

# ARTHROPODS ON ISLANDS: Colonization, Speciation, and Conservation

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Rosemary G. Gillespie and George K. Roderick

*Environmental Science, Policy, and Management, Division of Insect Biology, University of California, Berkeley, California 94720-3112; e-mail: gillespi@nature.berkeley.edu; roderick@nature.berkeley.edu*

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■ **Abstract** Islands have traditionally been considered to be any relatively small body of land completely surrounded by water. However, their primary biological characteristic, an extended period of isolation from a source of colonists, is common also to many situations on continents. Accordingly, theories and predictions developed for true islands have been applied to a huge array of systems, from rock pools, to single tree species in forests, to oceanic islands. Here, we examine the literature on islands in the broadest sense (i.e., whether surrounded by water or any other uninhabitable matrix) as it pertains to terrestrial arthropods. We categorize islands according to the features they share. The primary distinction between different island systems is “darwinian” islands (formed *de novo*) and “fragment” islands. In the former, the islands have never been in contact with the source of colonists and have abundant “empty” ecological niche space. On these islands, species numbers will initially increase through immigration, the rate depending on the degree of isolation. If isolation persists, over time species formation will result in “neo-endemics.” When isolation is extreme, the ecological space will gradually be filled through speciation (rather than immigration) and adaptive radiation of neo-endemics. Fragment islands are fundamentally different. In these islands, the ecological space will initially be filled as a consequence of connection to the source of colonists prior to insularization. Species numbers will decrease following fragmentation through the process of relaxation. If these islands become more isolated, species will eventually arise through relictualization with the formation of “paleo-endemics.” Given sufficient time, this process can result in generic level endemism on ancient fragment islands, a phenomenon well illustrated in Madagascar and New Zealand. Recognizing the distinction between the different kinds of islands is fundamental for understanding emerging patterns on each, in particular speciation, biodiversity (e.g., neo-endemics versus paleo-endemics), and conservation (e.g., naiveté in interactions with alien species).

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## INTRODUCTION

The common characteristic uniting all island systems is isolation, which can result in properties such as a microcosmal nature and a uniquely evolved biota. Scientific interest in islands started when explorers first began sailing the oceans, and studies of the relationship between species number and both island size and fragmentation date back to voyages of the eighteenth and nineteenth centuries (19). The importance of evolutionary processes on islands was first recognized in Charles Darwin's work on the Galapagos (38). However, the inaccessibility of many of the more remote islands made entomological surveys challenging. Nevertheless, the intrigue of islands for entomologists remained, and the late-nineteenth and early-twentieth centuries saw a tremendous boom in collecting efforts. For example in the Pacific, the British Royal Society's initial studies in the Hawaiian Islands, conducted by R.C.L. Perkins (140), led to the publication of the *Fauna Hawaiiensis*, which continues to serve as a foundation for entomological studies on the islands. Subsequently the Bishop Museum's Pacific Entomological Survey (3) led

to considerable enhancement of the knowledge of the insects in French Polynesia. Additional expeditions in the Pacific took place mostly in the 1930s and 1940s (73), with associated major publications [e.g., *The Insects of Micronesia* (69)]. A bibliography of some of the major papers on insects of the Pacific islands is given by S.E. Miller (121).

More recently, the concept of islands has been expanded to include habitats within a continental landmass that are isolated from similar habitats by inhospitable terrain. Such habitat islands have been studied intensively over the past few decades with the development of the field of conservation biology and concepts of reserve size, fragmentation, and corridors (41, 194). Here, much more than for islands in the ocean, the perception of an isolated habitat as an island depends on the organism in question.

