecosystem function has long been a central point of concern (Ehrlich and Mooney, 1983; Ehrlich and Wilson, 1991; Kareiva et al., 1993), the majority of conservation and restoration projects on islands still fail to take species interactions, particularly plant–animal mutualisms, into consideration in both planning and implementation phases. Furthermore, the same neglect is often repeated if and when ongoing or finished projects are subsequently being monitored and evaluated. Thus, the real challenge to preserving and restoring biodiversity on islands is not only to focus on species themselves, but more importantly on maintaining and restoring the integrity of interactions between species. Indeed, one common problem for restoration projects are the often “fuzzy targets” (Simberloff, 1990), i.e. what is the desired state we are restoring towards? Mutualistic interactions provide a good template for evaluating success and help to more clearly define targets of restoration projects.

Here, we focus on pollination and seed dispersal interactions on oceanic and para-oceanic islands (i.e. comparatively small islands of a continental origin that behave like oceanic ones, mainly because they have been isolated during millions of years; e.g. Balearics, the granitic Seychelles). On islands, pollinators and seed dispersers are likely to be strong interactors in the overall functioning of an ecosystem (Cox et al., 1991). Thus, we believe that these two categories of mutualistic plant–animal interactions on islands are eminently suited for a broad-scale comparative approach within and between archipelagos and regions, especially compared to taxon-specific work, which by nature differs a lot even between islands within archipelagos due to high levels of endemism at most taxonomical levels. Furthermore, working with endangered species and interactions should not only be seen as ‘emergency-aid’ to an ecosystem; it is possible to address and combine both basic evolutionary ecological research and applied conservation biology in such scenarios. Indeed, all else being equal, it could be argued that there should be a moral imperative to direct research funding towards basing studies on ecological and evolutionary studies in endangered ecosystems.

In this paper we highlight and discuss (1) evolutionary and ecological similarities of plant–animal interactions across islands, (2) threats to mutualistic plant–animal interactions in island ecosystems, (3) the challenges inherent to and opportunities offered by these interactions with regards to conservation and restoration, and (4) how recently proposed but controversial restoration strategies can be gainfully applied to island settings.

Evolutionary and ecological similarities of insular plant–animal mutualisms

The floras and faunas of oceanic islands are typically depauperate and disharmonic compared to continental ones (MacArthur and Wilson, 1967). Species diversity on islands arises from rare, selective colonisation events and subsequent evolution in which many lineages have radiated, resulting in high degrees of endemism. Island species have evolved in relative isolation often released from previous competitors or predators and typically, compared to mainland ecosystems, in smaller populations. These conditions of spatial isolation, ecological release and small population sizes have resulted in the oft-repeated sentiment that islands are simple systems that form ‘natural laboratories’ for evolutionary and ecological studies. It is the similarity of disparate evolutionary scenarios within and between archipelagos, and the structural similarity of different insular ecosystems, which have fascinated scientists from their initial discovery until today.

This similarity is also reflected in traits related to pollination and seed dispersal interactions on different islands and to the resulting ecosystem- and network-level patterns of such interactions. Below, we identify three evolutionarily and ecologically intertwined groupings of similar traits and patterns between islands. These groupings provide a firm basis for understanding how basic ecological and evolutionary research questions can be fruitfully integrated with applied conservation and restoration management on islands.

Generalised interactions

While a number of specific interactions have evolved on islands, many studies have shown that generalised interactions—one plant species interacting with many animal mutualists and vice versa—predominant in plant–pollinator communities on islands (Fig. 1A; Barrett, 1996; Bernardello et al., 2001; Rathcke, 2001; Olesen et al., 2002; Anderson, 2003; Dupont et al., 2003; Kaiser-Bunbury et al., 2009) and other studies have suggested similar patterns for plant–disperser communities (Cox et al., 1991; Meehan et al., 2002; M. Nogales et al., unpublished data). Moreover, it is common to find native *super-generalist* species (sensu Olesen et al., 2002), i.e., species that interact with a much higher number of mutualists compared to the average in the community. Most known super-generalist island pollinators are bees (e.g. *Xylocopa darwinii* on Galápagos, McMullen, 1993; *Bombus canariensis* on the Canary Islands, Olesen, 1985; *Halictus* sp. on the Azores, Olesen et al., 2002; and *Lasioglossum mahense* on the Mahé, Seychelles, CNKB, unpublished data), but also include a beetle (*Mausoleopsis aldabrensis* on Aldabra, Woodell, 1979), and a gecko (*Phelsuma ornata* on Ile aux Aigrettes, Mauritius, Olesen et al., 2002; Nyhagen et al., 2001). Similarly, some island plants are super-generalist species, being visited by a much higher than average number of flower visitors; examples include *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands (Dupont et al., 2003); *Azorina vidalii* (Campanulaceae), Azores (Olesen et al., 2002), *Psiadia terebinthina* (Asteraceae) and *Aphloia theiformis* (Aphloiaceae), Mauritius (Kaiser, 2006), and *Nephrosperma vanhoutteanum* (Arecaceae), Seychelles (CNKB, unpublished data).

There are unfortunately no similarly detailed studies of community-level insular seed dispersal interactions available. However, it is likely that some insular frugivores should be considered super-generalist seed dispersers. The twin features of ecological release and niche broadening in island vertebrates compared to congeners at mainland sites (Cox and Ricklefs, 1977; Diamond, 1978; Feinsinger et al., 1982; Grant, 1998) have frequently resulted in an

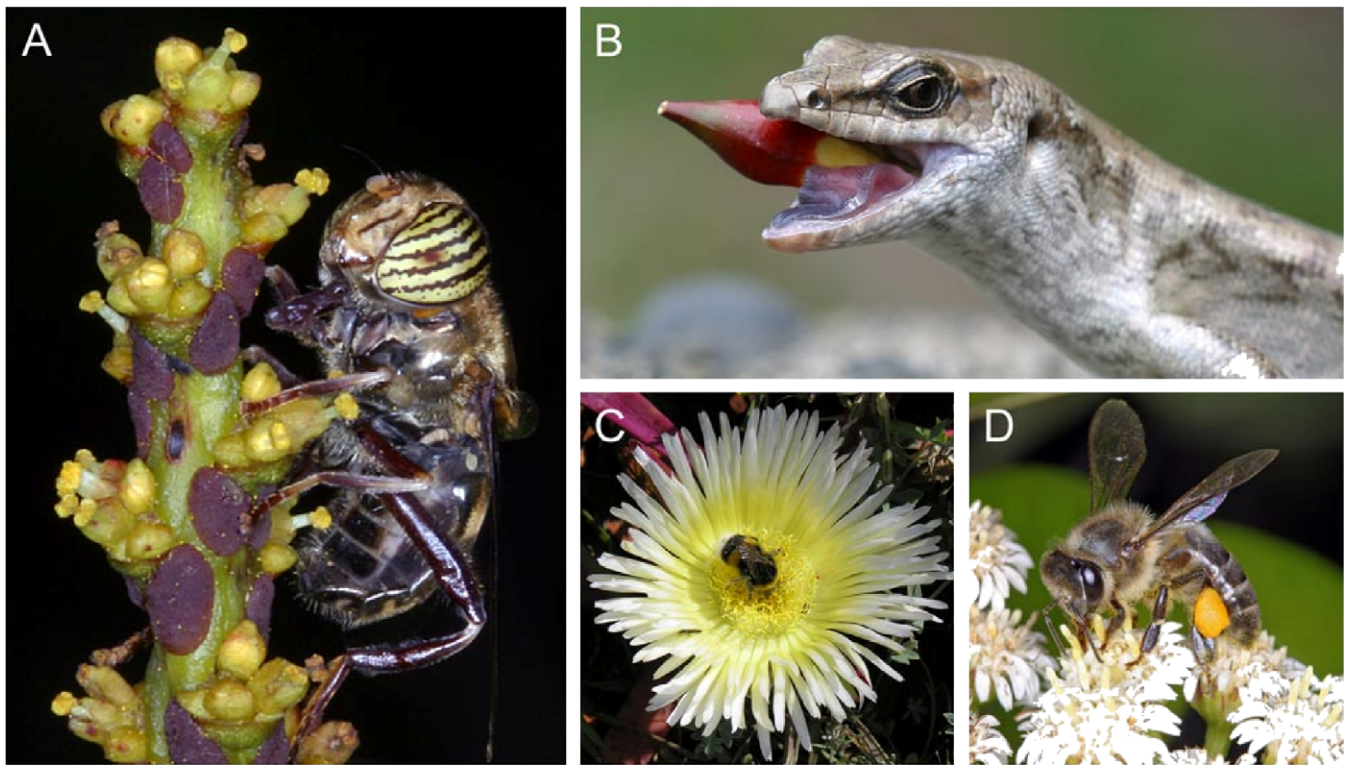


Fig. 1. Plant–animal mutualisms and their threats on oceanic islands. Native plant–animal mutualisms on oceanic islands often include generalised interactions; for example, the generalist hover fly *Eristalinus flaveolus* visiting the small, easily accessible flowers of *Stillingia lineata* (Euphorbiaceae) in Mauritius (A), or the omnivorous skink *Leiolopisma telfairii* eating a drupe of *Pandanus vandermeerschii* (Pandanaceae) on Round Island, Mauritius (B). However, these highly generalised interactions also facilitate invasions of both introduced plants and animals into the native interaction networks. For example, the native *Bombus terrestris* visiting flowers of the introduced *Carpobrotus edulis* (Aizoaceae) on Mallorca, Balearic Islands (C), or an introduced honeybee *Apis mellifera* harvesting pollen of the native *Psidium terebinthina* (Asteraceae) in Mauritius (D).

increase in population density of particular species—an island phenomenon also described as ‘density compensation’ (MacArthur et al., 1972; Rodda et al., 2001; Rodda and Dean-Bradley, 2002). The niche broadening observed in reptiles towards consuming plant material, causing reptiles in turn to serve as effective pollinators and seed dispersers for a variety of plants, is one of the best examples (Fig. 1B; reviewed in Olesen and Valido, 2003). Endemic lizards, for example, often include a great variety of fruits in their diet (e.g. Sáez and Traveset, 1995; Valido and Olesen, 2007; M. Nogales et al., unpublished data). Similarly, shifts in the diet of birds from insects and seeds to nectar and fruits have been described, for example, in the Hawaiian honeycreepers (Ziegler, 2002), the white-eyes in the Indian Ocean (Cheke, 1987; Hansen et al., 2002; Micheneau et al., 2006), and generalised passerines in the Canary Islands (Vogel et al., 1984; Dupont et al., 2004a, 2004b; Valido et al., 2004).

Readjustment of plant reproductive traits

The depauperate and disharmonic fauna on islands implies that upon arrival, for successful establishment, plants that rely on outcrossing will often have to ‘fit’ with some of the few available pollinators. Thus, even though no data are yet available to demonstrate this, plants with generalist syndromes could be expected to have a higher probability of initial establishment than those requiring highly specialized interactions. Otherwise, plant species must often modify their reproductive traits to enter into successful mutualisms with available pollinators and seed dispersers (e.g. Armbruster and Baldwin, 1998). A readjustment in corolla size, for instance, might result from an adaptation to a

new group of floral visitors. Indeed, Inoue et al. (1996) showed that flower size is larger in continental populations of *Campanula* spp. than in populations on the Izu Islands in Japan, corresponding closely to the size of the regional floral visitors (large bumblebees on the continent versus small halictids on the islands) (see also Kobayashi et al., 1997). Similarly, Schueller (2007) showed that island plants of the recently introduced alien species *Nicotiana glauca* have detectably longer corollas and are visited by hummingbirds with longer bills on Santa Catalina and Santa Cruz, two California Channel Islands, compared to plants on the mainland. Another example has been reported from the Juan Fernández Archipelago, where several originally insect-pollinated plant lineages switched to wind- or bird-pollination after arrival, possibly due to the poor insect pollinator fauna (Bernardello et al., 2001). Lastly, floral nectar composition may be a labile trait responding quickly to the presence of general avian pollinators on oceanic islands (e.g. on the Canary Islands: Dupont et al., 2004a, 2004b).

