

Biodiversity dynamics in isolated island communities: interaction between natural and human-mediated processes

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Abstract

The flora and fauna of oceanic islands have inspired research since the early scientific explorations. Islands can be considered ‘nature’s test tubes’ — simple systems with multiple replicates. Our research has used the simplicity of island systems to understand ecological community dynamics and to compare the properties of island communities with those in more complex mainland systems. Here, we present three topics: (i) current patterns of biodiversity on isolated islands of the Pacific; (ii) current patterns of disturbance and invasion on islands; and (iii) future trajectories inferred from these patterns. We examine features of islands (in particular, topography and isolation) that have allowed for given levels and distribution of endemism. The extent to which island communities are impacted by, resist or accommodate disturbance and/or invasions by nonindigenous species appears to be dictated to a large extent by properties of the native communities and how these communities were originally assembled. Accordingly, patterns of disturbance and invasion are very different for high (montane) islands that are extremely isolated compared to those that are nearer to a source of natural migrants. As with all biotas, those on islands are dynamic entities. However, the unique aspect of islands is their isolation, and extreme isolation has largely been lost over the course of the last few centuries due to the development of transportation routes. We argue that such a modified dynamic will affect the future of the biota and the processes that gave rise to the biota. Specifically for isolated habitats, ecological processes will become increasingly more likely to generate biodiversity than evolutionary processes which have been relatively more important in the past. In the short term, island biotas and other similar biotas that occur in montane habitats may fare well as species are often abundant locally in the habitat to which they are indigenous, and may demonstrate considerable resistance and resilience to invasion. However, island biotas — and other biotas that show high local endemism — will likely not fare well in the face of prolonged disturbance. The biotas in these areas generally display a relatively low dispersal capacity; therefore, under conditions of long-term habitat modification, isolated biotas are likely to be swamped by non-natives, which — simply because of random processes and higher propagule pressure — will move more readily into available habitats. Thus, despite the importance of incorporating the evolutionary process into conservation efforts, we must also be careful to evaluate the likely form that the processes will take when the context (specifically, extent of isolation) has been highly modified.

Keywords: adaptive radiation, cloud forest, community assembly, dispersal, gene flow, invasive species, neutral theory, niche, propagule pressure

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Introduction

Isolated archipelagos can serve as natural laboratories for studies of both ecological (MacArthur & Wilson 1967) and evolutionary (Grant 1998) processes. Ecological studies have highlighted the role of island size and isolation in

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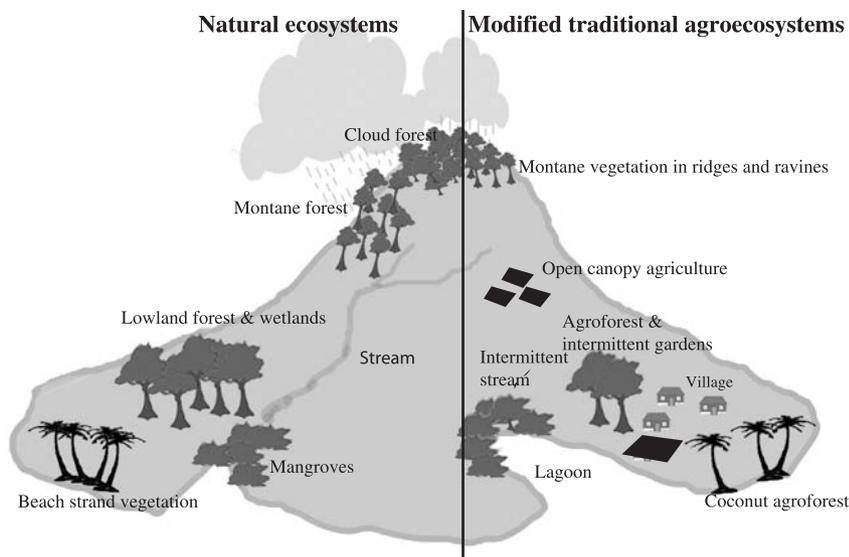


Fig. 1 Features of a remote high-elevation island showing different topographic features that change with elevation (redrawn after Office of Technology Assessment 1987).

dictating species diversity: larger islands are associated with reduced extinction (and, in some cases, increased immigration, Toft & Schoener 1983), while isolated islands are associated with reduced immigration (Simberloff & Wilson 1969). Studies on more remote islands have highlighted phenomena such as adaptive radiation, with immigration of different species being largely replaced by speciation as the process that generates diversity; thus, species diversity arises through evolutionary processes (Simon & Sugden 1987). Whether species diversity stems from immigration or evolution, larger islands support greater numbers of species (Paulay 1994; Gillespie & Roderick 2002). The Pacific Ocean is particularly well known for its remote oceanic islands, of which it contains about 25 000, more than the rest of the world's oceans combined. Besides their extraordinary evolutionary history, the biotas of distant islands are well known for their large numbers of endangered species and high rates of extinction. Moreover, because the isolation of these islands has recently been reduced with the development of transportation routes, they present an opportunity to examine the interplay between evolutionary and more recent ecological processes in shaping biodiversity. Here, we use this context of past evolutionary history and current ecological threats to examine biodiversity dynamics of remote islands and assess potential future trajectories.

Terrestrial habitat on remote Pacific islands

Terrestrial habitats on the remote islands of the central Pacific can be classified by vegetation type, which is determined largely by elevation and precipitation, both of which are strongly correlated with island size (Fig. 1). Strand habitat is found on almost all Pacific islands. Accordingly, although many of the islands are very small,

these kinds of habitats are relatively abundant. On the other hand, mid-elevation forest and cloud forest are restricted to islands that have elevations of at least 100 m. Cloud forests are the most distinctive habitats in the Pacific islands, the upper and lower limits of which are determined by the altitude of a persistent cloud zone, generally set by the elevation of the winds and by temperature and humidity. These cloud forests are characterized by an abundance of mosses, ferns and other epiphytic plants (Merlin & Juvik 1992; Manner *et al.* 1999), with reduced tree stature and increased stem density, and waterlogged soils. Compared to cloud forests of continents, those on small islands tend to occur at lower elevations. On the wet side of the Hawaiian islands, these habitats descend somewhat below 1000 m up to almost 2000 m (Mueller-Dombois & Fosberg 1998; Wagner *et al.* 1999); in the islands of Micronesia as low as 450–500 m (Raynor 1995); and in French Polynesia, the islands of the Societies and Marquesas, and Rapa, to approx. 300 m on windward slopes and 600 m on leeward slopes (Meyer & Florence 1996; Meyer 2004). However, there are only very few islands in the Pacific that have elevations sufficient to support cloud forests. Indeed, in all of Micronesia, Pohnpei and Kosrae have the only remaining patches of montane cloud forest. Hawaii is unusual in that the highest islands extend above the trade-wind inversion layer (3000 m); here, the cloud forest gives way to an even higher alpine zone that is cold and dry, with sparse vegetation.

Characteristics of biota on remote Pacific islands

Under natural conditions, propagules can only reach remote oceanic islands with difficulty, and those propagules that colonized these islands prior to human occupation tended to be small and easily dispersed. Accordingly, taxonomic

representation is biased towards such groups, a phenomenon termed 'taxonomic disharmony'. For example, many animal taxa are characteristically absent or scarce from the indigenous biota of very remote islands, including mammals (except bats), amphibians, terrestrial snakes, freshwater insects and freshwater fish (Gressitt 1974). Species that managed to colonize and get established on remote islands have diversified largely through adaptive radiation, accentuating the taxonomic disharmony and resulting in high levels of endemism. Characteristics of species of remote islands include reduced dispersal capabilities (Darwin 1859) and development of unusual traits for a given lineage (arising, presumably, in response to open ecological space). Change in body size is also commonly observed on islands, with species showing a tendency towards size extremes, both gigantism and dwarfism; for example, large mammal species that colonize relatively remote islands tend to get smaller while small species tend to get larger (Case 1978). In plants, reproductive changes are common and include the development of dioecy, asexual reproduction and low rates of reproduction (Sakai *et al.* 1995).