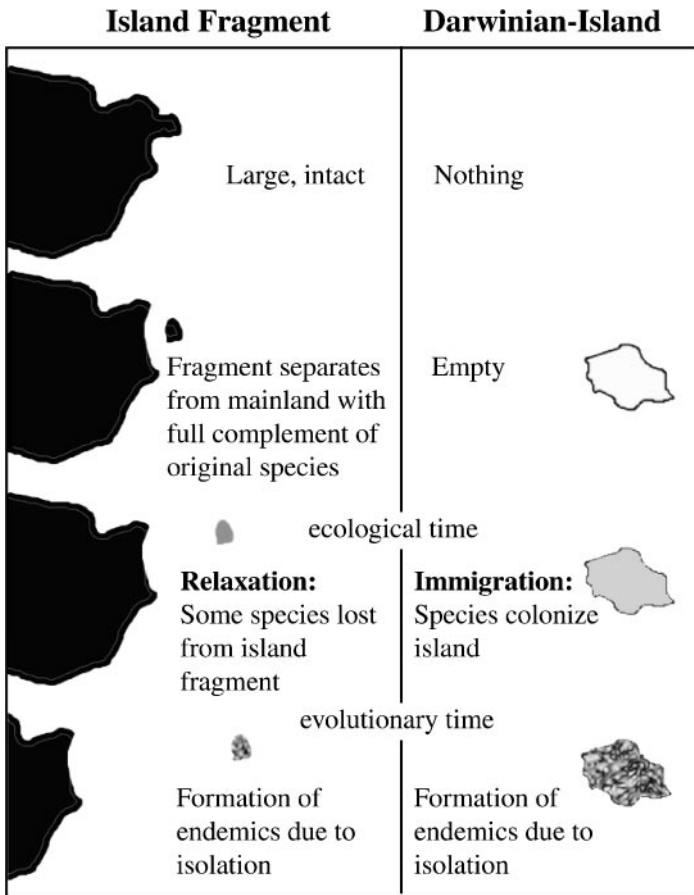
The literature on islands has continued to expand, with theories originally developed for islands surrounded by water now applied to a huge array of systems and associated problems in ecology, evolution, and conservation biology, from metapopulations, demographics of small populations, conservation fragments, and alien invasions, to mechanisms of speciation and adaptive radiation. The term island has been used across a wide range of levels of isolation, from individuals on trees in a forest (129) to dissected patches of vegetation (42), rock pools (174), and tussocks, as well as landmasses, up to the size of Australia, in the middle of the ocean. Clearly, when the discussion becomes so broad clarification is needed of properties of islands and the fundamental differences that lead to adaptive radiation in some situations and conservation concern in others.

The purpose of this review is to provide a context for studies of islands, using examples derived almost exclusively from the literature on terrestrial arthropods, so that similar insular situations can be compared and theories (e.g., equilibrium theory, ecological release, adaptive radiation) can be applied appropriately. We define island as any discrete habitat isolated from other such habitats by inhospitable matrix. As we will discuss, the primary differences between islands relate not so much to the matrix surrounding the island, but rather to island history and scale of isolation relative to the organism in question.

## ISLAND UNIQUENESS: THE IMPORTANCE OF HISTORY AND ISOLATION

A critical feature of all island systems is that they are, by definition, isolated to some degree from a source pool. However, the properties of two islands with the same level of isolation may differ radically depending on the history of the island. This distinction has been recognized for a long time. Darwin (38) advocated the view, controversial at the time, that many islands were formed *de novo*, and organisms must have dispersed there from continents. However, Wallace (186) viewed islands as fragments of continents, based on his studies of the islands of Indonesia. The arguments developed by Darwin and Wallace are fundamental

to understanding islands. If an island has ever been close to, or in contact with, a source, such as a mainland landmass, it will be open to immigration such that the biota will be similar to the source, except as a result of accidents of sampling. As a consequence, the ecological niche space will already be largely filled at the point of isolation (Figure 1). This is true even if the island becomes, over geological time, more removed from the mainland: It will still be unavailable for exploitation by most taxa that do manage to colonize it. On the other hand, islands that have never been in contact with a mainland source will inevitably have ecological space that is open and available when they first appear. However, it should be noted that, because niches are defined by the organisms that occupy them, the concept of open niche space is notoriously problematical. In addition, there has been much debate as to the degree of Hutchinsonian space that allows for maximal species packing



**Figure 1** Historical creation of fragment and darwinian islands.

and whether most continental communities have all their niches filled (148). That being said, unoccupied ecological space on newly formed islands that are the result of fragmentation will almost certainly be less than that on comparable new islands that are formed initially without life.