Little is known about the change of seed and fruit traits related to dispersal mechanisms on oceanic islands, but the larger continental island of New Zealand may provide important insights. Here, 70% of the woody species produce fleshy fruits (in comparison to 39% in temperate mainland forest, 39% in Mediterranean shrubland, and 46% in Neotropical dry forest; Jordano, 1992), possibly an adaptation to the dominance of frugivorous bird and lizard species on the islands (Webb and Kelly, 1993). Seed dispersal by lizards has also been linked to the association between shrubs with white and blue fleshy fruits and divaricate growth, small size of diaspores and open habitats in New Zealand (Lord and Marshall, 2001). Although these authors argue that reptiles could have exerted strong selection towards the evolution of small fleshy

fruits with pale colours on the islands (Lord et al., 2002), a recent review found no support for such association of characters as a general pattern (Valido and Olesen, 2007).

Strong disharmony in taxonomical groups of mutualists

A disharmonic flora and fauna refers to the over- and under-representation of certain taxonomic groups on islands compared to neighbouring continental systems. Consequently, one pattern that seems to be general across pollination interactions on islands is the dominance of one or a few taxa in the community and a scarcity or total absence of others, e.g. insect pollinators with long probosces. For instance, hymenopterans, which are the main pollinators on continents, are very rare or even absent on Samoa (Bryan, 1931), Aldabra (Woodell, 1979), and Izu (Inoue, 1993). Similarly, on Galápagos only one pollinating bee has been described, the carpenter bee *Xylocopa darwinii* (McMullen, 1987; Philipp et al., 2006). Hummingbirds, common pollinators on the American continent, are absent from the Galápagos archipelago, although two species of finches and several species of mockingbirds visit the flowers of native and alien plant species (Grant and Grant, 1981; P. Hoek pers. commun.). A disharmony in the pollinator assemblage is also found in Hawaii, where larger bees species are almost absent, native bees are only represented by one genus (but with > 60 spp.), and a few species of sphingids, small moths and flies may dominate the pollinator communities (Howarth and Mull, 1992). In the Izu islands, the number of pollinator species declines with increasing distance to the continent; possible explanations may include dispersal limitations and, in the case of bumblebees, a lack of food provided by plant species on small islands to maintain the colonies (Inoue, 1993). On oceanic islands in general, there is a disproportionately high representation of small insects, which may be due to their greater arrival probability facilitated by strong winds—as suggested by Barrett (1996). Small insects are likely to be generalist pollinators, visiting a large variety of floral shapes and sizes (Barrett, 1996).

The disharmony is also evident in seed disperser guilds, even though fewer studies have investigated these patterns in any detail. There is an obvious absence of large, non-volant frugivorous mammals on oceanic islands and their niche is occupied by comparatively large birds and reptiles similar across islands (Whittaker and Fernández-Palacios, 2007). However, also the composition of avian frugivores on islands tends to differ from continental ones. Several common continental avian frugivore taxa, for example hornbills and toucans, are not found on oceanic islands that instead tend to be dominated by columbid and passerine frugivores.

Past and present threats

Since the first human settlers arrived on remote oceanic islands 2–3 millennia ago, their biotas have undergone three substantial types of anthropogenic modification, namely species extinctions, species introductions (see also Kueffer et al., 2010) and habitat loss, all severely affecting plant–animal mutualisms.

Species extinctions

The ongoing wave of extinction is occurring at an exceptional rate and spatial scale, and has largely been documented for vertebrate species, specifically birds, mammals and large reptiles. There is little direct evidence on the degradation of insect pollination on islands, mainly because before- and after-disturbance

studies are rare. However, there are multiple records of declining insect pollinators worldwide (Allen-Wardell et al., 1998; Kearns et al., 1998; Larsen et al., 2005; Steffan-Dewenter et al., 2005; Biesmeijer et al., 2006), which, supported by available studies from islands, suggest that insect pollinator diversity and abundance may also be declining in many island sites (see also Motala et al., 2007; Gerlach, 2008). For example, insect collections from Mauritius at the beginning of the 20th century recorded a rich butterfly diversity. Ten out of 35 species are now considered extinct, nearly extinct or extremely rare (Davis and Barnes, 1991). It is likely that with the loss of each butterfly species, a number of plants become negatively affected. On Hawaii, 20 out of 60 species of native *Hylaeus* bees, which are important pollinators of many native plants, are considered extremely rare or extinct (Magnacca, 2007). Furthermore, the extinction of one third of the 52 endemic Hawaiian birds was likely a major driver of the extinction of at least 31 plant species in the family Campanulaceae (Cox and Elmqvist, 2000).

The high rate of extinctions and declines within large-bodied frugivores has led to the disruption of seed dispersal mutualisms on many islands. Indeed, many islands have been hit harder than most continental regions in relative terms (Hansen and Galetti, 2009). The disappearance of large frugivores is causing a lower recruitment of plant species with large, fleshy fruits. This has been reported from Tonga (Meehan et al., 2002; McConkey and Drake, 2006), Mauritius (Baider and Florens, 2006; Hansen et al., 2008), Pitcairn Island (Kingston and Waldren, 2005) and has been suggested in the Canary Islands (Valido, 1999).

Compared to extinction rates of animals, plants have suffered relatively fewer extinctions on islands (Sax et al., 2002). However, even though one recent study questions exactly how many island plants have gone extinct (Sax and Gaines, 2008), there is solid evidence that the extinction debt is large and looming. Many island floras are today on the edge of mass extinction, at least in the wild. For example, in Hawai'i, some 50% of native plant species are at risk (Sakai et al., 2002), many of which are down to between one and 50 plants on some of the islands (Burney and Burney, 2007). An even more dire situation faces the flora of Mauritius, where out of 680 native plant species, some 80 are already considered extinct. Another 155 species are critically endangered (with 79 of these known from less than 10 individuals), and 93 species are endangered and 241 vulnerable, making 82% of the native flora and 94% of the endemic flora of Mauritius threatened according to IUCN criteria (Mauritian Wildlife Foundation, unpublished database). How many interactions have been lost is sadly anyone's guess, but doubtlessly a higher number than for species.

Species introductions

While in the past many island species were reduced in population density or brought to extinction by direct, human-driven effects such as hunting and habitat loss, current threats imposed on mutualistic systems on many islands are primarily driven by alien species and their direct and indirect competition for pollination and seed dispersal (plants) and for floral resources and fruits (animals) (e.g. Fritts and Rodda, 1998; Hansen et al., 2002; Traveset and Richardson, 2006; Kaiser et al., 2008). Invasive plants, for example, can compete for mutualistic services with native plants (Fig. 1C; e.g. Aigner, 2004; Moragues and Traveset, 2005; Morales and Traveset, 2009; but see Kaiser-Bunbury and Müller, 2009) and their integration into resident communities can be facilitated by generalist pollinators and dispersers that include nectar and pollen or fleshy fruits in their diets (Morales and Aizen, 2006; Traveset and Richardson, 2006; Aizen et al., 2008;

Linnebjerg et al., 2009). This facilitation is likely to occur frequently in island ecosystems, in which a large number of native mutualists have widened their trophic niches in comparison to that in mainland systems (see earlier section for details). For instance, invasive *Opuntia* cacti on the Canary Islands and the Balearic Islands are pollinated by a variety of native generalist insect species and dispersed also by generalist lizards of the genus *Gallotia* in the Canary Islands and by generalist turtles and mammals in the Balearics (Padrón et al., 2009; Padrón et al., unpublished data). Other species originally from South Africa are highly invasive on many Mediterranean islands. Amongst them are *Carpobrotus* spp. on Mallorca where they are pollinated by a large diversity of native insects that are attracted by their abundant and attractive flowers (Fig. 1C; Moragues and Traveset, 2005).

Many oceanic islands have lost a large proportion of frugivorous bird species, but avian species richness has remained largely unchanged because extinction has been balanced by colonisation and naturalisation of alien bird species (e.g. Sax et al., 2002; Foster and Robinson, 2007). So far, there is little information, however, on whether those alien species act as functional surrogates of and occupy the same frugivorous niches as the extinct native birds. For example, Mandon-Dalger et al. (2004) report that the red-whiskered bulbul on Réunion almost entirely disperses seeds of invasive plant species, while Cole et al. (1995) and Foster and Robinson (2007) show that alien birds can act as reliable dispersers of native understorey shrubs on Hawaii. However, Kelly et al. (2006) found the contribution of alien species to seed dispersal of native plants in New Zealand to be unexpectedly small.

More is known about disruption of plant–pollinator systems by alien species. Examples include native megachilid bees displaced from flowers in Tasmania by alien bumble bees (Hingston and McQuillan, 1999; Hingston et al., 2002), small solitary bees endemic to the Bonin Islands, Japan, displaced by alien honey bees (Kato et al., 1999), and, both in Mauritius, white-eyes displaced by honey bees (Hansen et al., 2002), and endemic geckos displaced by invasive ants (Hansen and Müller, 2009). The Argentine ant *Iridomyrmex humilis*, introduced to Hawaii, significantly reduced the abundance of two important pollinators, the moth *Agrotis* sp. and the solitary bee *Hylaeus volcanica*, with potentially severe negative effects on the seed set of many native plant species (Cole et al., 1992). The most intensively studied alien pollinators are the honey bee *Apis mellifera* and the bumblebee *Bombus terrestris*, both super-generalists and well integrated into the pollinator networks of many invaded island communities on, e.g. Japan (Kato et al., 1999; Abe, 2006; Abe et al., 2008), Tasmania (Hingston et al., 2002), the Mascarene Islands (Fig. 1D; Olesen et al. 2002; Kaiser-Bunbury et al., 2009), the Seychelles (CNKB, unpublished data) and the Canary Islands (Dupont et al., 2004a, 2004b). Such introductions have had devastating effects on native bees (see Goulson, 2003 and reference therein), for example, as a direct result of competition for floral resource (e.g. Kato et al., 1999) or competition for nest sites (e.g. Wenner and Thorp, 1994). Introduced bees can affect plant fitness by actively reducing pollination of native plants (physical interference with native pollinators on the flowers; Gross and Mackay, 1998) or by altering pollen dispersal (e.g. Westerkamp, 1991; Paton, 1993; Celebrezze and Paton, 2004). Hansen et al. (2002) showed experimentally that the exclusion of bird pollinators reduced the seed set of two Mauritian tree species that were otherwise visited primarily by alien honey bees—possibly due to higher levels of within-plant foraging behaviour of honey bees compared to bird pollinators, a pattern also described by Paton (1993). Furthermore, such reduced outcrossing rates mediated by alien bees can result in a reduced gene flow and/or promote hybridization between native plants

(England et al., 2001; Dick et al., 2003). On islands, these detrimental effects are possibly magnified, due to low population sizes, fewer specialized interactions, and/or unpredictability of resources (e.g. Abe, 2006).