A primary concern of this paper is the biotas of cloud-forest habitats on remote islands of the central Pacific. Biodiversity can be relatively high in such forests with endemism often extremely high (Hamilton *et al.* 1995). The particular floristic elements of these habitats are generally not related to those of lower elevations on the same mountain mass, but rather have biogeographical affinities with northern or southern temperate regions (Meyer 2004). The same is likely true for the fauna, though this notion has not been examined critically.

Human impact on remote Pacific islands

One of the clearest demonstrations of human impact on remote islands is the high proportion of known extinct species. The majority of documented global extinctions since the 1500s has occurred on islands, most of these being birds (Baillie *et al.* 2004) and much of the remaining native biota of remote islands — especially birds — is threatened with extinction. Consequently, much emphasis is placed on protecting the remaining biota of isolated islands. The primary threats to biodiversity, as in most parts of the world, are invasive species (discussed below) and habitat modification, including climate change. Islands, in particular island cloud forests, have become a major focus of concern because of their known sensitivity to climate change (Still *et al.* 1999) coupled with high levels of endemism (Pounds *et al.* 1999; Nadkarni & Solano 2002). Rising sea levels and loss of lowland areas are immediate issues and will undoubtedly lead to greater pressure on mid-elevation habitats for agriculture, which in turn will likely lead to increased erosion. Historical biological and climatic data suggest that climate warming has raised the average altitude at the base of the orographic cloud bank, as predicted by

the lifting-cloud-base hypothesis (Still *et al.* 1999). Accordingly, because cloud-forest habitat on small islands, where it does occur, is limited to the topmost elevations, the status of such island cloud-forest habitats is extremely precarious.

Although human-mediated ecological change has been discussed extensively for islands, less well understood is the interaction of these processes in the context of the history of island biotas, which have been formed largely through evolutionary processes. For example, what form will the biota take in the future, and how will current impacts affect the natural ecological and evolutionary processes that created the indigenous biota that we see today? Here, we attempt to address the origin of biodiversity in the islands of the Pacific and to infer the future trajectories of these communities. We use published data from the islands of the Hawaiian archipelago, archipelagoes of French Polynesia (Societies, Marquesas and Australs), as well as the high islands of Eastern Micronesia (Kosrae and Pohnpei). Each of these sites is characterized by a combination of strand vegetation, mid-elevation forest, and cloud forest. Because strand vegetation is similar on the different islands, the focus here is limited to mid-elevation forest and cloud forest. We first examine patterns of endemism on the different islands in order to assess the relative roles of colonization and adaptive radiation in accounting for indigenous biodiversity. We confine our analysis to data available for plants and invertebrates; birds — the only indigenous vertebrate group that is well represented in such areas — have already suffered extensive extinction (Steadman 1995), making it more difficult to use them for assessment of indigenous diversity. We then consider recent colonization on the same islands to assess factors responsible for invasion success, including the timing of colonization, disturbance and propagule pressure. Finally, we use this information to predict the future trajectories of ecological and evolutionary processes that govern biodiversity dynamics on islands and the extent to which this information can be applied to continental communities.

Results and Discussion

Indigenous biodiversity: evolutionary patterns and process

In order to assess the future trajectory of species occurring in forests on remote islands, we must first understand the processes responsible for their history and diversification. Accordingly, we examined six features of remote islands and their component indigenous species to determine the relative roles played by colonization and speciation in building communities: (i) *isolation and endemism*; (ii) *dispersal of colonists and island species*; (iii) *origins of new species*; (iv) *specialization through time*; (v) *speciation and habitat shifts*; and (vi) *available habitat*.

Is endemism associated with isolation? To assess the relationship between endemism and isolation and the role of unique habitat features of cloud forests in this relationship, we compiled data on levels of endemism estimated for flowering plants from different islands across the Pacific (data from Florence 1987; Florence 1993, 1997; Florence & Lorence 1997; Eldredge & Evenhuis 2003; Merlin & Raynor 2005).

There are several indices of isolation for islands (I), the most commonly used being

$$I_i = (\sqrt{d_i} + \sqrt{d_a} + \sqrt{d_c}), \quad (\text{eqn 1})$$

where d_i , d_a and d_c are the distances to the nearest equivalent or larger island, the nearest archipelago and the nearest continent, respectively (Daehler 2006; Dahl 1998). This measure is a simple one in that it is based on distances only and ignores biological elements, such as dispersal ability of particular taxa. More significantly, this method disregards biogeographical affinities. For example, island cloud forests are unique environments, often with many endemic species that are phylogenetically distinct from those at lower elevations on the same mountain (Meyer 2004). Accordingly, isolation of cloud forest might be better considered in the context of the nearest *high* land mass (i.e. a large island of sufficient size to generate its own climate). Some measures of isolation do consider island elevation in the context of isolation, but they do not include biogeographical affinities, such as those associated with island cloud forests (Rolett & Diamond 2004).

For the current study, isolation to the nearest suitable habitat (I_h) was also calculated, as

$$I_h = (2\sqrt{d_a} + \sqrt{d_c}). \quad (\text{eqn 2})$$

This index is similar in form to the standard measure (I_i), in that it sums 3-values of the square root of distance, but it weights doubly the distance to the nearest archipelago with a high elevation island capable of sustaining a cloud forest (d_a), rather than the distance to the nearest island *per se*, which is ignored. Other weightings, of course, are also possible.

For vascular plants on remote Pacific islands, we examined the relationship between isolation and endemism in three ways: (i) low elevation islands using the original isolation statistic, I_i ; (ii) high elevation islands using the same isolation statistic, I_i ; and (iii) high elevation islands using the isolation statistic that emphasizes the distance to the nearest high islands, I_h . Adding high islands in the analysis (i vs. ii), increased the observed endemism, and only the high islands had values of endemism well above 15% (Fig. 2). For low islands (i) the relationship between isolation and endemism was not statistically significant. For

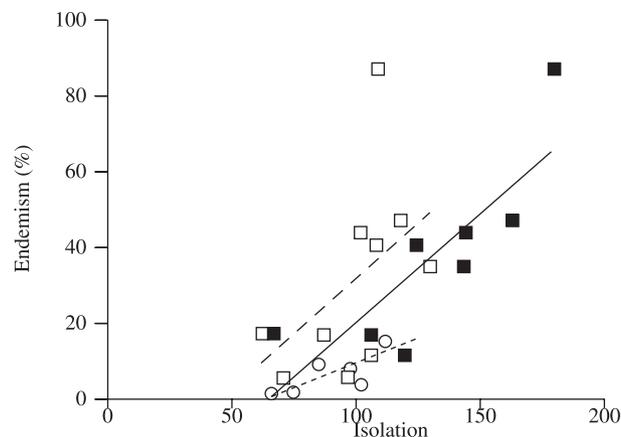


Fig. 2 Endemism of vascular plants on different Pacific islands as a function of isolation, using a standard indicator of isolation that includes the distance from the island to nearest island for (a) low-elevation islands (open circles, small dashed line), (b) high-elevation islands (open squares, large dashed line) and (c) using a modified indicator for isolation that includes the distance from the archipelago to nearest high elevation habitat capable of sustaining a cloud forest (closed squares, solid line). See text for additional explanation of these indices. Only the high islands (b, c) have endemism well above 15%. The relationship between endemism and isolation calculated the traditional way was not significant for low islands (a) and barely significant for high islands (b, Spearman $\rho = 0.64$, $P = 0.048$), while the relationship that includes distance to the nearest high islands (c) was highly significant ($\rho = 0.88$, $P = 0.0039$). Best-fit lines are shown only for illustrative purposes.

high islands the relationship using the traditional measure of isolation (ii) was barely significant (Spearman $\rho = 0.64$, $P = 0.048$) but greatly improved when isolation emphasized the distance to the nearest high islands (c, $\rho = 0.88$, $P = 0.0039$). This result supports the idea that higher-elevation forests are more isolated than lower-elevation habitats. While lower-elevation forests may have also many indigenous species (R. Gillespie, *unpublished*), their uniqueness (endemism) is less pronounced.