Over time and with isolation, the number of species on islands created by fragmentation will, if anything, decline. Populations on these islands may diverge genetically from the source over evolutionary time either through changes in the island or in the source population. On islands created without life, however, the number of species will initially only increase. This increase may lead to a balance between immigration and extinction. However, when isolation on these islands is such that most species never colonize (rate of immigration slower than the rate of species formation), then adaptive radiation can occur. Because of the fundamental importance of island history in dictating species composition, a clear distinction should be made between (*a*) darwinian islands, i.e., those envisioned by Darwin, which we define as any newly created habitat that appears within an unlike matrix; and (*b*) fragment islands, which we define as any habitat that has broken off from a larger habitat and in so doing has become separated by an expanse of unlike matrix (Figure 1; Table 1). The best known darwinian islands are certainly oceanic islands, which by definition arise from the floor of the ocean basin and hence have never been connected to continental landmasses. However, there are a number of other isolated habitats that are not oceanic yet are created *de novo* and therefore share the biological properties of oceanic islands (described below). By contrast, the best known fragment islands are perhaps continental islands that were originally part of a continental mass but have broken off through geological processes, or have become isolated by rising sea levels. However, numerous isolated habitats within continents share the biological properties of continental islands and so should also be considered as fragment islands (also described below).

Besides history, the composition of the fauna of an island is dictated largely by the scale of isolation, with time playing a role (Table 1). First, the degree of isolation of an island depends on the dispersal abilities of a taxon. For example, the Hawaiian Islands are often considered to be the most isolated archipelago in the world (168): Yet, although these islands are undoubtedly remote for most terrestrial organisms, they are merely stop-offs for certain sea birds and winter feeding grounds for whales. At the other extreme, for certain wingless and specialized organisms, a few meters between patches of suitable habitat may serve as isolating barriers.

The nature of the matrix surrounding an island is also important in dictating the isolation of the island. Islands that are separated from a primary source population by a matrix of sea water are generally colonized from the primary source. However, aquatic invertebrates are known to colonize oceanic island streams from the sea water matrix (150). Likewise, caves represent islands within a terrestrial environment, although a cave may be colonized, not only by migration from another cave, but also by immigration of individuals from the matrix and subsequent adaptation.

**TABLE 1** Summary of island type, history, ecological and evolutionary processes

Island type	Darwinian (newly created) islands	Fragment islands
<b>Island history</b>	no prior contact with source; ecological niche space entirely open at outset	connected to source prior to insularization; ecological niche space filled before island forms
<b>Scale of isolation</b>	<b>Low<sup>a</sup></b>	<b>Low</b>
<b>Examples<sup>d</sup></b>	mangrove islands, rock pools	remnant trees & forest patches
<b>Ecological change in species number</b>	increases as result of colonization	decreases as result of relaxation
<b>Rate of immigration</b>	rapid	rapid
<b>Disharmony</b>		intermediate
<b>Ecological time</b>	low	low
<b>Evolutionary time</b>	low	intermediate
<b>Colonization</b>	many colonists	many colonists
<b>Success of initial colonists</b>	high (open ecological space)	low (little vacant ecological space)
<b>Ecological changes subsequent to colonization</b>	ecological release (associated with open ecological space)	little ecological change (ecological space largely "filled")
<b>Evolutionary changes subsequent to colonization</b>	no endemism	no endemism
	neo-endemism, single species	paleo-endemism (increases with isolation) through relictualization
<b>Conservation issues—invasions</b>		
<b>Vulnerability to alien species</b>	not unusually vulnerable	not unusually vulnerable
	intermediate	intermediate
	very high owing to naiveté of neo-endemics	intermediate
		may be high among paleo-endemics

<sup>a</sup>Insufficient for population divergence; <sup>b</sup>sufficient for population divergence; <sup>c</sup>zero or otherwise slower than the evolutionary rate of species formation; <sup>d</sup>dependent on species in question.

In the case of habitat islands, the degree to which one area is isolated depends on the dissimilarity of the matrix surrounding it.