Introduced vertebrates are well known to have detrimental effects on the native island flora and fauna (e.g. North et al., 1994; Mack et al., 2000) and thereby affect native mutualisms indirectly (e.g. Campbell and Donald, 2005; Nogales et al., 2004, 2005, 2006; Traveset and Riera, 2005; Kelly et al., 2006; Traveset et al., 2009). The negative impact of, for example, introduced goats, rats and parrots on plant fitness and dispersal can be multifold. It includes the direct consumption of vegetative or reproductive parts of native plants and, more indirectly, the reduction of populations of legitimate seed dispersers (Riera et al., 2002; Traveset and Richardson, 2006). There is evidence that rodents, cats, opossums, and invasive ants—like *Linepithema humilis* or *Wasmannia auropunctata*—have devastating effects on native seed dispersers (e.g. Jourdan et al., 2001; García 2002, Nogales et al., 2004; Kelly et al., 2006; Towns et al., 2006; Hansen and Müller, 2009).

Despite the plentiful evidence that invasive species degrade ecosystems, resulting in changes to the structure and the functioning of the system (Naeem et al., 1994; Cronk and Fuller, 1995; D'Antonio and Dudley, 1995; Callaway et al., 2004), a general synthesis of the impact of invasive species on ecosystem functions remains elusive.

Fragmentation

In the 21st century there is little left on most islands that we could call natural ecosystems. Not only has a lot of habitat been lost, but what remains is often heavily fragmented, even within small islands. Medium-sized fragments of semi-natural habitat remain in inaccessible areas on mountains on individual islands of archipelagos such as Hawaii, Kauai and Maui in the Hawaiian Islands, Mahé and Silhouette in the Seychelles, Réunion in the Mascarenes, Gran Canaria in the Canary Islands, parts of Mallorca in the Balearic Islands, and many small SE Asian and Western Pacific islands, harbouring isolated communities. Island ecosystems have been severely exploited for natural resources, and native habitat has been converted into agricultural and urbanised land. Islands are *per se* small systems with small population sizes, high extinction rates and reduced colonisation rates (metapopulation processes; see Hanski 1994), and fragmentation of island habitats thus results in smaller fragments, which may lead to a disproportional amount of edge effects with small or entirely absent unaffected core areas. While habitat fragmentation may have particularly severe consequences for insular mutualistic interactions, there is little direct evidence. In fragmented mainland systems, plant–pollinator interactions are disrupted by declines in pollinator richness, abundance and composition (see Feinsinger and Aizen, 2003, and references within); both are likely to act in similar or amplified ways in insular settings, partly due to the lower functional redundancy here (Olesen and Jordano, 2002). This is certainly the case for seed dispersers where lower functional redundancy has been highlighted for several island systems (e.g. Traveset and Riera, 2005; McConkey and Drake, 2006; Hansen and Galetti, 2009). Moreover, larger insect pollinators, capable of long-distance pollen dispersal, are under-represented on islands, exacerbating the impact of fragmentation on community-level pollination interactions here. For seed dispersal, there is a tendency towards fewer volant and more ground-dwelling dispersers than in mainland systems, reflected e.g. by the dominance of lizards as seed dispersers on islands (Valido and Olesen, 2007) as well as the presence of large or giant frugivorous tortoises and flightless birds (Worthy et al., 1999;

Hansen and Galetti, 2009). Furthermore, frugivore vertebrates are more likely to become locally extinct in small fragments (Cordeiro and Howe, 2003; Rodríguez-Cabal et al., 2007).

Opportunities and challenges in conservation and restoration of mutualistic interactions

Conservation of island ecosystems benefits greatly from these systems being comparatively simple, with generally smaller and spatially restricted populations. On the other hand, small island states are frequently limited by a lack of financial and human resources as many island groups belong to developing countries (Pelling and Uitto, 2001). Furthermore, these states are small in area and thus cannot afford to set aside relatively large areas for conservation, and human population density is high, resulting in a strong anthropogenic pressure on natural resources (e.g. Gillespie et al., 2008; Caujapé-Castells et al., 2010).

It is advantageous, however, that most islands around the globe encounter similar obstacles with respect to mutualisms, which provides the opportunity to bundle resources and transfer knowledge between islands. To paraphrase Quammen (1996): Islands are unique ecosystems but they are unique in similar ways. Similarities among native insular ecosystems, particularly for taxonomic affinities and derived functional traits, are often greater between islands within archipelagos than between archipelagos within a region, and between archipelagos within a region than between regions. Below, we outline four areas where we present and discuss options and ideas that highlight the opportunities and challenges pertaining to the conservation and restoration of mutualistic interactions. Those areas are based on the three groups of trait similarities between island mutualisms outlined earlier and, most importantly, refer directly to the conservation goals which (1) ensure functional levels of vital native mutualisms, (2) enhance the diversity of species interactions, and (3) restore completely or partially lost groups of mutualistic interactions. Furthermore, inherent to each area is the potential for addressing broad ecological and evolutionary questions, a few examples of which we highlight.

The network approach: basis for restoration and conservation of mutualistic interactions

Mutualistic networks describe plant–animal interactions on a community level, and the use of such an approach in conservation and restoration of pollination and seed dispersal interactions is particularly useful on islands due to the simplicity of ecosystems. Insights gained through an increasing number of mutualistic networks from islands encompass similar interaction patterns at the guild- or ecosystem-level between island groups, providing opportunities for the restoration of such interactions on the community level.

Pollination networks on islands, for example, are often generalised systems where many open and easily accessible flowers are predominately pollinated by flies and beetles, with few bee pollinators (Anderson et al., 2001; Rathcke, 2001), and mostly diverse in vertebrate pollinators, including birds and lizards (Traveset and Sáez, 1997; Dupont et al., 2003; Kaiser-Bunbury et al., 2009). With the high degree of generalisation most island pollination networks show a dominance of asymmetric interactions, which suggest high redundancy and resilience to perturbations (Bascompte et al., 2006). Asymmetric interactions describe links between specialist and generalist species, and they are common in networks that are generally small, have a core of highly generalised species, and are therefore able to provide

stable interaction partners to rare specialists (Olesen et al., 2002; Bascompte et al., 2003; Dupont et al., 2003; Kaiser, 2006; Kaiser-Bunbury et al., 2009). However, this also means that any loss of the relatively few highly generalised pollinators may result in a subsequent sharp decline of plant diversity (see Memmott et al., 2004). Thus, a primary mission of conservation should be to identify and manage or restore species that interact strongly with others (Jackson et al., 2001; Dupont et al., 2003), also described as keystone mutualists (Gilbert, 1980). For example, Cox and Elmquist (2000) reviewed the loss of pollinator species on Pacific Ocean Islands, and found that such losses can reduce plant reproductive success (e.g. Jennersten, 1988), or result in a complete breakdown of breeding systems (e.g. Washitani, 1996).

For insular seed dispersal networks, due to the great isolation of many oceanic islands and the restricted dispersal ability of vertebrates compared to small invertebrates, pristine seed dispersal communities consisted of few vertebrate frugivores. In the western Indian Ocean, for example, Mauritius used to harbour 23 mostly or partly frugivorous bird, reptile and mammal species, Réunion had 16, Rodrigues 11, the granitic Seychelles islands 14, and similar numbers were found on the other side of Africa, on the Canary islands, with Tenerife harbouring 14 and La Palma 12 species. The high rate of extinctions has affected most of these communities, sometimes literally decimating their number of frugivore species. For example, on Rodrigues only one native frugivore, the Rodrigues fruitbat *Pteropus rodricensis*, remains. Thus, extant seed dispersal networks can be obtained with little effort. In fact, the simplicity of species pools should make it easier to restore lost dynamics in dysfunctional insular networks because you need to restore proportionally fewer nodes to achieve a relatively high number of restored links. However, as a result of high levels of endemism on islands, the loss of a keystone species on one island is often global. There is therefore a pressing need to consider alien species to replace missing native nodes (see below). Furthermore, network studies are a useful tool to assess potential positive and negative consequences of introducing alien species to mutualistic interactions and ecosystems in general (Henneman and Memmott, 2001; Memmott and Waser, 2002).

One major challenge in contemporary mutualistic network studies is to adequately capture and describe spatial and temporal dynamics (Bascompte and Jordano, 2007; Olesen et al., 2008; Tylianakis, 2008). Studies from mainland plant–pollinator communities have shown that within- and between-year variation in species richness and abundance can fluctuate strongly (Herrera, 1988; Alarcón et al., 2008; Petanidou et al., 2008). To our knowledge, only one study recently compared temporal variation between mainland and island pollination networks, suggesting that island and mainland system are similar in their degree of species and interaction turnover (Dupont et al., 2009). However, the authors note that the available data may be insufficient to draw strong conclusions due to sampling effects. We propose that island ecosystems are ideally suited to advance our understanding in these areas given their relatively low species richness. Here, species pools may change less over time within and between seasons, especially for seed dispersers as, for instance, most frugivorous birds on oceanic islands are not migratory like they are in many mainland ecosystems (e.g. columbids and passerines). However, for islands with a high altitudinal range, some animal mutualists may migrate more-or-less seasonally between upland and lowland habitats (e.g. giant tortoises on some Galapagos islands; birds in Hawaii). Overall, analyses of island mutualistic networks should therefore be minimally constrained by between-season species turnover (Herrera, 1988; Cane and Payne, 1993).



Fig. 2. Restoration of plant–animal mutualisms on oceanic islands. Options for restoring native pollination and seed dispersal interactions are manifold. They include weeding or eradicating alien invasive species, as well as actively facilitating increases in populations of native species, or even replacing extinct species with taxon substitutes. For example, while manual weeding of introduced and invasive plant species in restoration areas in Mauritius creates a lot of initial disturbance (A; compare right-hand side, weeded area with left-hand side, unweeded area), it rapidly results in an increase in interactions between native plants and native flower visitors, compared to non-weeded areas (Kaiser-Bunbury et al., 2009). On extremely degraded islands, such as Rodrigues in the Indian Ocean, another option is to recreate native habitats from scratch. Here, in the Francois Leguat Reserve, some 100,000 native seedlings have been planted in 2007 (B). In another conservation area on Rodrigues, Grande Montagne, similar plantings in 1998 have already resulted in a low forest of 3–6 m in height (C), with many plants already flowering and producing fruits. A next logical step would be to rewild such habitats with taxon substitutions, replacing extinct endemic frugivores with extant analogues, for example Aldabra giant tortoises *Aldabrachelys gigantea* to replace the two extinct *Cylindraspis* giant tortoises (D).

Mutualistic interactions as biodiversity monitoring tools

The conventional methods of biodiversity monitoring focus on species numbers and population sizes (e.g. Yoccoz et al., 2001; Marsh and Trenham, 2008). One reason may be that species richness and populations are simply easier to quantify than ecological interactions. However, to more fully encapsulate ecosystem health it is pivotal to monitor changes to the underlying biostructure instead of only monitoring species diversity patterns (McCann, 2007). We here argue that plant–pollinator interactions, specifically flower visitation rates and the resulting reproductive success of plants, represent a comprehensible and easily quantifiable way of monitoring a vital part of the biostructure of an ecosystem. Alternatively, determining pollen limitation is a suitable method to monitor pollination effectiveness, and it can

easily be demonstrated empirically when supplemental pollination of flowers increases their seed and fruit set compared to open-pollinated controls. Combining the monitoring of the interactions themselves and their outcome, i.e., seed production and dispersal, allows us to identify conservation targets and prioritise restoration efforts towards system-relevant species or species groups, even during ongoing habitat restoration projects (see Fig. 2A).