What is the relative distribution and associated dispersal ability of island endemics as compared to colonists? We examined the dispersal dynamics of species of remote islands and the role that dispersal, or lack thereof, may play in diversification, by comparing range size and dispersal ability between the presumed colonists and current island taxa. Remote islands are known for their extraordinary local endemism of species. At the same time, the colonists that gave rise to the diversity of species in the islands are related to taxa that include some of the most widespread and dispersive species known. Loss of dispersal ability among island forms has long been recognized and hypothesized to be an adaptation against the high probability of being blown out to sea (Darwin 1859).

We explored the extent to which dispersal ability has been curtailed on the islands in two ways. First, we compared the geographical ranges of species on islands to that of their continental relatives. For long-jawed *Tetragnatha* spiders (Araneae, Tetragnathidae), we estimated the area occupied by the endemic Hawaiian species with the areas occupied by the closest outgroups. We found that the average area occupied by a clade of endemic *Tetragnatha* species ($n = 17$) in the Hawaiian islands is 598 km² (SD = 768 km²) (Gillespie 1991; Gillespie 2002), while that of three outgroup species from the mainland US (*Tetragnatha pallescens*, *T. versicolor* and *T. elongata*) is approximately 8.5×10^6 km² (SD = 3.0×10^6 km²). This represents an average decrease in geographical range of more than four orders of magnitude among the native species since colonization of the islands. While a small range does not necessarily translate into limited dispersal, there are three reasons to suggest that dispersal is indeed limited in island taxa: (i) although similar habitats occur on the different volcanoes of the Hawaiian islands, many (perhaps most) indigenous arthropods are endemic to a single volcano (Carson & Clague 1995); (ii) where populations of a single species occur on multiple islands, evidence suggests that gene flow between volcanoes is either absent or minimal (Piano *et al.* 1997; Gillespie & Oxford 1998; Pons & Gillespie 2004); and (iii) when populations occur in a fragmented landscape of tiny forest patches separated from each other by narrow tracts of lava (10–100 m wide), significant genetic differences can be found between populations in the different patches (Carson & Sato 1969; Vandergast *et al.* 2004).

Second, we considered how organisms on islands lose their dispersal ability. In insects, one expression of loss of dispersal ability is the loss or reduction of wings, and such reductions are observed on islands. For example, on Campbell Island, New Zealand, 40% of 183 indigenous insect species show some degree of wing reduction; on Tristan de Cunha, 18 of 20 endemic beetles show reduced wings and in Hawaii, 10 of 11 orders of alate (winged) species have evolved flightlessness (Gillespie & Roderick 2002). Moreover, taxa such as spiders that do not have wings but disperse by 'ballooning', have also tended to lose their ability to balloon (Gillespie 2005). The correlation between island colonization and loss of dispersal is not absolute. For example, some island species need wings for vertical movement within their habitat, which may explain at least why three species of delphacid planthoppers (Hemiptera) in Hawaii are macropterous (having long wings) out of 72 species that are primarily brachypterous (short wings) or polymorphic (Denno 1994): all three macropterous species are associated with host plants that exceed 20 m in height, while the other species are specialists on hosts less than 5 m in height. A similar phenomenon may explain why only some lineages of birds have become flightless. It should be noted that loss of dispersal is not unique to oceanic

islands; it is also found in isolated continental habitats, in particular high elevation habitats and habitats that persist unaltered for extended periods (Denno *et al.* 1991; Roff 1994).

Does native diversity originate from colonization events or in situ speciation? To assess the relative importance of immigration vs. *in situ* speciation in generating species diversity, we examined the number of colonization events that gave rise to various groups of taxa. Considering the Hawaiian islands, the flora of 1009 species appears to be derived from only about 270 colonists, not including purposeful introductions or doubtfully native taxa (Price 2004). For Hawaiian terrestrial arthropods overall, it is estimated that as few as 350–400 colonization events gave rise to the 8000–10 000 known species (Howarth & Mull 1992). Indeed, most groups that are well-represented on remote islands are descended from only one, or a few, natural colonizations; far fewer than the number of species in each group, illustrating the overwhelming effect of *in situ* diversification in producing biodiversity. For example, for *Tetragnatha* spiders in Hawaii, there were likely three colonization events that together have given rise to approximately 50 species (Gillespie 2005). For delphacid sap-feeding planthoppers in Hawaii, Ashe (1997) hypothesized that there were five or six introductions for a group that numbers 81 species. For broad-nosed weevils in the genus *Rhyncogonus* (Coleoptera), there appears to have been a single colonization of the central Pacific giving rise to the 112 described species (Claridge 2006). For these weevils, phylogenetic studies suggest that there have been three separate colonizations to the Austral Islands (25 species), Marquesas (22 species) and Hawaiian islands (47 species), though there have been multiple colonizations of islands within each archipelago.

Do lineages show a predictable pattern of specialization through time? To determine the likely evolutionary trajectory of native species, we examined evidence for a predictable pattern of specialization through time. Colonization of an island is often followed by ecological range expansion, or 'ecological release' (Losos & De Queiroz 1997). Wilson (1961) suggested for ants in Melanesia that most colonists disperse through lowland marginal habitats and then extend their distributions into forested and montane habitats on progressively more remote islands — a progression from generalist to specialist distribution he termed the 'taxon cycle'. Such a cycle has also been identified through detailed molecular phylogenetic studies of West Indian birds (Ricklefs & Bermingham 1999, 2001, 2002). These observations led to the suggestion that less specialized taxa have more evolutionary potential and more specialized species are on a trajectory towards extinction. We examined this idea using data from Hawaiian spiders and sets of

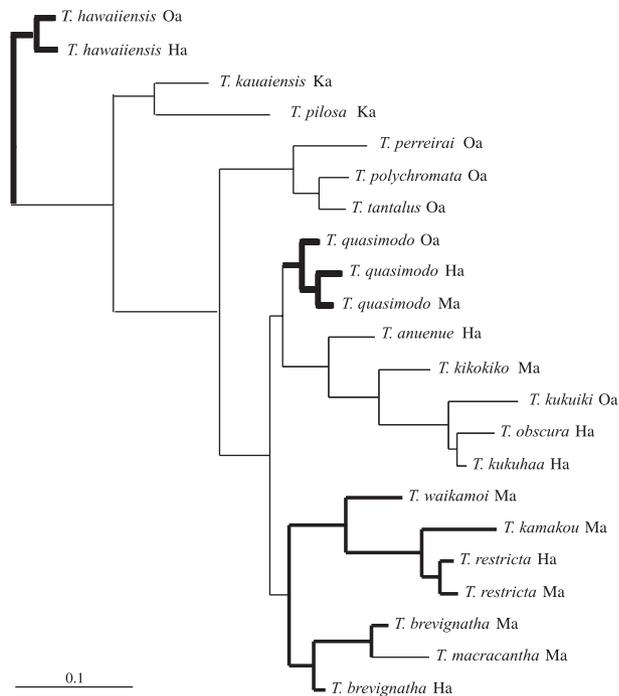


Fig. 3 Phylogenetic analysis of the radiation of Hawaiian spiny-leg *Tetragnatha* spiders showing that shifts of ecological range over phylogenetic history within the radiation are not directional. The tree shown is based on mitochondrial DNA (Gillespie 2004), with the same topology found using allozymes and minisatellite DNA (Pons & Gillespie 2004). There is no overall pattern in ecological range from widespread generalist species to more ecologically specialized species (i.e. 'taxon cycle') within the Hawaiian radiation, as widespread species appear intermittently within the radiation. For example, *Tetragnatha quasimodo* is a widespread generalist spider that has arisen within a clade of more specialized species (Gillespie 2004). Thick lines denote species found throughout the islands; medium lines show species on 2 islands/volcanoes; and thin lines represent species found on one volcano.

specialized herbivorous insects. For the Hawaiian spiny-leg *Tetragnatha* spiders, although colonization of the islands is associated with an immediate reduction in range (described above) and much greater specialization in ecological affinity relative to the outgroup (Gillespie 2005), there is no general tendency for generalist species to give rise to progressively more specialized species as they become more derived (Fig. 3). Widespread generalist species, relative to others within the island lineage, are a common component of Hawaiian radiations, but most appear to arise within the radiation (i.e. these generalist species arise from species that are more specialized). In addition to the *Tetragnatha* example, the happy face spider *Theridion grallator* is a widespread Hawaiian endemic species that has arisen within a radiation of species that have more restricted ranges (Arnedo *et al.* 2007). Likewise, the picture-winged fly *Drosophila grimshawi* is a widespread

species that has arisen within the radiation of Hawaiian *Drosophila* (Kambysellis & Craddock 1997).