Isolation of more remote islands may also depend on the availability of islands closer to the source that can serve as "stepping stones." Without doubt, it is possible for islands to serve as stepping stones, although they do not necessarily serve this function. For example, the faunas of some remote eastern Pacific islands (Society, Marquesas, Pitcairn, Henderson, and Juan Fernandez islands) have components in common (54), a phenomenon that could readily be explained if the islands served as stepping stones from one archipelago to the next (70). However, it is also well known that the native taxa that are well represented on these islands exhibit high levels of endemism and tend to have reduced dispersal abilities—many are flightless (168). Accordingly, the native species of one such archipelago may be unlikely colonizers of other archipelagoes. Another explanation for the similarity in the faunas is that there are certain taxa that disperse well, and successful colonization of more remote islands of the Pacific is largely confined to these taxa. This explanation is supported by molecular data for tetragnathid spiders and delphacid planthoppers that suggest multiple, yet independent, colonization events of different remote archipelagoes in the Pacific (R. Gillespie & G. Roderick, unpublished data).

Finally, the availability of suitable transportation vectors can play a role in determining island isolation. For example, organisms that are transported by wind or water are subject to prevailing currents. In some areas, wind and water currents are persistent and directional (e.g., trade winds of the Pacific and Atlantic subtropical oceans, which blow westward and toward the equator, and the westerlies at higher latitudes, which blow eastward). Mona, an island in the Antilles, equidistant between Hispaniola and Puerto Rico, provides an example. Of its 46 species of butterflies, 9 are shared with Puerto Rico but none with Hispaniola. It has been suggested that wind currents from the direction of Puerto Rico toward Mona are responsible for this unequal distribution (169).

How does isolation translate into genetic divergence? Exactly how much gene flow (number of immigrants) must be reduced to allow island populations to diverge through random genetic drift from the source depends on the geographical model and the degree to which migrants are representative of the species as a whole. For a genetic island model in which islands are almost completely isolated from an infinitely large panmictic population, strong differentiation of neutral genes can occur only if the number of migrants averages two or fewer per generation (196). When the immigrants each island receives are not wholly representative of the species, then genetic differentiation can occur even in the face of much higher levels of gene flow. For example, if as few as 10% of the genes are represented in the immigrant population, then there can be strong differentiation even if the number of migrants is as high as 20 per generation. This situation could also occur when a large population is broken up into numerous partially isolated demes (as may occur on fragment islands). Such estimates should be taken with some caution, however, and are best interpreted as null models. In particular, selective pressures on islands are also clearly important in causing genetic change and likely play

a significant role in differentiation between islands and source populations and between populations on different islands and even in different habitats (155).

The following examples illustrate the interaction of both history and isolation in dictating the nature of arthropod communities that develop on islands.

## Darwinian Islands

Darwinian islands, exemplified by oceanic islands, are formed without life. Thus, the number of species represented on these islands starts from nothing and increases at a rate that depends on the interplay of isolation and time. When isolation is low, the number of species colonizing will be high, and species may exist as metapopulations similar to those on fragment islands. Islands such as the raised coral rock islands of Palau (69) and some mangrove islands (166) are darwinian islands of variable age, in which species occur as metapopulations, their composition at any one point in time being dictated by the dynamics of immigration and extinction (68). Rock pools and rocks in streams represent habitat "islands" for many arthropods. Beetles in rock pools show characteristics of a dynamic metapopulation (174). Rocks in streams, by their nature, have never been contiguous and thus represent habitats that emerge by rolling into a given part of the stream. The insect fauna under rocks of differing size in a river in Finland exhibit a strong species-area relationship (104), although habitat differences between stones may also play an important role in dictating species numbers (79).