Moreover, interactions are likely more sensitive to changes. While species may continue to persist for a long time, and thus remain in an ecosystem's species inventory, interactions and their strength within an ecosystem may respond faster to changes (e.g. Kaiser, 2006; Morales and Aizen, 2006; Aizen et al., 2008; CNKB unpublished data). To identify and apply conservation measures before species extinction has set in, we need to develop tools that detect early stages of changes to an ecosystem and that do not

rely on slow-responding indicators such as species diversity. Potential problems detected by observing major shifts in interaction strength and identity can be addressed more swiftly because the participant species are still present in the system. Ideally, this would be accomplished by regular re-sampling of entire communities. Achieving this level of detail on a regular basis, however, is in most cases impossible. This is almost certainly the case when omnibus surveillance monitoring is applied, i.e. monitoring that is not guided by *a priori* hypotheses (Nichols and Williams, 2006). Contrary to such an *ad-hoc* approach, it is comparatively easy to establish *a priori* hypotheses and to collect fine-scale data about the structure of focal species interactions instead of species lists (see Hansen et al., 2008; Kaiser et al., 2008). In addition, interaction monitoring on islands is facilitated by the simplicity (i.e. generalised plants and pollinators, disharmonic taxonomical groups) of the systems. Specifically, as mentioned above, island pollinator and seed dispersal communities potentially show higher seasonal and annual consistency in species composition and abundance, an island characteristic which requires further investigation. Thus, resulting interaction networks would display higher interaction consistency than communities on mainland sites, many of which show high temporal variation (Herrera, 1988; Willson and Whelan, 1993; Jordano, 1994; Elberling and Olesen, 1999; Alarcón et al., 2008; Petanidou et al., 2008). Thus, interaction monitoring on islands should be able to rapidly detect phenological uncoupling and spatial mismatches between mutualists.

To conclude, targeted monitoring of mutualistic interactions is ideally suited to further our ecological understanding on how common threats to island biodiversity modify ecosystem structure.

Pollination or seed dispersal: setting priorities

Both pollination and seed dispersal interactions may require restoration in degraded island ecosystems. Depending on the context, priorities may differ. Here, we discuss the reasoning behind prioritising restoration of pollination or seed dispersal interactions, and outline the opportunities of combined efforts.

Pollination on islands is dominated by invertebrates, while seed dispersal is largely carried out by vertebrates. As the requirements and life cycles of these taxa operate on very different spatial and temporal scales, restoration that addresses pollination does not necessarily create favourable conditions for maintaining native seed dispersal interactions, and vice versa. Given the resource and space limitations on islands, restoring pollination interactions in small habitat patches may be more easily achieved than restoring the integrity of seed dispersal interactions. For example, recent experimental evidence has shown that Janzen-Connell patterns, i.e., a disproportionately large negative effect on progeny close to maternal trees caused by host-specific seed predators, seedling herbivores or pathogens, act strongly in present-day island ecosystems (Hansen et al., 2008), with further indirect evidence from other islands (Galapagos: Clark and Clark, 1981; Pacific islands: Lee, 1985; Wiles et al., 1996; and Canary Islands: Arévalo and Fernández-Palacios, 2003). Seeds therefore may often require dispersal within fairly large habitats of sufficient quality for successful establishment and growth. Since vertebrate frugivores have substantially larger minimum habitat size requirements than invertebrate pollinators, many restoration areas on islands are too small to maintain self-sustaining resident seed disperser populations. It may be possible, though, with minimal husbandry to maintain resident or semi-resident populations of seed-dispersing vertebrates in larger habitats (e.g. giant tortoises on Cousine Island, Seychelles;

Samways et al., 2009; on Round Island and Ile aux Aigrettes, Mauritius, Griffiths et al., *in press*). Resurrecting thus at least part of the lost mutualisms, if not quite achieving self-sustaining mutualist animal populations, is in our point of view preferable to more heavy-handed human-driven management. Furthermore, one advantage of focusing on the restoration of plant–vertebrate interactions is the comparatively larger availability of vertebrate conservation- and restoration-related information.

Conservation and restoration priorities on islands are inherently idiosyncratic and it may not always be possible to address pollination and seed dispersal when restoring a habitat. Although both interactions are vital parts to plant reproduction, there is a necessary priority towards restoring pollination dynamics if fruit set is low due to pollinator limitation (quantity of pollination). The quality of pollination is partly dependent on the genetic diversity within a plant population, i.e. generally speaking with an increase in population size one would expect an increase in genetic diversity (Frankham, 1996; Hedrick, 2001; Ouborg et al., 2006) and in the diversity of pollinators visiting the plant. If restoration aims to restore quality of pollination more than quantity of pollination, seed dispersal and pollination can be addressed simultaneously. In this case, restoration of dispersal interactions would lead to an increase in plant population size, which could consequently result in a larger genetic diversity and higher quality pollination services, if both sufficient genetic diversity and pollinators are still present within the island.

Overall, a positive outcome of restoration is more easily achieved for pollination interactions on a smaller spatial scale, in a shorter time period, and with an increased likelihood of creating higher functional integrity (i.e. a combination of the conservation goals described above) in plant–pollinator communities, than for restoring plant–disperser interactions. This is especially true when considering the predominately generalised nature of interactions and the disproportionate role of certain groups of pollinators in insular systems, which allows conservationists to focus on a few core groups for maximum conservation value. In the medium- to long-term, however, restoration has to tackle both pollination and seed dispersal interactions to avoid genetic deterioration of the plant community. Small populations of restored plant species will maintain relatively little genetic diversity, which reduces the chance of successful adaptation to small- or large-scale alterations such as e.g. climate change. Hence, in a second step, large-scale restoration needs to be carried out to account for seed dispersal interactions to eventually result in reproductively self-sustaining communities.

Alien invasive species and mutualistic interactions

Alien species and their invasion into new habitats are most commonly perceived as detrimental to native species. However, depending on the level of invasion and degree of degradation, the presence of alien species in insular habitats may also have facilitative effects, particularly on ecosystem processes such as mutualistic interactions. In the following two sections we discuss the potential role of alien mutualists in native, degraded habitats and highlight their potential for restoring island ecosystems.

Recent studies have shown that alien species may integrate substantially in native mutualistic networks (Memmott and Waser, 2002; Olesen et al., 2002; Morales and Aizen, 2006; Lopezaraiza-Mikel et al., 2007). While alien species increase their number and strength of links within the network, which can ultimately result in the disconnection of natives from the network, many network parameters such as connectivity, nestedness, level of asymmetry, compartmentalization, and modularity remain largely unaffected by the presence of invasive species

(Aizen et al., 2008; CNKB, unpublished data; but see Bartomeus et al., 2008). A less ambiguous pattern may be revealed by analyzing shifts in dependence strength or quantitative evenness between mutualistic partners during invasion processes, patterns that were shown by Tylianakis et al. (2007) in antagonistic host–parasitoid networks.

In contrast to evidence provided by network analysis, we have highlighted how “single-species” studies (see earlier section “Species introductions”) demonstrate that alien species can interfere with native mutualistic interactions (Fig. 1C and D). This suggests that, although individual alien invasive species may have a negative impact on one or several native mutualistic interactions, their effect on the overall community may be neutral or even positive with regards to the outcome of mutualistic interactions. For example, in some heavily degraded island systems honey bees may step in as pollinators of native species and thus contribute positively to the native plant fitness. In Mauritius, honey bees were the major flower visitors of 43 out of 74 plant species (58%) in a weeded conservation management area (Fig. 2A; Kaiser, 2006), and, in addition to substituting native pollinators in the system, they are potentially important for the reproductive success of these native plants. While studies on the role of alien invertebrate pollinators draw variable conclusions, island systems are ideally suited to contribute further evidence from differently degraded systems to advance our understanding of these processes. Similarly, the following section advances the idea of using alien species as a management tool as they could provide beneficial interactions to systems where native mutualists have disappeared.

Rewilding, a current controversial issue in conservation biology: islands at the forefront again?

Work on islands has contributed significantly to advances in modern conservation and restoration, and many techniques and methods were pioneered and developed here, particularly in subjects such as single-species conservation and eradication of alien species (Townsend et al., 1990; Veitch and Clout, 2002).

A recently developed, but highly controversial, concept for restoration is to rewild ecosystems by introducing extant species, taxon substitutions, as functional replacements or ecological analogues for extinct native species. Rewilding with taxon substitutions has been proposed for several continents and continental islands (Mauritius: Jones 2002; Hansen et al., 2008; Griffiths et al., in press; New Zealand: Atkinson, 1988; Madagascar: Burney, 2003; South America: Galetti, 2004; Siberia: Zimov, 2005; North America: Donlan et al., 2005; Martin, 2005; Donlan et al., 2006), especially where the focal extinct native species were keystone or ecosystem engineer species (e.g. Griffiths et al., in press). However, the use of functional but alien substitute species is a controversial issue, with several scientists arguing caution (Caro, 2007), or being in direct opposition (Cajal and Tonni, 2006; Rubenstein et al., 2006), so comparison between native and alien functional traits (e.g. Kueffer et al., 2009) may thus be required to assess the substitutes' impact on the ecosystem. It is clear, however, that the rewilding approach has the potential to excite the public (and funding agencies) about conservation in general, as it transcends the all-too-familiar ‘doom and gloom’ scenarios that are otherwise prevalent when conservation scientists and professionals communicate with the public (Donlan et al., 2006; Nicholls, 2006; Stolzenburg, 2006).

The implementation of rewilding projects was originally suggested and discussed for large-scale continental scenarios—which also partly explains their controversial nature. A major current roadblock to objective discussion of the applicability of rewilding is a lack of broad empirical evaluation of methods and

outcomes. We believe that highly degraded island ecosystems offer some of the most well-suited scenarios for smaller scale, rapid implementation and evaluation of rewilding projects, especially in relation to plant–animal interactions. In particular, because many island ecosystems have only little to lose and a lot to gain. That is, ironic as it may sound, some of the most devastated island ecosystems may offer the best prospects for being turned into frontrunners for the development of restoration and conservation practices of the future. This is simply because the most badly afflicted islands and islets have already suffered so much extinction, invasion and degradation that almost any action will lead to an improvement in ecosystem function. Indeed, such sentiments were recently reflected in Burney and Burney (2007), who stated that “The Hawaiian Islands are ripe for new conservation ideas ... the situation there is dire.” Or, even more forcefully, as the poetic words ascribed to conservation biologist Richard Lewis in Douglas Adam's book ‘Last chance to see’ put it in the case of Mauritius: “Everything that shouldn't be done to an island has been done to Mauritius. Except, perhaps, nuclear testing” (Adams and Carwardine, 1990, p. 188).

Among the first questions to ask in any rewilding project is which extant species to use, and which criteria (e.g. relatedness, ecology, functional traits, behaviour) to use when selecting them (Nicholls, 2006). On islands, in relation to rewilding projects in continental areas, the planning phase often has a critical advantage: the history of extinction and loss is comparatively recent, and has been well documented for some islands (e.g. Seychelles: Stoddart, 1984; Lord Howe Islands: Hutton et al., 2007; Mauritius: Cheke and Hume, 2008).

Good examples of potential taxon substitution projects with animal mutualists include the pigeon *Hemiphysalis novaeseelandiae* from mainland New Zealand to Norfolk Island, the pollinating and seed-dispersing bellbird *Anthornis melanura* from New Zealand to the Chatham Islands (Atkinson, 1988), or bulbuls (*Hypsipetes*; Jones, 2008) and blue pigeons (*Alectroenas*) between islands in the western Indian Ocean. Insular tortoise taxon substitutions also hold great promise. For example, the proposed intra-archipelago introductions of replacements for extinct tortoises on some of the Galapagos islands (Hamann, 1993).

In fact, some current projects already utilise taxon substitutions in restoration projects: In the western Indian Ocean, two extant species of large and giant tortoises (*Astrochelys radiata* and *Aldabrachelys gigantea*) are used as replacements for four extinct species of giant tortoises from the genus *Cylindraspis*. In Mauritius, as part of ongoing large-scale restoration projects, these tortoise species have been introduced to two islets, Ile aux Aigrettes (*A. gigantea* only) and Round Island (*A. gigantea* and *A. radiata*) (Griffiths et al., in press; Jones, 2008). In Rodrigues, both *A. gigantea* and *A. radiata* are used as analogues in an ecotourism and ecosystem restoration project, with great potential for additional future projects (See Fig. 2B–D; Weaver and Griffiths, 2008).