For herbivorous insects on islands, many groups with species that are now host specialists appear to have originated from continental or other island taxa that are also specialized (Roderick & Percy 2008). Examples in Hawaii include *Nesosydne* sap-feeding planthoppers (Hemiptera: Delphacidae), as well as *Sarona*, *Nesiomiris* and *Cryptolepis* bugs (Hemiptera: Miridae). The same observation appears to hold for *Miocalles* weevils (Paulay 1985) and carabid beetles (Liebherr 1997), with no indication of unidirectional shifts toward specialization through the history of a lineage within an island radiation.

Is speciation associated with habitat shifts? To assess the ease with which species can switch to new habitats over their evolutionary history, and hence their potential ability to adapt to habitat modification in the future, we examined the extent to which speciation has been associated with major habitat shifts, or alternatively, with smaller microhabitat shifts within a major habitat type. Adaptive radiation is often associated with ecological speciation (Schluter 2001). Moreover, adaptive radiation appears frequently to lead to a deterministic pattern of community assembly (Losos *et al.* 1998; Glor *et al.* 2003; Blackledge & Gillespie 2004; Gillespie 2004). Accordingly, we counted the number of times that speciation within an adaptive radiation was associated with large shifts in habitat use or alternatively with smaller changes within a habitat. Wet forest habitats on different islands of the Hawaiian chain are broadly similar above approximately 600–1000 m, up to the subalpine zone (above approximately 2000 m). Below these elevations, the habitats are very disturbed; above, the climate is dry and cold (Daehler 2005). We used the phylogenetic framework of Hawaiian spiny-leg *Tetragnatha* (see, Gillespie 2004) to examine whether speciation is associated more often with shifts to different major habitat types or to different microhabitats within a habitat type. The phylogeny shows that almost all the native species and/or populations on younger islands stem from similar habitats (wet forest) on older islands within the archipelago. Thus, speciation appears to be associated with adaptation *within* a habitat (i.e. to a specific microhabitat) rather than a change to a *different* habitat type. Ecological change between major habitat types (i.e. habitats with major differences in aridity or temperature) is very uncommon (Fig. 4). Although one switch to so-called 'dry forest' has occurred, such habitats are characterized by extensive cloud cover that promotes the growth of mosses and lichens which cover the trees; accordingly, conditions are unlikely to be very dry for organisms living in this habitat. Colonization of high-elevation alpine shrubland habitats above the inversion layer, which would require physiological adaptation to a very dry and arid environment,

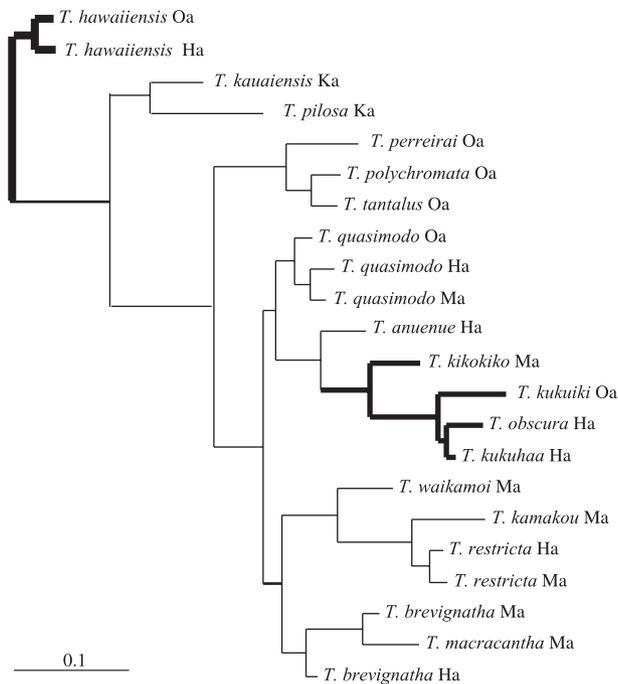


Fig. 4 Phylogenetic analysis of the radiation of Hawaiian *Tetragnatha* spiders showing ecological shifts through time. Source of data as in Fig. 3. Ecological change *between* major habitat types (for example, low elevations to wet montane habitats, and montane forest to mesic habitats) is uncommon. Thick lines denote species found in low elevation habitats; medium lines show montane cloud/dry forest species; and thin lines represent species in montane wet forests.

has never occurred in the spiny-leg *Tetragnatha* spiders; only once in a large clade of web-spinning spiders (R. Gillespie, *unpublished*) and only rarely in other groups (Howarth & Mull 1992).

Are isolated islands more ecologically 'open' to colonizing species? To assess the extent to which island habitats are available to invasive species, we examined evidence for the idea that island habitats are more ecologically 'open'. Previous studies of the evolutionary history of different groups of endemic species in the Hawaiian Islands have shown a very clear and marked tendency for organisms to colonize in the direction of open ecological space; a phenomenon referred to as the 'progression rule' (Funk & Wagner 1995) which applies also to most, but not all, groups of terrestrial arthropods (Roderick & Gillespie 1998). Island age has long been used as a predictor of diversity, the logic being that species diversity increases with time (Emerson & Kolm 2005). Indeed, the native spider (Gillespie 2004) and *Rhyncogonus* weevil (Paulay 1994) communities on the youngest island of Hawaii appear still to be in the early stages of community development relative to the older islands. This effect is not found in all arthropods; for example, gryllid crickets and

drosophilid flies are both very diverse on the youngest island, presumably as a result of more rapid speciation accelerated through sexual selection (Mendelson & Shaw 2005). Taken together, these results show that communities on these islands, in general, have developed only over very long time periods, although the time may vary between lineages. Indeed, the fact that some recent colonists have been able to colonize 'backwards' up the island chain from younger to older islands (Magnacca & Danforth 2006) suggests that ecological opportunity still exists even on the oldest islands. These observations are consistent with the well-publicized susceptibility of islands to invasion by non-native species, which may be explained in part by the time required for community development. Because species are formed only very slowly through evolutionary processes, open niche space may remain available for a very long time, and even for the oldest islands there may have been insufficient time to develop an 'equilibrium' number of species in some groups.

Evolutionary trajectories

Based on the arguments presented in the section above, we can conclude, first, that cloud forests play a key role in the high levels of endemism that characterize the remote islands of the Pacific. In addition, for the arthropod studies presented, the native biota that has colonized the islands has generally undergone a marked reduction in dispersal ability subsequent to colonization, and compared to their continental counterparts, dispersal ability is low for taxa on remote islands. Subsequent species diversity has arisen largely from *in situ* speciation. However, lineages thus formed show no evidence of a predictable pattern of specialization through time; that is, there is no evidence of a taxon cycle *within* an archipelago (Fig. 3). Rather, even though many island species are already specialized in habitat use, relatively widespread species can be derived from lineages that are more specialized, as well as from those lineages that are less specialized. Speciation is associated largely with smaller ecological shifts within a habitat rather than switches between habitats (Fig. 4), and colonization of new habitats (i.e. those with novel climatic regimes) occurs relatively infrequently. Finally, colonization is heavily biased in the direction of open ecological space. Moreover, the large amount of time required for communities to develop species through evolutionary processes on these islands may mean that, at least in some groups, 'equilibrium' numbers are never reached. This may explain the overall tendency of remote islands to be more open to invasive species, an argument that is developed further below. In summary, these individual patterns give a picture of a biota that shows high local endemism, with little tendency to disperse or switch habitat types, with communities having arisen over evolutionary time.

Non-native biodiversity: ecological patterns and process

Since humans arrived on remote islands, dynamics have changed considerably. In particular, islands are now characterized by invasions of nonindigenous species, most of which evolved in very different settings. In order to assess the future of the native biodiversity, it is necessary to understand the ecological and evolutionary dynamic of the nonindigenous species on these islands.