Darwinian islands of intermediate isolation are those in which colonization is sufficiently low to allow populations to diverge genetically from the source, but occurs too frequently to allow adaptive radiation. Species formation (neo-endemics) will be possible through isolation of colonists. Some excellent studies have been conducted on these kinds of islands in many different situations. In particular, the islands of the Lesser Antilles fall into this category and perhaps also some of the Greater Antilles, although others have been formed as fragments (43). The Bahamas were entirely submerged in the Pliocene, so that their fauna is likely to be the result of more recent dispersal from the nearby landmasses of Cuba, Hispaniola, and Florida. There are many insects that are endemic to these islands (18, 81). Caves are "islands" of subterranean environments that have been created in the midst of a terrestrial environment. However, because the surface environment is more permeable than the ocean, immigration into caves can occur through colonization from the surface environment (83). The facility with which taxa adapt to caves is unresolved. Some studies have shown that caves are like darwinian islands, with colonization of the new land mass occurring through adaptation of surface species (85). Other arguments portray caves more as fragments, with speciation associated with relictualization (13).

On darwinian islands of high isolation, the number of colonizing species is close to zero, with the rate of immigration slower than the rate at which new species can form through evolutionary processes. Here, multiple neo-endemics may form through adaptive radiation (65). This outer limit of dispersal has been termed the

radiation zone (114), the location of which clearly depends on the dispersal abilities of an organism. Evolution on such islands is discussed below.

## Fragment Islands

Fragment islands include most continental and habitat islands. Here, unlike darwinian islands, which are initially without life, the available niche space has usually been filled to a large extent prior to isolation. Following isolation, the number of species represented will decrease over ecological time as a result of relaxation, or reduction in species number, simply because of the reduced area (188). Relaxation has been well documented for vertebrates on Barro Colorado Island in Panama and is now well known on island fragments (132), including habitat islands [e.g., (149)]. However, again depending on an interplay between isolation and time, species will diverge from the original stock through relictualization, with the formation of paleo-endemics (36).

There are numerous examples of fragment islands that show only low levels of isolation, ranging from offshore islands (101) to patches of suitable habitat (176) and to single trees (129) within an inhospitable matrix. For example, insects in acacia tree canopies in northeast Tanzania show a species-area relationship (described below) characteristic of islands (103). Insect species on such fragment islands can often be studied as metapopulations in the same way as for darwinian islands. For example, a forest of deciduous *Pistacia* trees, destroyed by fire, was found to regenerate quickly into a network of sparsely scattered trees that served as ecological islands for aphids, with population extinction and recolonization every year (195). The checkerspot butterfly, *Euphydryas editha bayensis* (Nymphalidae) in the Jasper Ridge Preserve of California, occurs in one large patch ('mainland') and 60 small patches (fragment islands). The mainland patch is a permanent population, whereas the fragment patches are subject to extinctions through demographic accidents. These patches can readily be recolonized subsequent to extinction, provided they are close to the mainland patch (78). Similar results were obtained in a study of silver-studded blue butterflies *Plebejus argus* (Lycaenidae) in the United Kingdom (176) and another of spiders in the Bahamas (158). In the latter study, the islands (metapopulations) have a "source-sink" relationship, with small patches being colonized from the larger source and serving as a sink for excess individuals from the larger source.

In recent years, there has been increasing concern for protection and conservation of native species that are confined to small fragment islands of vegetation, isolated by an inhospitable matrix, either urban (53, 131) or agricultural (44, 177). For example, a number of studies have examined vacant lots or parks in cities in the context of islands. Diptera and Coleoptera, isolated in such parks, can show a species-area relationship (53). As land becomes increasingly fragmented through urbanization and agriculture, the presence and dynamics of such fragment island patches are becoming increasingly important in a wide variety of situations throughout the world (2, 42).

As isolation increases, the opportunity for genetic differentiation between patches increases. Within the island of Hawaii, small forest fragments (kipukas) surrounded by a 150-year old lava flow foster genetic differentiation among populations of both *Drosophila* flies (25) and *Tetragnatha* spiders that are confined to the kipukas (A. Vandergast, unpublished data). It is possible that these kipukas serve as “crucibles” for evolution and adaptive radiation in the Hawaiian Islands (25), although whether they have indeed served in such a capacity has not yet been demonstrated.