An important common feature in the abovementioned species and examples is that they are all vertebrates. This is simply because our understanding of insect conservation—and even more so for insect restoration—is much less developed than for vertebrates (e.g. Seddon et al., 2005), especially so on islands (Motala et al., 2007; Gerlach, 2008). For example, a recent special issue of Journal of Insect Conservation, dealing with conservation of island insects (New, 2008), contains only two papers dealing specifically with translocation of insect species as a conservation tool—both on giant weta species in New Zealand (Stringer and Chappell, 2008; Watts et al., 2008), which, admittedly, are also seed dispersers (Duthie et al., 2006).

Similarly, very few proposed rewilding projects on islands are specifically aiming at replacing extinct plant species with similar

extant ones—and none of these projects seem to have resurrection of lost interactions as the main goal of such substitutions. One example is from Lord Howe Island, where Hutton et al. (2007) suggest replacing the extinct plant *Solanum bauerianum* species with the widespread Pacific species *S. viride*. However, comparatively few plants are known to have gone extinct on oceanic islands (Sax and Gaines, 2008), and the chronically limited conservation funds are probably better applied to boosting population sizes of extant endangered native and endemic species.

Overall, rewilding offers hope of restoring regeneration dynamics in even some of the most devastated island ecosystems. Indeed, there is a growing interest in re-building native ecosystems in areas where few if any native plants or animals remain, or even in abandoned agricultural land. One example comes from some Hawaiian islands, where this kind of ‘inter-situ’ plant conservation is rapidly recreating native plant communities of several hectares in size (Burney and Burney, 2007). Another example is found on the island of Rodrigues in a restoration project in the Grande Montagne reserve, where today, 10 years after planting, several hectares of 5–6 m tall native forest have replaced the formerly dense, monospecific stands of invasive *Syzygium jambos* trees (Fig. 2C; Cheke and Hume, 2008; CNKB and DMH, pers. obs.). Both of these projects already now offer suitable habitats that could be used in animal rewilding projects, particularly for generalised herbivores and frugivores. Similarly encouraging early results come from Cousine Island, Seychelles, where native plant species have formed a canopy only 10 years after planting—replacing what used to be almost entirely alien plants (Samways et al., 2009).

Lastly, even though it is not an oceanic island, the restoration of the heavily human-modified Mana Island, New Zealand (Timmins et al., 1987; Miskelly, 1999), may offer many valuable lessons for similar projects on oceanic islands. For example, on this island, introduced European starlings and endemic geckos are already providing valuable seed dispersal of native plant species being restored (Ferguson and Drake, 1999), suggesting that an early addition of generalised frugivores to an otherwise frugivore-empty ecosystem under restoration may be desirable.

To conclude, rewilding projects on islands offer unique opportunities to advance our understanding of basic ecological processes, particularly in the fields of ecological networks, community assembly and colonisation. We would thus encourage any such projects to go beyond a simple ‘all-or-nothing’ approach, and plan and execute projects in a way that maximizes basic scientific as well as applied management outputs.

Conclusion

We have highlighted the importance and suitability of pollination and seed dispersal interactions for understanding and advancing of ecology, conservation, and restoration in oceanic island ecosystems. The restoration of species without knowledge of their interactions neglects the pivotal role of these dynamics. For instance, habitat restoration that focuses on replanting of native trees runs the risk of creating “just ‘plant communities’” (Atkinson, 1988), i.e., a botanical garden requiring continuous human management (see Fig. 2). We propose that island conservation and restoration programmes that aim, for example, to meet the CBD targets of achieving a significant reduction in the current rate of biodiversity loss should prioritise the monitoring of ecological interactions as an indicator of biodiversity change. Ideally, scientists and organisations should work towards designing and implementing standardised monitoring schemes of mutualistic interactions that are compatible both within the

same archipelago as well as between regions. Instead of “reinventing the wheel” in battling threats to ecological interactions, what is needed is a platform that facilitates rapid and timely exchange and dissemination of lessons learned on the conservation and restoration of native mutualistic interactions, freed from the constraints of peer-reviewed publication.

We have argued that mutualistic interactions are inherently suitable for inter-island comparisons despite idiosyncrasies between islands. These interactions provide the opportunity to fruitfully combine natural science with applied conservation and restoration, a combination that often is deemed incompatible. Most importantly, during all stages of conservation and restoration, i.e. planning, implementation, and monitoring, the outcomes of such efforts need to be immediately and widely disseminated between islands, ideally at all geographical levels.

Acknowledgements

We would like to thank the editors of this Special Issue who invited us to participate and to C. Kueffer and two anonymous reviewers for constructive comments on earlier versions of the manuscript. CNKB thanks the Swiss National Science Foundation (PBZHA3-117022) and J. Ghazoul at the ETH Zurich for funding and support. AT thanks the Spanish Ministry of Education and Science for financing a project on mutualistic networks on islands (project CGL2007-61165/BOS) and Manuel Nogales for sending his unpublished manuscript. DMH thanks the Velux Foundation (Project #442) for funding.

References

- Abe, T., 2006. Threatened pollination systems in native flora of the Ogasawara (Bonin) Islands. *Ann. Bot.* 98, 317–334.
- Abe, T., Makino, S.I., Okochi, I., 2008. Why have endemic pollinators declined on the Ogasawara Islands? *Biodiv. Conserv.* 17, 1465–1473.
- Adams, D., Carwardine, M., 1990. In: *Last Chance to See*. William Heinemann Ltd., London, pp. 208.
- Aigner, P.A., 2004. Ecological and genetic effects on demographic processes: pollination, clonality and seed production in *Dithyrea maritima*. *Biol. Conserv.* 116, 27–34.
- Aizen, M.A., Morales, C.L., Morales, J.M., 2008. Invasive mutualists erode native pollination webs. *PLoS Biol.* 6, 396–403.
- Alarcón, R., Waser, N.M., Ollerton, J., 2008. Year-to-year variation in the topology of a plant–pollinator interaction network. *Oikos* 117, 1796–1807.
- Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J., Cox, P.A., Dalton, V., Feinsinger, P., Ingram, M., Inouye, D., Jones, C.E., Kennedy, K., Kevan, P., Koopowitz, H., Medellin, R., Medellin-Morales, S., Nabhan, G.P., Pavlik, B., Tepedino, V., Torchio, P., Walker, S., 1998. The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conserv. Biol.* 12, 8–17.
- Anderson, G.J., Bernardello, G., Stuessy, T.F., Crawford, D.J., 2001. Breeding system and pollination of selected plants endemic to Juan Fernandez Islands. *Am. J. Bot.* 88, 220–233.
- Anderson, S.H., 2003. The relative importance of birds and insects as pollinators of the New Zealand flora. *N.Z. J. Ecol.* 27, 83–94.
- Arévalo, J.R., Fernández-Palacios, J.M., 2003. Spatial patterns of trees and juveniles in a laurel forest of Tenerife, Canary Islands. *Plant Ecol.* 165, 1–10.
- Armbruster, W.S., Baldwin, B.G., 1998. Switch from specialized to generalized pollination. *Nature* 394, 632.
- Atkinson, I.A.E., 1988. Opportunities for ecological restoration. *N.Z. J. Ecol.* 11, 1–12.
- Baider, C., Florens, F.B.V., 2006. Current decline of the “Dodo Tree”: a case of broken-down interactions with extinct species or the result of new interactions with alien invaders? In: Laurance, W.F., Peres, C.A. (Eds.), *Emerging Threats to Tropical Forests*. Chicago University Press, Chicago, pp. 199–214.
- Barrett, S.C.H., 1996. The reproductive biology and genetics of island plants. *Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci.* 351, 725–733.
- Bartomeus, I., Vilà, M., Santamaría, L., 2008. Contrasting effects of invasive plants in plant–pollinator networks. *Oecologia* 155, 761–770.
- Bascompte, J., Jordano, P., 2007. Plant–animal mutualistic networks: the architecture of biodiversity. *Annu. Rev. Ecol. Syst.* 38, 567–593.
- Bascompte, J., Jordano, P., Melian, C.J., Olesen, J.M., 2003. The nested assembly of plant–animal mutualistic networks. *Proc. Natl. Acad. Sci. USA* 100, 9383–9387.
- Bascompte, J., Jordano, P., Olesen, J.M., 2006. Asymmetric coevolutionary networks facilitate biodiversity maintenance. *Science* 312, 431–433.