Island invasion. Invasive species are common on islands (Howarth & Ramsay 1991; Cox 1999). These species are not a random selection of taxa since they are largely preadapted for human transport. Invasive species tend to be widely distributed across islands, as predicted based on the well-known population abundance-range-size relationships of many different taxa (Brown 1984; Gaston 1990, 1994; Lawton 1993; Blackburn *et al.* 1997; Kotze *et al.* 2003). Indeed, the extent of distribution of species is often used as an indicator of time of arrival (Elton 1958; Snyder & Evans 2006). However, these ecological attributes alone are not sufficient to indicate that a species is a recent invader (R. Gillespie unpublished). In the remote islands of the Pacific, common invasive species include rodents, mongoose, the cane toad and ungulates such as pigs and goats. Evolution and adaptation can occur rapidly in such groups in response to the new biotic and abiotic conditions (Millien & Damuth 2004; Phillips *et al.* 2006).

Isolated islands tend to be more invulnerable than continents and islands nearer to a source of colonists (Lonsdale 1999), and the indigenous biotas appear to be particularly susceptible to new introductions (Lonsdale 1999; Sax 2001; Denslow 2003; but see Simberloff 1995). Suggested explanations for invulnerability of islands have been based largely on functional traits, generally attributable to lower species richness (Mondor *et al.* 2007) and reduced competitive ability of native species (e.g. Cox 1999). However, such explanations are not entirely adequate (Levine & D'Antonio 1999) as species richness may have either positive or negative effects on invulnerability (Kennedy *et al.* 2002; Levine *et al.* 2002; Gross *et al.* 2005). More recently, emphasis has been placed on whether differences in species pools — i.e. the set of species whose propagules can reach a given community in reasonable time and establish there (Zobel 1997) — can affect invulnerability through neutral processes (Herben 2005; Gimeno *et al.* 2006). For example, in a comparison between Hawaii and Taiwan, it was shown that the high propagule pressure of invasives relative to indigenous species may account for a substantial portion of the difference in invulnerability (Daehler 2006).

Are 'open' habitats more invulnerable? For plant communities it has been demonstrated that invasion resistance is related

to the degree of niche overlap between resident species and invaders (Mwangi *et al.* 2007); likewise for invertebrate communities, species diversity can play a key role in community invulnerability (Beisner *et al.* 2006). Accordingly, if habitats can be protected from disturbance, the biota in those habitats can likely be maintained for long periods of time. However, when a habitat opens as a result of disturbance or modification through geological, climatological or biological — including human-mediated — causes, it becomes available for colonization. Under such circumstances, the original biota can move back in or, alternatively, a different biota might move into the area. The extent to which invasive species move in to open ecological space is in part a function of propagule pressure (Lockwood *et al.* 2005). On an ecological timescale, studies examining the colonization of younger substrates have indicated the effect of habitat or community age on invulnerability. On the island of Hawaii, lava from Mauna Loa has carved up the habitat on a number of occasions, leaving a patchwork of forested fragments dissected by young successional forest on the open lava flows. On an 1881 lava flow following removal of birds, a large increase in nonindigenous spiders was observed (Gruner 2005). On an 1885 lava flow in the same area, nonindigenous spiders were found to invade the lava flows but were never found in the 'kipukas', the remnants of the original forest in the area (Vandergast & Gillespie 2004). These studies support the notion that the open habitat created by the lava flows facilitates invasion by nonindigenous species. Likewise, hurricanes and other catastrophic events can open up habitats to invasive species. However, given a sufficient density of indigenous propagules relative to nonindigenous ones at a site, it appears that native forest habitats can — and do — recover well (Harrington *et al.* 1997).

Interaction between native and non-native biota

The discussion above highlights some marked differences between species that form *in situ* on islands vs. those that arrived through recent invasion. The deterministic pattern of community assembly that has been shown in a number of radiations of endemic species contrasts markedly with the results obtained from studies of communities of invasive species. The differences parallel those between the classical 'niche assembly perspective' on communities vs. the 'dispersal assembly perspective', the latter suggesting that recent invasion may simply parallel a neutral process (Hubbell 2001). From the neutral perspective, the density of individuals in an area provides the best predictor of patterns of colonization in a given environment, and the resulting communities represent a steady-state equilibrium of transient species. The difference in these perspectives in the context of islands may simply be a consequence of time. During the process of adaptive radiation, coexistence of

similar species occurs through evolutionary divergence of a small number of similar taxa over very long periods. By contrast, large numbers of nonindigenous species are now arriving continually on even the most remote islands; accordingly, neutral effects will likely play a more dominant role in the future assembly of communities.

Relative to introduced (and particularly invasive) species, the reduced propagule pressure of most indigenous species may lead to the lower indigenous 'species pool' on islands, which in turn may account for most, if not all, of the differences in invasibility between islands and continental habitats (Herben 2005). Indeed, the few species in the Hawaiian Islands that have retained high dispersal abilities (e.g. the fern *Dicranopteris*) thrive in disturbed habitats (Follet *et al.* 2003). At the same time, propagule pressure alone cannot account for higher invasibility of islands: for example, the diversity of non-native plant species has increased the overall diversity of Hawaiian plants (Sax 2001), suggesting that the islands could accommodate more species than they originally held. In contrast, the influx of nonindigenous birds in Hawaii has only compensated for the loss of diversity of indigenous species (Lockwood 2006), suggesting that native bird diversity was at equilibrium prior to recent extinction. Although many of these patterns may also be explained by neutral models, they do indicate the importance of available niche space in the islands compared to continental habitats.

The overall pattern of enhanced invasibility on islands therefore appears to be interpretable in the context of time and evolution on the islands: on remote islands such as those of the Hawaiian chain, immigration is extremely slow; the rarity of such events exacerbated by the tendency of species that arrive in the islands to undergo an almost immediate reduction in dispersal ability (Darwin 1859). Accordingly, in any given habitat, the historical infrequency of natural immigration has meant that *in situ* evolution of new species generally took place more rapidly than immigration and much of the diversity arose through evolution as opposed to ecological colonization. The youngest island of Hawaii is still in the earliest stages of species diversification and has abundant available niche space. Older islands may have been super-saturated for a few groups but still have had opportunity for new groups to have colonized recently in evolutionary time (e.g. Magnacca & Danforth 2006). The corollary of this observation is that older islands should currently be less open to invasion than younger islands, given the same propagule pressure. Moreover, the generally very low propagule pressure of indigenous species compared to introduced species suggests that it is more likely for introduced species to colonize the open space.

Adaptation to invasion? Several studies have now shown that native species can respond and adapt to introduced species and the re-shuffled communities thus created

(reviewed by Strauss *et al.* 2006). Responses observed include altered antipredator defences, changes in the spectrum of resources and habitats used and other adaptations that permit coexistence of native species in sites that have been invaded. Much of the evidence for the evolution of native species in response to introduced species comes from interactions between phytophagous insects and their hosts on continents. For several cases, evolutionary (genetic) shifts have now been demonstrated where insects switch to nonindigenous host plants (Tabashnik 1983; Thomas *et al.* 1987; Filchak *et al.* 2000; Carroll *et al.* 2001, 2003, 2005; Malausa *et al.* 2005). Lack of similar evidence for island species may be due to the small effective population sizes and low genetic variation characteristic of many native island populations preventing rapid response to new selective regimes (Strauss *et al.* 2006). An alternative explanation may be the low propagule pressure of indigenous species compared to introduced species. Thus, rather than being able to adapt to a new selective regime, an indigenous species in an isolated habitat may simply be displaced, as there will be insufficient numbers to make up for the influx of nonindigenous species.

Future of island biodiversity. We can now make some assessment of the future of island biotas. First, in the long term it is clear that remote islands are no longer as isolated as before. For example, considering the Hawaiian islands where an estimated 270 colonists are thought to have given rise to the known native flora (Price 2004), if colonization commenced on the oldest current high-elevation island of Kauai (which appears to be true for most groups), 54 successful colonizations per million years would be required to give rise to the current biota. By contrast, in the year 2003 approx 7.5 million overseas passengers deplaned in the Hawaiian islands (State of Hawaii 2007). Likewise, 184 328 tons of cargo and 46 515 tons of mail from overseas were taken off planes in the same year. If only one of every 10 000 passengers plus one out of 10 000 pieces of cargo and mail (assuming, conservatively, that the average cargo package weighs 1000 lbs and mail 2 lbs) each carried a stray seed, and just 1% of these seeds became established, this would still represent an increase in the rate of colonization to the islands of more than one million fold! Therefore, the processes that created the pattern of historical diversity have been lost, and examining the propensity of given lineages to speciate has little practical conservation significance. The basis for this assertion is that, as new land mass appears, isolated habitats will tend to be colonized through immigration of alien species simply because these have greater dispersal ranges and higher propagule pressure than indigenous species. Thus, the effect will be to shift what creates/determines biodiversity from evolutionary processes to ecological, with species diversity being a balance between immigration (greater on islands with

more trade) and extinction (greater on smaller islands). At the same time, except when habitats are modified, current communities show surprising resistance and resilience to invasion by nonindigenous species.

Climate change results in a somewhat different scenario in that it will likely lead to a rise in the elevation of cloud-forest habitats. Pacific-island cloud forests are particularly vulnerable to climate change because relatively small climate shifts are likely to trigger major local shifts in rainfall, cloud cover and humidity (Loope & Giambelluca 1998). On islands such as Pohnpei, Kosrae, Moorea, and Rapa, the cloud forests are already restricted to the very highest elevations. Accordingly, given even a small change in climatic regime, these habitats will disappear. Extinction — associated with stochastic processes due to small population size — would seem to be the inevitable fate of the biota, as all the evidence we have suggests that, for native species, speciation within similar habitats occurs much more readily than adaptation to new habitats (see above, Fig. 4). Taxa at lower elevations may then move up the mountain; but perhaps more likely, the newly modified habitats will be filled by invasive species which may colonize more rapidly and in greater numbers.

Application to mainland habitats

The current study shows first, that isolated environmental regimes — in particular the unusual conditions that lead to cloud forest — have led to the formation of uniquely evolved sets of biota on each of the remote high islands of the Pacific. Second, key factors involved in the formation of remote island communities, often through adaptive radiation, appear to have been very low dispersal ability, with speciation occurring more rapidly than immigration. The primary difference between remote islands and continents is that in many continental regions, indigenous species have not lost the ability to disperse, so disturbed habitats are not always likely to be filled by invasive species at the expense of local species. However, some mountain habitats demonstrate marked isolation, with taxa that have also suffered a much reduced ability to disperse (Roff 1994). Like those on islands, many of these species are locally abundant (Pimm 2002; Reif *et al.* 2006) and hence are likely to show resistance or resilience to invasion. However, if their populations decline or are pushed into marginal habitats, the opened habitat will likely be filled by nonindigenous propagules in the same way as described for islands.

Conclusions

Islands clearly illustrate the power of evolution in shaping communities and the ability of populations and species to adapt, diversify and fill available ecological space.

However, in the process of adaptive radiation, which accounts for the rich diversity of isolated islands, speciation has occurred more rapidly than colonization. Speciation itself is a slow process, although can be accelerated greatly by natural — and in particular sexual — selection, and by genetic drift and other processes when population sizes are small (Carson 1990; Slatkin 1996; Otto & Whitlock 1997). But whatever the mechanism, reduced dispersal is a major factor not only in allowing island populations to diverge from source populations, but also in accelerating adaptive change. With the recent increase in global transportation and trade, few habitats remain isolated. Therefore, species in island-type habitats — where most taxa home propagules that establish relatively infrequently — may fare well if left undisturbed, or even if disturbance does not result in prolonged change. However, it is generally easier for species to move than to adapt. Therefore, if the habitat changes, the probability of preadapted nonindigenous species moving in to the modified habitat will be greater than the chance of adaptation by the few indigenous propagules. Thus, while a laudable goal of conservation efforts is to preserve the evolutionary process, one must also be careful to evaluate the likely form that the process will take when the context has been significantly modified.

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References

- Arnedo MA, Agnarsson I, Gillespie RG (2007) Molecular Insights into the phylogenetic structure of the spider genus *Theridion* (Araneae, Theridiidae) and the origin of the Hawaiian *Theridion*-like fauna. *Zoologica Scripta*, **36**, 337–352.
- Asche M (1997) A review of the systematics of Hawaiian planthoppers (Hemiptera: Fulgoroidea). *Pacific Science*, **51**, 366–376.
- Baillie JEM, Hilton-Taylor C, Stuart SN (2004) *A Global Species Assessment: 2004 IUCN Red List of Threatened Species* (ed. Commission TISS). IUCN, Gland, Switzerland and Cambridge, UK.
- Beisner BE, Hovius J, Hayward A, Kolasa J, Romanuk TN (2006) Environmental productivity and biodiversity effects on invertebrate community invasibility. *Biological Invasions*, **8**, 655–664.
- Blackburn TM, Gaston KJ, Quinn RM, Arnold H, Gregory RD (1997) of mice and wrens: The relation between abundance and