- Berglund, H., Järemo, J., Bengtsson, G., 2009. Endemism predicts intrinsic vulnerability to nonindigenous species on islands. *Am. Nat.* 174, 94–101.
- Bernardello, G., Anderson, G.J., Stuessy, T.F., Crawford, D.J., 2001. A survey of floral traits, breeding systems, floral visitors, and pollination systems of the angiosperms of the Juan Fernandez Islands (Chile). *Bot. Rev.* 67, 255–308.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M., Ohlemüller, R., Edwards, M., Peeters, T., Schaffers, A.P., Potts, S.G., Kleukers, R., Thomas, C.D., Settele, J., Kunin, W.E., 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313, 351–354.
- Bolger, D.T., Alberts, A.C., Soule, M.E., 1991. Occurrence patterns of bird species in habitat fragments—sampling, extinction, and nested species subsets. *Am. Nat.* 137, 155–166.
- Bond, W.J., 1994. Do mutualisms matter—assessing the impact of pollinator and disperser disruption on plant extinction. *Philos. Trans. R. Soc. Lond. Ser. B-Biol. Sci.* 344, 83–90.
- Bryan, E.H., 1931. Insects of Samoa: a review. *Proc. Hawaiian Entomol. Soc.* 7, 445–451.
- Buchmann, S.L., Nabhan, G.P., 1996. In: *The Forgotten Pollinators*. Island Press, Washington, DC.
- Burney, D.A., 2003. Madagascar's prehistoric ecosystems. In: Goodman, S., Benstead, J. (Eds.), *The Natural History of Madagascar*. University of Chicago Press, Chicago, pp. 47–51.
- Burney, D.A., Burney, L.P., 2007. Paleocology and “inter-situ” restoration on Kaua’i, Hawai’i. *Frontiers Ecol. Environ.* 5, 483–490.
- Cajal, J.L., Tonni, E.P., 2006. Re-wilding in South America: is it possible? *Mastozoöl. Neotropical* 13, 281–282.
- Callaway, R.M., Thelen, G.C., Rodriguez, A., Holben, W.E., 2004. Soil biota and alien plant invasion. *Nature* 427, 731–733.
- Campbell, K., Donald, C.J., 2005. Feral goat eradication on islands. *Conserv. Biol.* 19, 1369–1374.
- Cane, J.H., Payne, J.A., 1993. Regional, annual, and seasonal variation in pollinator guilds: intrinsic traits of bees (Hymenoptera: Apoidea) underlie their patterns of abundance at *Vaccinium ashei* (Ericaceae). *Ann. Entomol. Soc. Am.* 86, 577–588.
- Caro, T., 2007. The Pleistocene re-wilding gambit. *Trends Ecol. Evol.* 22, 281–283.
- 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., Gomes, I., Kueffer, C., 2010. Conservation of oceanic island floras: present and future global challenges. *Perspect. Plant Ecol. Evol. Syst.* 12, 107–129.
- Celebrezze, T., Paton, D.C., 2004. Do introduced honeybees (*Apis mellifera*, Hymenoptera) provide full pollination service to bird-adapted Australian plants with small flowers? An experimental study of *Brachyloma ericoides* (Epacridaceae). *Aust. Ecol.* 29, 129–136.
- Cheke, A.S., 1987. The ecology of the smaller land birds of Mauritius. In: Diamond, A.W. (Ed.), *Studies of Mascarene Island Birds*. Cambridge University Press, Cambridge, pp. 151–207.
- Cheke, A.S., Hume, J.P., 2008. In: *Lost Land of the Dodo*. Christopher Helm, London, pp. 464.
- Clark, D.A., Clark, D.B., 1981. Effects of seed dispersal by animals on the regeneration of *Bursera graveolens* (Burseraceae) on Santa Fe Island. *Galápagos. Oecol.* 49, 73–75.
- Cole, F.R., Loope, L.L., Medeiros, A.C., Raikes, J.A., Wood, C.S., 1995. Conservation implications of introduced game birds in high-elevation Hawaiian shrubland. *Conserv. Biol.* 9, 306–313.
- Cole, F.R., Medeiros, A.C., Loope, L.L., Zuehlke, W.W., 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology* 73, 1313–1322.
- Cordeiro, N.J., Howe, H.F., 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proc. Natl. Acad. Sci. USA* 100, 14052–14056.
- Cox, G.W., Ricklefs, R.E., 1977. Species-diversity and ecological release in Caribbean land bird faunas. *Oikos* 28, 113–122.
- Cox, P.A., Elmqvist, T., 2000. Pollinator extinction in the Pacific Islands. *Conserv. Biol.* 14, 1237–1239.
- Cox, P.A., Elmqvist, T., Pierson, E.D., Rainey, W.E., 1991. Flying foxes as strong interactors in South-Pacific island ecosystems—a conservation hypothesis. *Conserv. Biol.* 5, 448–454.
- Cronk, Q.C.B., Fuller, J.L., 1995. In: *Plant Invaders: the Threat to Natural Ecosystems*. Chapman & Hall, London, pp. 241.
- D’Antonio, C.M., Dudley, T.L., 1995. Biological invasions as agents of change on islands versus mainland. In: Vitousek, P.M., Loope, L.L., Adersen, H. (Eds.), *Islands: Biological Diversity and Ecosystem Functions*. Springer, Heidelberg, pp. 103–117.
- Davis, P.M.H., Barnes, M.J.C., 1991. The butterflies of Mauritius. *J. Res. Lepid.* 30, 145–161.
- Diamond, J.M., 1978. Niche shifts and rediscovery of interspecific competition. *Am. Sci.* 66, 322–331.
- Dick, C.W., Etchelecu, G., Austerlitz, F., 2003. Pollen dispersal of tropical trees (*Dinizia excelsa*: Fabaceae) by native insects and African honeybees in pristine and fragmented Amazonian rainforest. *Mol. Ecol.* 12, 753–764.
- 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., Greene, H.W., 2006. Pleistocene rewilding: an optimistic agenda for twenty-first century conservation. *Am. Nat.* 168, 660–681.
- Donlan, C.J., Greene, H.W., Berger, J., Bock, C.E., Bock, J.H., Burney, D.A., Estes, J.A., Foreman, D., Matrin, P.S., Roemer, G.W., Smith, F.A., Soule, M.E., 2005. Rewilding North America. *Nature* 436, 913–914.
- Dupont, Y.L., Hansen, D.M., Olesen, J.M., 2003. Structure of a plant–flower–visitor network in the high-altitude sub-alpine desert of Tenerife, Canary Islands. *Ecography* 26, 301–310.
- Dupont, Y.L., Hansen, D.M., Rasmussen, J.T., Olesen, J.M., 2004a. Evolutionary changes in nectar sugar composition associated with switches between bird and insect pollination: the Canarian bird–flower element revisited. *Funct. Ecol.* 18, 670–676.
- Dupont, Y.L., Hansen, D.M., Valido, A., Olesen, J.M., 2004b. Impact of introduced honey bees on native pollination of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. *Biol. Conserv.* 118, 301–311.
- Dupont, Y.L., Padrón, B., Olesen, J.M., Petanidou, T., 2009. Spatio-temporal variation in the structure of pollination networks. *Oikos* 118, 1261–1269.
- Duthie, C., Gibbs, G., Burns, K.C., 2006. Seed dispersal by Weta. *Science* 311, 1575.
- Ehrlich, P.R., Mooney, H.A., 1983. Extinction, substitution, and ecosystem services. *Bioscience* 33, 248–254.
- Ehrlich, P.R., Wilson, E.O., 1991. Biodiversity studies—science and policy. *Science* 253, 758–762.
- Elberling, H., Olesen, J.M., 1999. The structure of a high latitude plant–flower visitor system: the dominance of flies. *Ecography* 22, 314–323.
- England, P.R., Beynon, F., Ayre, D.J., Whelan, R.J., 2001. A molecular genetic assessment of mating system variation in a naturally bird-pollinated shrub: contributions from birds and introduced honeybees. *Conserv. Biol.* 15, 1645–1655.
- Feinsinger, P., Aizen, M.A., 2003. Bees not to be? Responses of insect pollinator faunas and flower pollination to habitat fragmentation. In: Bradshaw, G.A., Marquet, P.A. (Eds.), *How Landscapes Change: Human Disturbance and Ecosystem Fragmentation in the Americas*. Springer, Berlin, pp. 111–129.
- Feinsinger, P., Wolfe, J.A., Swann, L.A., 1982. Island ecology: reduced hummingbird diversity and the pollination biology of plants, Trinidad and Tobago, West Indies. *Ecology* 63, 494–506.
- Ferguson, R.N., Drake, D.R., 1999. Influence of vegetation structure on spatial patterns of seed deposition by birds. *N.Z. J. Bot.* 37, 671–677.
- Foster, J.T., Robinson, S.K., 2007. Introduced birds and the fate of Hawaiian rainforests. *Conserv. Biol.* 21, 1248–1257.
- Frankham, R., 1996. Relationship of genetic variation to population size in wildlife. *Conserv. Biol.* 10, 1500–1508.
- Fritts, T.H., Rodda, G.H., 1998. The role of introduced species in the degradation of island ecosystems: a case history of Guam. *Annu. Rev. Ecol. Syst.* 29, 113–140.
- Galetti, M., 2004. Parks of the Pleistocene: recreating the Cerrado and the Pantanal with megafauna. *Nat. Conserv.* 2, 93–100.
- García, J.D.D., 2002. Interaction between introduced rats and a frugivore bird–plant system in a relict island forest. *J. Nat. Hist.* 36, 1247–1258.
- Gerlach, J., 2008. Preliminary conservation status and needs of an oceanic island fauna: the case of Seychelles insects. *J. Insect Conserv.* 12, 293–305.
- Gilbert, L.E., 1980. Food web organisation and the conservation of Neotropical diversity. In: Soulé, M.E., Wilcox, B.A. (Eds.), *Conservation Biology: An Evolutionary-Ecological Perspective*. Sinauer, Sunderland, MA, pp. 11–33.
- Gillespie, R.G., Claridge, E.M., Roderick, G.K., 2008. Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes. *Mol. Ecol.* 17, 45–57.
- Goulson, D., 2003. Effects of introduced bees on native ecosystems. *Annu. Rev. Ecol. Evol. Syst.* 34, 1–26.
- Grant, B.R., Grant, P.R., 1981. Exploitation of *Opuntia* cactus by birds on the Galápagos. *Oecologia* 49, 179–187.
- Grant, P.R., 1998. Patterns on islands and microevolution. In: Grant, P.R. (Ed.), *Evolution on Islands*. Oxford University Press, Oxford, pp. 334.
- Griffiths, C.J., Jones, C.G., Hansen, D.M., Puttoo, M., Tatayah, R.V., Müller, C.B., Harris, S., in press. The use of extant non-indigenous tortoises to replace extinct ecosystem engineers: a restoration tool. *Restor. Ecol.*, doi: 10.1111/j.1526-100X.2009.00612.x.
- Groombridge, B. (Ed.), 1992. *Global Biodiversity: Status of the Earth's Living Resources*. A Report Compiled by the World Conservation Monitoring Centre. Chapman & Hall, London, UK.
- Gross, C.L., Mackay, D., 1998. Honeybees reduce fitness in the pioneer shrub *Melastoma affine* (Melastomataceae). *Biol. Conserv.* 86, 169–178.
- Hamann, O., 1993. On vegetation recovery, goats and giant tortoises on Pinta Island, Galápagos. *Ecuador. Biodiv. Conserv.* 2, 138–151.
- Hansen, D.M., Galetti, M., 2009. The forgotten megafauna. *Science* 324, 42–43.
- Hansen, D.M., Kaiser, C.N., Müller, C.B., 2008. Seed dispersal and establishment of endangered plants on oceanic islands: the Janzen–Connell model, and the use of ecological analogues. *PLoS ONE* 3, e2111.
- Hansen, D.M., Müller, C.B., 2009. Invasive ants disrupt gecko pollination and seed dispersal of the endangered plant *Roussea simplex* in Mauritius. *Biotropica* 41, 202–208.
- Hansen, D.M., Olesen, J.M., Jones, C.G., 2002. Trees, birds and bees in Mauritius: exploitative competition between introduced honey bees and endemic nectarivorous birds? *J. Biogeogr.* 29, 721–734.
- Hanski, I., 1994. Patch-occupancy dynamics in fragmented landscapes. *Trends Ecol. Evol.* 9, 131–135.
- Hedrick, P.W., 2001. Conservation genetics: where are we now? *Trends Ecol. Evol.* 16, 629–636.
- Henneman, M.L., Memmott, J., 2001. Infiltration of a Hawaiian community by introduced biological control agents. *Science* 293, 1314–1316.
- Herrera, C.M., 1988. Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biol. J. Linn. Soc.*, 95–125.