- geographic rangesize in British mammals and birds. *Philosophical Transactions of the Royal Society London, Series B: Biological Sciences*, **352**, 419–427.
- Blackledge TA, Gillespie RG (2004) Convergent evolution of behavior in an adaptive radiation of Hawaiian web-building spiders. *Proceedings of the National Academy of Sciences, USA*, **101**, 16228–16233.
- Brown JH (1984) The relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.
- Carroll SP, Dingle H, Famula TR, Fox CW (2001) Genetic architecture of adaptive differentiation in evolving host races of the soapberry bug, *Jadera haematoloma*. *Genetica*, **112**, 257–272.
- Carroll SP, Marler M, Winchell R, Dingle H (2003) Evolution of cryptic flight morph and life history differences during host race radiation in the soapberry bug, *Jadera haematoloma* Herrich-Schaeffer (Hemiptera: Rhopalidae). *Annals Entomological Society of America*, **96**, 135–143.
- Carroll SP, Loye JE, Dingle H, Mathieson M, Famula TR, Zalucki M (2005) And the beak shall inherit – evolution in response to invasion. *Ecology Letters*, **8**, 944–951.
- Carson HL (1990) Increased genetic variance after a population bottleneck. *Trends in Ecology and Evolution*, **5**, 228–230.
- Carson HL, Clague DA (1995) Geology and biogeography of the Hawaiian Islands. In: *Hawaiian Biogeography Evolution on a Hot Spot Archipelago* (eds Wagner WL, Funk VA), Smithsonian Institution Press, Washington, DC.
- Carson HL, Sato JE (1969) Microevolution within 3 species of Hawaiian *Drosophila*. *Evolution*, **23**, 493–501.
- Case TJ (1978) A general explanation for insular body size trends in terrestrial vertebrates. *Ecology*, **59**, 1–18.
- Claridge EM (2006) *The Systematics and Diversification of Rhynogonus Weevils (Entiminae: Curculionidae) in the Central Pacific*. University of California, Berkeley, CA.
- Cox GW (1999) *Alien Species in North America and Hawaii*. Island Press, Washington, DC.
- Daehler C (2005) Upper-montane plant invasions in the Hawaiian Islands: Patterns and opportunities. *Perspectives in Plant Ecology, Evolution and Systematics*, **7**, 203–216.
- Daehler CC (2006) Invasibility of tropical islands by introduced plants: Partitioning the influence of isolation and propagule pressure. *Preslia*, **78**, 389–404.
- Dahl AL (1998) Island directory. United Nations Environment Programme, URL: <http://islands.unep.ch>.
- Darwin CR (1859) *On the Origin of Species by Means of Natural Selection*. John Murray, London, UK.
- Denno RF (1994) Life history variation in planthoppers. In: *Planthoppers Their Ecology and Management* (eds Denno RF, Perfect TJ), pp. 163–215. Chapman & Hall, New York.
- Denno RF, Roderick GK, Olmstead KD, Döbel HG (1991) Density-related migration in planthoppers: the role of habitat persistence. *American Naturalist*, **138**, 1513–1541.
- Denslow JS (2003) Weeds in paradise: thoughts on the invasibility of tropical islands. *Annals of the Missouri Botanical Garden*, **90**, 119–127.
- Eldredge LG, Evenhuis NL (2003) Hawaii's biodiversity: a detailed assessment of the numbers of species in the Hawaiian Islands. *Bishop Museum Occasional Papers*, **76**, 1–28.
- Elton C (1958) *The Ecology of Invasions by Plants and Animals*. Methuen, London.
- Emerson BC, Kolm N (2005) Species diversity can drive speciation. *Nature*, **434**, 1015–1017.
- Filchak KE, Roethele JB, Feder JL (2000) Natural selection and sympatric divergence in the apple maggot *Rhagoletis pomonella*. *Nature*, **407**, 739–742.
- Florence J (1987) Endemisme et evolution de la flore de la Polynesie française. *Bulletin de la Société Zoologique de France*, **112**, 369–380.
- Florence J (1993) La vegetation de quelques iles de Polynesie française. In: *Atlas de la Polynesie Française* (ed. Dupon JF), l'ORSTOM, Paris.
- Florence J (1997) *Flore de la Polynesie Française* l'ORSTOM, Paris.
- Florence J, Lorence DH (1997) Introduction to the flora and vegetation of the Marquesas Islands. *Allertonia*, **7**, 226–237.
- Follet PA, Anderson-Wong P, Johnson MT, Jones VP (2003) Revegetation in dead *Dicranopteris* (Gleicheniaceae) fern patches associated with Hawaiian rain forests. *Pacific Science*, **57**, 347–357.
- Funk VA, Wagner WL (1995) Biogeographic patterns in the Hawaiian Islands. In: *Hawaiian Biogeography: Evolution on a Hot Spot Archipelago* (eds Wagner WL, Funk VA), Smithsonian Institution Press, Washington, DC.
- Gaston KJ (1990) Patterns in the geographical ranges of species. *Biological Review*, **65**, 105–129.
- Gaston KJ (1994) *Rarity*. Chapman & Hall, London.
- Gillespie RG (1991) Hawaiian spiders of the genus *Tetragnatha*: I. Spiny leg clade. *Journal of Arachnology*, **19**, 174–209.
- Gillespie RG (2002) Hawaiian Spiders of the Genus *Tetragnatha*: IV: New, Small Species in the Spiny Leg Clade. *Journal of Arachnology*, **30**, 159–172.
- Gillespie RG (2004) Community assembly through adaptive radiation in Hawaiian spiders. *Science*, **303**, 356–359.
- Gillespie RG (2005) The ecology and evolution of Hawaiian spider communities. *American Scientist*, **93**, 122–131.
- Gillespie RG, Oxford GS (1998) Selection on the color polymorphism in Hawaiian happy-face spiders: evidence from genetic structure and temporal fluctuations. *Evolution*, **52**, 775–783.
- Gillespie RG, Roderick GK (2002) Arthropods on islands: evolution, speciation, and conservation. *Annual Review of Entomology*, **47**, 595–632.
- Gimeno I, Vilà M, Hulme PE (2006) Are islands more susceptible to plant invasion than continents? A test using *Oxalis pescaprae* L. in the western Mediterranean. *Journal of Biogeography*, **33**, 1559–1565.
- Glor RE, Kolbe JJ, Powell R, Larson A, Losos JB (2003) Phylogenetic analysis of ecological and morphological diversification in Hispaniolan trunk-ground anoles (*Anolis cybotes* group). *Evolution*, **57**, 2383–2397.
- Grant PR (1998) *Evolution on Islands*, p. 334. Oxford University Press, Oxford.
- Gressitt JL (1974) Insect biogeography. *Annual Review of Entomology*, **19**, 293–321.
- Gross KL, Mittelbach GG, Reynolds HL (2005) Grassland invasibility and diversity: Responses to nutrients, seed input, and disturbance. *Ecology*, **86**, 476–486.
- Gruner DS (2005) Biotic resistance to an invasive spider conferred by generalist insectivorous birds on Hawai'i Island. *Biological Invasions*, **7**, 541–546.
- Hamilton LS, Juvik JO, Scatena FN (1995) Tropical montane cloud forests. In: *Ecological Studies 110*. Springer-Verlag, New York.
- Harrington RA, Fownes JH, Scowcroft PG, Vann CS (1997) Impact of Hurricane Iniki on native Hawaiian *Acacia koa* forests: Damage and two-year recovery. *Journal of Tropical Ecology*, **13**, 539–558.
- Herben T (2005) Species pool size and invasibility of island communities: a null model of sampling effects. *Ecology Letters*, **8**, 909–917.

- Howarth FG, Mull WP (1992) *Hawaiian Insects and Their Kin*. University of Hawaii Press, Honolulu.
- Howarth FG, Ramsay GW (1991) The conservation of island insects and their habitats. In: *The Conservation of Insects and Their Habitats* (eds Collins NM, Thomas JA). Academic Press, London.
- Hubbell SP (2001) *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton University Press, Princeton, NJ.
- Kambysellis MP, Craddock EM (1997) Ecological and reproductive shifts in the diversification of the endemic Hawaiian *Drosophila*. In: *Molecular Evolution and Adaptive Radiation* (eds Givnish TJ, Sytsma KJ), Cambridge University Press, New York.
- Kennedy TA, Naeem S, Howe KM, Knops JMH, Tilman D, Reich P (2002) Biodiversity as a barrier to ecological invasion. *Nature*, **417**, 636–638.
- Kotze DJ, Niemelä J, O'Hara RB, Turin H (2003) Testing abundance-range size relationships in European carabid beetles (Coleoptera, Carabidae). *Ecography*, **26**, 553–566.
- Lawton JH (1993) Range, population abundance and conservation. *Trends in Ecology and Evolution*, **8**, 409–413.
- Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.
- Levine JM, Kennedy T, Naeem S (2002) Neighborhood scale effects of species diversity on biological invasions and their relationship to community patterns. In: *Biodiversity and Ecosystem Functioning – Synthesis and Perspectives* (eds Loreau M, Naeem S, Inchausti P), Oxford University Press, Oxford.
- Liebherr JK (1997) Dispersal and vicariance in Hawaiian platynine carabid beetles (Coleoptera). *Pacific Science*, **51**, 424–439.
- Lockwood JL (2006) Life in a double-hotspot: the transformation of Hawaiian passerine bird diversity following invasion and extinction. *Biological Invasions*, **8**, 449–457.
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology and Evolution*, **20**, 223–228.
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- Loope LL, Giambelluca TW (1998) Vulnerability of island tropical montane forests to climate change, with special reference to East Maui, Hawaii. *Climate Change*, **39**, 503–517.
- Losos JB, De Queiroz K (1997) Evolutionary consequences of ecological release in Caribbean *Anolis* lizards. *Biological Journal of the Linnean Society*, **61**, 459–483.
- Losos JB, Jackman TR, Larson A, De Queiroz K, Rodriguez-Schettino L (1998) Contingency and determinism in replicated adaptive radiations of island lizards. *Science*, **279**, 2115–2118.
- MacArthur RH, Wilson EO (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.
- Magnacca KN, Danforth BN (2006) Evolution and biogeography of native Hawaiian *Hylaeus* bees (Hymenoptera: Colletidae). *Cladistics*, **22**, 393–411.
- Malausa T, Bethenod MT, Bontemps A, Bourguet D, Cornuet JM, Ponsard S (2005) Assortative mating in sympatric host races of the European corn borer. *Science*, **308**, 258–260.
- Manner HL, Mueller-Dombois D, Rapaport M (1999) Terrestrial ecosystems. In: *The Pacific Islands: Environment Society* (ed. Rapaport M), The Bess Press, Honolulu.
- Mendelson TC, Shaw KL (2005) Sexual behaviour: Rapid speciation in an arthropod. *Nature*, **433**, 375–376.
- Merlin MD, Juvik JO (1992) Relationships among native and alien plants on Pacific islands with and without significant human disturbance and feral ungulates. In: *Alien Plant Invasions in Native Ecosystems of Hawaii: Management and Research* (eds Stone CP, Smith CW, Tunison JT), University of Hawai'i Cooperative National Park Resource Studies Unit, Honolulu.
- Merlin M, Raynor W (2005) Kava cultivation, native species conservation, and integrated watershed resource management on Pohnpei Island. *Pacific Science*, **59**, 241–260.
- Meyer J-Y (2004) Threat of invasive alien plants to native flora and forest vegetation of eastern Polynesia. *Pacific Science*, **58**, 357–375.
- Meyer J-Y, Florence J (1996) Tahiti's native flora endangered by the invasion of *Miconia calvescens* D.C. (Melastomaceae). *Journal of Biogeography*, **23**, 775–781.
- Millien V, Damuth J (2004) Climate change and size evolution in an island rodent species: new perspectives on the island rule. *Evolution*, **58**, 1353–1360.
- Mondor EB, Tremblay MN, Messing RH (2007) Morphological and ecological traits promoting aphid colonization of the Hawaiian Islands. *Biological Invasions*, **9**, 87–100.
- Mueller-Dombois D, Fosberg FR (1998) *Vegetation of the Pacific Islands*. Springer-Verlag, New York.
- Mwangi PN, Schmitz M, Scherber C *et al.* (2007) Niche pre-emption increases with species richness in experimental plant communities. *Journal of Ecology*, **95**, 65–78.
- Nadkarni N, Solano R (2002) Potential effects of climate change on canopy communities in a tropical cloud forest: An experimental approach. *Oecologia*, **131**, 580–584.
- Office of Technology Assessment (1987) Integrated Renewable Resource Assessment for U.S. Insular Areas. In: *Office of Technology Assessment (OTA) Report F325*. Government Printing Office, Washington, DC.
- Otto SP, Whitlock MC (1997) Probability of fixation in populations of changing size. *Genetics*, **146**, 723–733.
- Paulay G (1985) Adaptive radiation on an isolated oceanic island: the Cryptorhynchinae (Curculionidae) of Rapa revisited. *Biological Journal of the Linnean Society*, **26**, 95–187.
- Paulay G (1994) Biodiversity on oceanic islands: its origin and extinction. *American Zoologist*, **34**, 134–144.
- Phillips BL, Brown GP, Webb JK, Shine R (2006) Invasion and the evolution of speed in toads. *Nature*, **439**, 803–803.
- Piano F, Craddock EM, Kambysellis MP (1997) Phylogeny of the island populations of the Hawaiian *Drosophila Grimshawi* complex: evidence from combined data. *Molecular Phylogenetics and Evolution*, **7**, 173–184.
- Pimm SL (2002) The Dodo went extinct (and other ecological myths). *Annals of the Missouri Botanical Garden*, **89**, 190–198.
- Pons J, Gillespie RG (2004) Evolution of satellite DNAs in a radiation of endemic Hawaiian spiders: Does concerted evolution of highly repetitive sequences reflect evolutionary history? *Journal of Molecular Evolution*, **59**, 632–641.
- Pounds JA, Fogden MPL, Campbell JH (1999) Biological response to climate change on a tropical mountain. *Nature*, **398**, 611–615.
- Price JP (2004) Floristic biogeography of the Hawaiian Islands: influences of area, environment and paleogeography. *Journal of Biogeography*, **31**, 487–500.
- Raynor W (1995) Montane cloud forests in Micronesia: Status and future management. In: *Tropical Montane Cloud Forests* (eds Hamilton LS, Juvik JO, Scatena FN). Springer-Verlag, New York.
- Reif J, Hořák D, Sedláček O, Riegert J, Pešata M, Hrázský Z, Janeček S, Storch D (2006) Unusual abundance–range size relationship in an Afrotropical bird community: the effect of geographical isolation? *Journal of Biogeography*, **33**, 1959–1968.

- Ricklefs RE, Bermingham E (1999) Taxon cycles in the Lesser Antillean avifauna. *Ostrich*, **70**, 49–59.
- Ricklefs RE, Bermingham E (2001) Nonequilibrium diversity dynamics of the Lesser Antillean avifauna. *Science*, **294**, 1522–1524.
- Ricklefs RE, Bermingham E (2002) The concept of the taxon cycle in biogeography. *Global Ecology and Biogeography*, **11**, 353–361.
- Roderick GK, Gillespie RG (1998) Speciation and phylogeography of Hawaiian terrestrial arthropods. *Molecular Ecology*, **7**, 519–531.
- Roderick GK, Percy DM (in press) Host plant use, diversification, and coevolution: Insights from remote oceanic islands. In: *Evolutionary Biology of Plant and Insect Relationships* (ed. Tilmon KJ), University of California Press, Berkeley, CA.
- Roff DA (1994) Habitat persistence and the evolution of wing dimorphism in insects. *American Naturalist*, **144**, 772–798.
- Rolett B, Diamond J (2004) Environmental predictors of pre-European deforestation on Pacific islands. *Nature*, **431**, 443–446.
- Sakai AK, Wagner WL, Ferguson DM, Herbst DR (1995) Biogeographical and ecological correlates of dioecy in the Hawaiian flora. *Ecology*, **76**, 2530–2543.
- Sax DF (2001) Latitudinal gradients and geographic ranges of exotic species: implications for biogeography. *Journal of Biogeography*, **28**, 139–150.
- Schluter D (2001) Ecology and the origin of species. *Trends in Ecology and Evolution*, **16**, 372–380.
- Simberloff D (1995) Why do introduced species appear to devastate islands more than mainland areas? *Pacific Science*, **49**, 87–97.
- Simberloff D, Wilson EO (1969) Experimental zoogeography of islands: The colonization of empty islands. *Ecology*, **50**, 278–296.
- Simon C, Sugden A (1987) Hawaiian evolutionary biology. *Trends in Ecology and Evolution*, **2**, 173–229.
- Slatkin M (1996) In defense of founder-flush theories of speciation. *American Naturalist*, **147**, 493–505.
- Snyder WE, Evans EW (2006) Ecological effects of invasive arthropod generalist predators. *Annual Review Ecology and Systematics*, **37**, 95–122.
- State of Hawaii (2007) Airport activity statistics by calendar year. In: *An Annual Statistical Publication of the State of Hawaii* (ed. Airports Planning Office HIA). Department of Transportation, Airports Division, Honolulu.
- Steadman DW (1995) Prehistoric extinctions of Pacific island birds: biodiversity meets zooarchaeology. *Science*, **267**, 1123–1131.
- Still CJ, Foster PN, Schneider SH (1999) Simulating the effects of climate change on tropical montane cloud forests. *Nature*, **398**, 608–610.
- Strauss SY, Lau JA, Carroll SP (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecology Letters*, **9**, 357–374.
- Tabashnik BE (1983) Host range evolution: the shift from native legume hosts to alfalfa by the butterfly, *Colias philodice eriphyle*. *Evolution*, **37**, 150–162.
- Thomas CD, Ng D, Singer MC, Mallet JLB, Parmesan C, Billington HL (1987) Incorporation of a European weed into the diet of a North American herbivore. *Evolution*, **41**, 892–901.
- Toft CA, Schoener TW (1983) Abundance and diversity of orb spiders on 106 Bahamian islands: biogeography at an intermediate trophic level. *Oikos*, **41**, 411–426.
- Vandergast AG, Gillespie RG (2004) Effects of natural forest fragmentation on a Hawaiian spider community. *Environmental Entomology*, **33**, 1296–1305.
- Vandergast AG, Gillespie RG, Roderick GK (2004) Influence of volcanic activity on the population genetic structure of Hawaiian *Tetragnatha* spiders: fragmentation, rapid population growth, and the potential for accelerated evolution. *Molecular Ecology*, **13**, 1729–1743.
- Wagner WL, Herbst DR, Sohmer SH (1999) *Manual of the Flowering Plants of Hawaii (Including Annual Updates Through 2003)*, Volumes 1 and 2. University of Hawaii Press, Honolulu.
- Wilson EO (1961) The nature of the taxon cycle in the Melanesian ant fauna. *American Naturalist*, **95**, 169–193.
- Zobel M (1997) The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends in Ecology & Evolution*, **12**, 266–269.

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