- Hingston, A.B., Marsden-Smedley, J., Driscoll, D.A., Corbett, S., Fenton, J., Anderson, R., Plowman, C., Mowling, F., Jenkin, M., Matsui, K., Bonham, K.J., Ilowski, M., McQuillan, P.B., Yaxley, B., Reid, T., Storey, D., Poole, L., Mallick, S.A., Fitzgerald, N., Kirkpatrick, J.B., Febey, J., Harwood, A.G., Michaels, K.F., Russell, M.J., Black, P.G., Emmerson, L., Visoiu, M., Morgan, J., Breen, S., Gates, S., Bantich, M.N., Desmarchelier, J.M., 2002. Extent of invasion of Tasmanian native vegetation by the alien bumblebee *Bombus terrestris* (Apoidea: Apidae). *Aust. Ecol.* 27, 162–172.
- Hingston, A.B., McQuillan, P.B., 1999. Displacement of Tasmanian native megachilid bees by the recently introduced bumblebee *Bombus terrestris* (Linnaeus, 1758) (Hymenoptera: Apidae). *Aust. J. Zool.* 47, 59–65.
- Howarth, F.G., Mull, W.P., 1992. In: *Hawaiian Insects and their Kin*. University of Hawaii Press, Honolulu, pp. 160.
- Hutton, I., Parkes, J.P., Sinclair, A.R.E., 2007. Reassembling island ecosystems: the case of Lord Howe Island. *Anim. Conserv.* 10, 22–29.
- Inoue, K., 1993. Evolution of mutualism in plant–pollinator interactions on islands. *J. Biosci.* 18, 525–536.
- Inoue, K., Maki, M., Masuda, M., 1996. Evolution of *Campanula* flowers in relation to insect pollinators on islands. In: Lloyd, D.G., Barrett, S.C.H. (Eds.), *Floral Biology: Studies on Floral Evolution in Animal-Pollinated Plants*. Chapman & Hall, New York, pp. 377–400.
- Jackson, J.B.C., Kirby, M.X., Berger, W.H., Bjørndal, K.A., Botsford, L.W., Bourque, B.J., Bradbury, R.H., Cooke, R., Erlandson, J., Estes, J.A., Hughes, T.P., Kidwell, S., Lange, C.B., Lenihan, H.S., Pandolfi, J.M., Peterson, C.H., Steneck, R.S., Tegner, M.J., Warner, R.R., 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293, 629–638.
- Janzen, D.H., 1974. Deflowering of Central America. *Nat. History* 83, 48–53.
- Jennersten, O., 1988. Pollination in *Dianthus deltoides* (Caryophyllaceae)—effects of habitat fragmentation on visitation and seed set. *Conserv. Biol.* 2, 359–366.
- Jones, C.G., 2002. Reptiles and amphibians. In: Perrow, M.R., Davy, A.J. (Eds.), *Handbook of Ecological Restoration*. Cambridge University Press, Cambridge, pp. 355–375.
- Jones, C.G., 2008. Practical conservation on Mauritius and Rodrigues: steps towards the restoration of devastated ecosystems. In: Cheke, A.S., Hulme, J.P. (Eds.), *Lost Land of the Dodo*. Christopher Helm, London, UK.
- Jordano, P., 1992. Fruits and frugivory. In: Fenner, M. (Ed.), *Seeds: The Ecology of Regeneration in Plant Communities*. CABI, Wallingford, UK, pp. 105–156.
- Jordano, P., 1994. Spatial and temporal variation in the avian–frugivore assemblage of *Prunus mahaleb*: patterns and consequences. *Oikos* 71, 479–491.
- Jourdan, H., Sadlier, R.A., Bauer, A.M., 2001. Little fire ant invasion (*Wasmannia auropunctata*) as a threat to New Caledonian lizards: evidences from a sclerophyll forest (Hymenoptera: Formicidae). *Sociobiology* 38, 283–301.
- Kaiser, C.N., 2006. In: *Functional Integrity of Plant–Pollinator Communities in Restored Habitats in Mauritius*. PhD Dissertation University of Zurich, Zürich, Switzerland.
- Kaiser, C.N., Hansen, D.M., Müller, C.B., 2008. Habitat structure affects reproductive success of the rare endemic tree *Syzygium mamillatum* (Myrtaceae) in restored and unrestored sites in Mauritius. *Biotropica* 40, 86–94.
- Kaiser-Bunbury, C.N., Memmott, J., Müller, C.B., 2009. Community structure of pollination webs of Mauritian heathland habitats. *Perspect. Plant Ecol. Evol. Syst.* 11, 241–254.
- Kaiser-Bunbury, C.N., Müller, C.B., 2009. Indirect interactions between invasive and native plants via pollinators. *Naturwissenschaften* 96, 339–346.
- Kareiva, P.M., Kingsolver, J.G., Huey, R.B., 1993. In: *Biotic Interactions and Global Change*. Sinauer, Sunderland, MA.
- Kato, M., Shibata, A., Yasui, T., 1999. Impact of introduced honeybees, *Apis mellifera*, upon native bee communities in the Bonin (Ogasawara) Islands. *Res. Popul. Ecol.* 41, 217–228.
- Kearns, C.A., Inouye, D.W., Waser, N.M., 1998. Endangered mutualisms: the conservation of plant–pollinator interactions. *Annu. Rev. Ecol. Syst.* 29, 83–112.
- Kelly, D., Robertson, A.W., Ladley, J.J., Anderson, S.H., McKenzie, R.J., 2006. Relative (un)importance of introduced animals as pollinators and dispersers of native plants. In: Allen, R.B., Lee, W.G. (Eds.), *Biological Invasions in New Zealand*. Springer, Berlin, pp. 227–245.
- Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibsch, P.L., Nowicki, C., Mutke, J., Barthlott, W., 2009. A global assessment of endemism and species richness across island and mainland regions. *Proc. Natl. Acad. Sci. USA* 106, 9322–9327.
- Kingston, N., Waldren, S., 2005. A conservation appraisal of the rare and endemic vascular plants of Pitcairn Island. *Biodiv. Conserv.* 14, 781–800.
- Kobayashi, S., Inoue, K., Kato, M., 1997. Evidence of pollen transfer efficiency as the natural selection factor favoring a large corolla of *Campanula punctata* pollinated by *Bombus diversus*. *Oecologia* 111, 535–542.
- Kueffer, C., Daehler, C.C., Torres-Santana, C.W., Lavergne, C., Meyer, J.-Y., Otto, R. and Silva, L. 2010. A global comparison of plant invasions on oceanic islands. *Perspec. Plant Ecol. Evol. Syst.* 12, 145–161.
- Kueffer, C., Kronauer, L., Edwards, P.J., 2009. Wider spectrum of fruit traits in invasive than native floras may increase the vulnerability of oceanic islands to plant invasions. *Oikos* 118, 1327–1334.
- Larsen, T.H., Williams, N.M., Kremen, C., 2005. Extinction order and altered community structure rapidly disrupt ecosystem functioning. *Ecol. Lett.* 8, 538–547.
- Lee, M.A.B., 1985. The dispersal of *Pandanus tectorius* by the land crab *Cardisoma carnifex*. *Oikos* 45, 169–173.
- Linneberg, J.F., Hansen, D.M., Olesen, J.M., 2009. Gut passage effect of the introduced red-whiskered bulbul (*Pycnonotus jocosus*) on germination of invasive plant species in Mauritius. *Aust. Ecol.* 34, 272–277.
- Lopezaraza-Mikel, M.E., Hayes, R.B., Whalley, M.R., Memmott, J., 2007. The impact of an alien plant on a native plant pollinator network: an experimental approach. *Ecol. Lett.* 10, 539–550.
- Lord, J.M., Markey, A.S., Marshall, J., 2002. Have frugivores influenced the evolution of fruits traits in New Zealand? In: Levey, D., Silva, W.R., Galetti, M. (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CABI Publishing, Wallingford, UK, pp. 544.
- Lord, J.M., Marshall, J., 2001. Correlations between growth form, habitat, and fruit colour in the New Zealand flora, with reference to frugivory by lizards. *N.Z. J. Bot.* 39, 567–576.
- MacArthur, R.H., Wilson, E.O., 1967. In: *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ, pp. 203.
- MacArthur, R.H., Diamond, J.M., Karr, J.R., 1972. Density compensation in island faunas. *Ecology* 53, 330–342.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A., 2000. Biotic invasions: causes, epidemiology, global consequences, and control. *Ecol. Appl.* 10, 689–710.
- Magnacca, K.N., 2007. Conservation status of the endemic bees of Hawai'i, *Hylaeus (Nesoprotopis)* (Hymenoptera: Colletidae). *Pac. Sci.* 61, 173–190.
- Mandon-Dalger, I., Clergeau, P., Tassin, J., Riviere, J.N., Gatti, S., 2004. Relationships between alien plants and an alien bird species on Réunion Island. *J. Trop. Ecol.* 20, 635–642.
- Marsh, D.M., Trenham, P.C., 2008. Current trends in plant and animal population monitoring. *Conserv. Biol.* 22, 647–655.
- Martin, P.S., 2005. In: *Twilight of the Mammoths—Ice Age Extinctions and the Rewilding of America*. California University Press, Berkeley, CA, pp. 250.
- McCann, K., 2007. Protecting biostructure. *Nature* 446, 29.
- McConkey, K.R., Drake, D.R., 2006. Flying foxes cease to function as seed dispersers long before they become rare. *Ecology* 87, 271–276.
- McMullen, C.K., 1987. Breeding systems of selected Galapagos Islands angiosperms. *Am. J. Bot.* 74, 1694–1705.
- McMullen, C.K., 1993. Flower-visiting insects of the Galapagos Islands. *Pan-Pacific Entomol.* 69, 95–106.
- Meehan, H.J., McConkey, K.R., Drake, D.R., 2002. Potential disruptions to seed dispersal mutualisms in Tonga, Western Polynesia. *J. Biogeogr.* 29, 695–712.
- Memmott, J., Waser, N.M., 2002. Integration of alien plants into a native flower–pollinator visitation web. *Proc. R. Soc. B* 269, 2395–2399.
- Memmott, J., Waser, N.M., Price, M.V., 2004. Tolerance of pollination networks to species extinctions. *Proc. R. Soc. B* 271, 2605–2611.
- Micheneau, C., Fournel, J., Paillet, T., 2006. Bird pollination in an angraecoid orchid on Reunion Island (Mascarene Archipelago, Indian Ocean). *Ann. Bot.* 97, 965–974.
- Miskelly, C., 1999. In: *Mana Island Ecological Restoration Plan*. New Zealand Department of Conservation, Wellington, pp. 1–136.
- Moragues, E., Traveset, A., 2005. Effects of *Carpobrotus* spp. on the pollination success of native plant species of the Balearic Islands. *Biol. Conserv.* 122, 611–619.
- Morales, C.L., Aizen, M.A., 2006. Invasive mutualisms and the structure of plant–pollinator interactions in the temperate forests of north-west Patagonia, Argentina. *J. Ecol.* 94, 171–180.
- Morales, C.L., Traveset, A., 2009. A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecol. Lett.* 12, 716–728.
- Motala, S.M., Krell, F.T., Mungroo, Y., Donovan, S.E., 2007. The terrestrial arthropods of Mauritius: a neglected conservation target. *Biodiv. Conserv.* 16, 2867–2881.
- Moulton, M.P., Pimm, S.L., 1986. Species introductions to Hawaii. In: Mooney, H.A., Drake, D.R. (Eds.), *Ecology of Biological Invasions of North America and Hawaii*. Springer Verlag, New York, pp. 231–249.
- Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., Woodfin, R.M., 1994. Declining biodiversity can alter the performance of ecosystems. *Nature* 368, 734–737.
- New, T.R., 2008. A special issue on insect conservation and islands. *J. Insect Conserv.* 12, 195.
- Nicholls, H., 2006. Restoring nature's backbone. *PLoS Biol.* 4, 893–896.
- Nichols, J.D., Williams, B.K., 2006. Monitoring for conservation. *Trends Ecol. Evol.* 21, 668–673.
- Nogales, M., Martín, A., Tershy, B.R., Donlan, C.J., Veitch, D., Puerta, N., Wood, B., Alonso, J., 2004. A review of feral cat eradication on islands. *Conserv. Biol.* 18, 310–319.
- Nogales, M., Nieves, C., Illera, J.C., Padilla, D.P., Traveset, A., 2005. Effect of native and alien vertebrate frugivores on seed viability and germination patterns of *Rubia fruticosa* (Rubiaceae) in the eastern Canary Islands. *Funct. Ecol.* 19, 429–436.
- Nogales, M., Rodríguez-Luengo, J.C., Marrero, P., 2006. Ecological effects and distribution of invasive non-native mammals on the Canary Islands. *Mammal Rev.* 36, 49–65.
- North, S.G., Bullock, D.J., Dulloo, M.E., 1994. Changes in the vegetation and reptile populations on Round Island, Mauritius, following eradication of rabbits. *Biol. Conserv.* 67, 21–28.
- Nyhamen, D.F., Kragelund, C., Olesen, J.M., Jones, C.G., 2001. Insular interactions between lizards and flowers: flower visitation by an endemic Mauritian gecko. *J. Trop. Ecol.* 17, 755–761.

- Olesen, J.M., 1985. The Macaronesian bird-flower element and its relation to bird and bee opportunists. *Bot. J. Linnean Soc.* 91, 395–414.
- Olesen, J.M., Bascompte, J., Elberling, H., Jordano, P., 2008. Temporal dynamics in a pollination network. *Ecology* 89, 1573–1582.
- Olesen, J.M., Eskildsen, L.L., Venkatasamy, S., 2002. Invasion of pollination networks on oceanic islands: importance of invader complexes and endemic super generalists. *Div. Distrib.* 8, 181–192.
- Olesen, J.M., Jordano, P., 2002. Geographic patterns in plant–pollinator mutualistic networks. *Ecology* 83, 2416–2424.
- Olesen, J.M., Valido, A., 2003. Lizards as pollinators and seed dispersers: an island phenomenon. *Trends Ecol. Evol.* 18, 177–181.
- Ouborg, N.J., Vergeer, P., Mix, C., 2006. The rough edges of the conservation genetics paradigm for plants. *J. Ecol.* 94, 1233–1248.
- Padrón, B., Traveset, A., Díaz, D., Nogales, M., et al., 2009. Impact of alien plant invaders on pollination networks in two archipelagoes. *PLoS ONE* 4 (7), e6275, doi:10.1371/journal.pone.0006275.
- Paton, D.C., 1993. Honeybees in the Australian environment: does *Apis mellifera* disrupt or benefit the native biota? *Bioscience* 43, 95–103.
- Pelling, M., Uitto, J.I., 2001. Small island developing states: natural disaster vulnerability and global change. *Global Environ. Change B Environ. Hazards* 3, 49–62.
- Petanidou, T., Kallimanis, A.S., Tzanopoulos, J., Sgardelis, S.P., Pantis, J.D., 2008. Long-term observation of a pollination network: fluctuation in species and interactions, relative invariance of network structure and implications for estimates of specialization. *Ecol. Lett.* 11, 564–575.
- Philipp, M., Bocher, J., Siegmund, H.R., Nielsen, L.R., 2006. Structure of a plant–pollinator network on a pahoehoe lava desert of the Galapagos Islands. *Ecography* 29, 531–540.
- Quammen, D., 1996. Song of the dodo: island biogeography in an age of extinction. Hutchinson, London.
- Rainbird, P., 2002. A message for our future? The Rapa Nui (Easter Island) ecodisaster and Pacific island environments. *World Archaeol.* 33, 436.
- Rathcke, B.J., 2001. Pollination and predation limit fruit set in a shrub, *Bourreria succulenta* (Boraginaceae), after hurricanes on San Salvador Island, Bahamas. *Biotropica* 33, 330–338.
- Riera, N., Traveset, A., García, O., 2002. Breakage of mutualisms by alien species: the case of *Cneorum tricocon* L. in the Balearic Islands (Western Mediterranean Sea). *J. Biogeogr.* 29, 713–719.
- Rodda, G.H., Dean-Bradley, K., 2002. Excess density compensation of island herpetofaunal assemblages. *J. Biogeogr.* 29, 623–632.
- Rodda, G.H., Perry, G., Rondeau, R.J., Lazell, J., 2001. The densest terrestrial vertebrate. *J. Trop. Ecol.* 17, 331–338.
- Rodríguez-Cabal, M.A., Aizen, M.A., Novaro, A.J., 2007. Habitat fragmentation disrupts a plant–disperser mutualism in the temperate forest of South America. *Biol. Conserv.* 139, 195–202.
- Rubenstein, D.R., Rubenstein, D.I., Sherman, P.W., Gavin, T.A., 2006. Pleistocene park: does re-wilding North America represent sound conservation for the 21st century? *Biol. Conserv.* 132, 232–238.
- Sáez, E., Traveset, A., 1995. Fruit and nectar feeding by *Podarcis lilfordi* (Lacertidae) on Cabrera Archipelago (Balearic Islands). *Herpetol. Rev.* 26, 121–123.
- Sakai, A.K., Wagner, W.L., Mehrhoff, L.A., 2002. Patterns of endangerment in the Hawaiian flora. In: *Symposium on Biodiversity, Systematics, and Conservation*; Bloomington, Indiana, pp. 276–302.
- Samways, M.J., Hitchins, P.M., Bourquin, O., Henwood, J., 2009. Restoration of a tropical island: Cousine Island, Seychelles. *Biodiv. Conserv.* doi:10.1007/s10531-008-9524-z in press.
- Sax, D.F., Gaines, S.D., 2008. Species invasions and extinction: the future of native biodiversity on islands. *Proc. Nat. Acad. Sci. USA* 105, 11490–11497.
- Sax, D.F., Gaines, S.D., Brown, J.H., 2002. Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *Am. Nat.* 160, 766–783.
- Schuller, S., 2007. Island–mainland difference in *Nicotiana glauca* (Solanaceae) corolla length: a product of pollinator-mediated selection? *Evol. Ecol.* 21, 81–98.
- Seddon, P.J., Soorae, P.S., Launay, F., 2005. Taxonomic bias in reintroduction projects. *Anim. Conserv.* 8, 51–58.
- Simberloff, D., 1990. Reconstituting the ambiguous—can islands be restored? In: Towns, D.R., Dougherty, C.H., Atkinson, I.A.E. (Eds.), *Ecological restoration of New Zealand islands*. New Zealand Department of Conservation, pp. 37–51.
- Simberloff, D., Boecklen, W., 1991. Patterns of extinction in the introduced Hawaiian avifauna—a reexamination of the role of competition. *Am. Nat.* 138, 300–327.
- Steadman, D.W., 1995. Prehistoric extinctions of Pacific island birds—biodiversity meets zooarchaeology. *Science* 267, 1123–1131.
- Steffan-Dewenter, I., Potts, S.G., Packer, L., 2005. Pollinator diversity and crop pollination services are at risk. *Trends Ecol. Evol.* 20, 651–652.
- Stoddart, D.R., 1984. In: *Biogeography and Ecology of the Seychelles Islands*. Junk, The Hague.
- Stolzenburg, W., 2006. Where the wild things were. *Conserv. Practice* 7, 28–33.
- Stringer, I.A.N., Chappell, R., 2008. Possible rescue from extinction: transfer of a rare New Zealand tusked weta to islands in the Mercury group. *J. Insect Conserv.* 12, 371–382.
- Timmins, S.M., Atkinson, I.A.E., Ogle, C.C., 1987. Conservation opportunities on a highly modified island—Mana Island, Wellington, New Zealand. *N.Z. J. Ecol.* 10, 57–65.
- Towns, D.R., Atkinson, I.A.E., Daugherty, C.H., 2006. Have the harmful effects of introduced rats on islands been exaggerated? *Biol. Invas.* 8, 863–891.
- Towns, D.R., Dougherty, C.H., Atkinson, I.A.E. (Eds.), 1990. *Ecological Restoration of New Zealand Islands*. New Zealand Department of Conservation, Wellington p. 320.
- Traveset, A., Nogales, M., Alcover, J., Delgado, J., López-Darias, M., Godoy, D., Igual, J., Bover, P., 2009. A review on the effects of alien rodents in the Balearic (Western Mediterranean Sea) and Canary Islands (Eastern Atlantic Ocean). *Biol. Invas.* 11, 1653–1670.
- Traveset, A., Richardson, D.M., 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecol. Evol.* 21, 208–216.
- Traveset, A., Riera, N., 2005. Disruption of a plant–lizard seed dispersal system and its ecological effects on a threatened endemic plant in the Balearic Islands. *Conserv. Biol.* 19, 421–431.
- Traveset, A., Sáez, E., 1997. Pollination of *Euphorbia dendroides* by lizards and insects: spatio-temporal variation in patterns of flower visitation. *Oecologia* 111, 241–248.
- Tylianakis, J.M., 2008. Understanding the web of life: the birds, the bees, and sex with aliens. *PLoS Biol.* 6, e47.
- Tylianakis, J.M., Tscharntke, T., Lewis, O.T., 2007. Habitat modification alters the structure of tropical host–parasitoid food webs. *Nature* 445, 202–205.
- Valido, A., 1999. *Ecología de la dispersión de semillas por los lagartos endémicos canarios (g. Gallotia, Lacertidae)*. PhD Dissertation. University of La Laguna Tenerife, Canary Islands, Spain.
- Valido, A., Dupont, Y.L., Olesen, J.M., 2004. Bird–flower interactions in the Macaronesian islands. *J. Biogeogr.* 31, 1945–1953.
- Valido, A., Olesen, J.M., 2007. Importance of lizards as frugivores and seed dispersers. In: Dennis, R., Green, R., Schupp, E., Westcott, D. (Eds.), *Seed Dispersal: Theory and its Application in a Changing World*. CABI Publishing, Wallingford, UK, pp. 124–147.
- Veitch, C.R., Clout, M.N. (Eds.) 2002. *Turning the tide: the eradication of invasive species*. In: *International Conference on Eradication of Island Invasives*. IUCN; Auckland, pp. 414.
- Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmanek, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. *N.Z. J. Ecol.* 21, 1–16.
- Vogel, S., Westerkamp, C., Thiel, B., Gessner, K., 1984. Ornithophily on the Canary Islands. *Plant Syst. Evol.* 146, 225–248.
- Washitani, I., 1996. Predicted genetic consequences of strong fertility selection due to pollinator loss in an isolated population of *Primula sieboldii*. *Conserv. Biol.* 10, 59–64.
- Watts, C., Stringer, I., Sherley, G., Gibbs, G., Green, C., 2008. History of weta (Orthoptera: Anostomatidae) translocation in New Zealand: lessons learned, islands as sanctuaries and the future. *J. Insect Conserv.* 12, 359–370.
- Weaver, E.A., Griffiths, O.L., 2008. In: *A guide to La Vanille Réserve des Mascareignes (Mauritius)*. Bioculture Press, Rivière des Anguilles, Mauritius.
- Webb, C.J., Kelly, D., 1993. The reproductive biology of the New Zealand flora. *Trends Ecol. Evol.* 8, 442–447.
- Wenner, A.M., Thorp, R.W., 1994. Removal of feral honey bee (*Apis mellifera*) colonies from Santa Cruz Island. In: Halvorson, W.L., Maender, G.L. (Eds.), *Fourth California Islands Symposium: Update on the Status of Resources*. Santa Barbara Museum of Natural History, Santa Barbara, CA, pp. 513–522.
- Westerkamp, C., 1991. Honeybees are poor pollinators—why? *Plants Syst. Evol.* 177, 71–75.
- Whittaker, R.J., Fernández-Palacios, J.M., 2007. In: *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford University Press, Oxford, pp. 401.
- Wiles, G.J., Schreiner, I.H., Nafus, D., Jurgensen, L.K., Manglona, J.C., 1996. The status, biology, and conservation of *Serianthes nelsonii* (Fabaceae), an endangered Micronesian tree. *Biol. Conserv.* 76, 229–239.
- Willson, M.F., Whelan, C.J., 1993. Variation of dispersal phenology in a bird-dispersed shrub, *Cornus drummondii*. *Ecol. Monogr.* 63, 151–172.
- Woodell, S.R.J., 1979. Role of unspecialised pollinators in the reproductive success of Aldabran plants. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 286, 99–108.
- Worthy, T.H., Anderson, A.J., Molnar, R.E., 1999. Megafaunal expression in a land without mammals—the first fossil faunas from terrestrial deposits in Fiji. *Senckenbergiana Biol.* 79, 237–242.
- Yoccoz, N.G., Nichols, J.D., Boulinier, T., 2001. Monitoring of biological diversity in space and time. *Trends Ecol. Evol.* 16, 446–453.
- Ziegler, A.C., 2002. *Hawaiian natural history, ecology, and evolution*. University of Hawai'i Press, Honolulu, HI.
- Zimov, S.A., 2005. Pleistocene park: return of the mammoth's ecosystem. *Science* 308, 796–798.