The characteristic feature of the fauna on fragment islands of intermediate isolation is some degree of population differentiation or species-level endemism through relictualization. Such islands are exemplified by the California Channel Islands (145) and the Chatham Islands off New Zealand. In the latter, the beetle fauna is closely related to that of New Zealand and shows high species-level endemism, though low generic-level endemism (47, 182). Within continents, a number of arthropods are endemic to mountaintops (sky islands) in North America (100, 116, 128) and northern Australia (11). The coastal forests of East Africa are characterized by a relict fauna, with high levels of local endemism, their isolation resulting historically from climatic desiccation of the surrounding areas, though more recently from human destruction (22).

Fragment islands well isolated for long periods are characterized by relictual lineages. In the western Pacific, fragmentation of island arcs has caused vicariant speciation in cicadas through relictualization on the isolated arc fragments (39). The phenomenon of relictualization is also well illustrated by certain habitat islands isolated for long periods of time, such as the tepuis of South America, which are ancient sandstone outcrops, created as large portions of the original sandstone plateau were eroded, followed by uplifting (147). Inselbergs, monuments, monadnocks, stacks, buttes, bornhardts, and tors are also isolated features formed as either protruding remnants of an igneous landmass, erosional outliers of nearby plateaus, or remnants of former highlands (144). The arthropod fauna of these fragments is poorly known.

## Mixed Islands

Many islands consist of a mixture of paleo-endemics derived from the original landmass coupled with neo-endemics stemming from more recent colonization. New Zealand represents a classic case of a mixed fragment and darwinian island. New Zealand broke away from the coast of Gondwana 80 million years ago, with all direct land routes to Antarctica/Australia severed (120), although apparently maintaining connections to New Caledonia until approximately 60 million years ago (171). Since then, it has been the largest Pacific island. Toward the end of the Miocene, increasing compression across the plate boundary caused massive uplift and mountain formation. Formation of new land in this previously small and inhospitable landmass that subsequently became isolated

would have created conditions permissible to adaptive radiation. Disharmony is marked in the current rich insect fauna of New Zealand (70). Many insect groups show close relationships with South America and New Caledonia groups and are likely ancient Gondwana relicts; other elements have relationships with Australia groups and are likely derived from more recent dispersal. This mixture of elements is well illustrated among beetles (99) and cicadas (21). For example, species of New Zealand cicada appear to have arisen from more than one colonization event after the split from Gondwana and have undergone relatively recent adaptive radiation (57), with rapid diversification of species according to ecological affinity (21). Likewise, Madagascar separated from Greater India approximately 88 million years ago (172), and many arthropod groups [e.g., (75)] show this ancient affinity. Subsequent volcanic activity has created new terrain that has allowed colonization and adaptive radiation in a number of taxa, such as tiger beetles (5) and ants (55, 56), which are both diverse with high levels of neo-endemism. The Seychelles, part of which broke off from India 64 million years ago, also have a number of paleo-endemics, but more recent neo-endemics appear to be derived from species of Malagasy, Laurasian/Malesian, and African origin (117).

Collision of islands can also lead to changes in biotic assemblages, with high species diversity along the margins of islands that have accreted terrain, such as along the northern margin of New Guinea (143). Indeed, the New Guinea fauna, a complex mixture of Southeast Asian, Indonesian, Philippine, and Australian groups, some of Gondwanan origin, is one of the richest and most extreme in the world (72).

## ISLAND UNIQUENESS: DISHARMONY

On darwinian islands, disharmony is a consequence of differential dispersal abilities and evolutionary distinctiveness, the latter effect being greatly increased by time and isolation. Islands that are more distant from the source have less harmonic faunas because successful colonization will be confined to few lineages (72). This has been termed attenuation. For many insect groups (23, 70, 115, 198) more isolated islands have only poor representation of faunas from the source landmasses at the family and genus levels. Such attenuation has, for example, been noted among the taxa colonizing the Canary Islands (93) but is particularly well illustrated as one crosses the Pacific Ocean from west to east (Fiji through Samoa, to the Society, Marquesas, and Hawaiian Islands). In Fiji (2700 km from Australia, the nearest continent; 800 km from the nearest island group), most insects would have colonized via oversea dispersal (70). However, Fiji is relatively close to the continental source and so has a rather rich fauna. Samoa (3800 km from Australia; 500 km from the nearest island group) is less rich than Fiji but still has many families and orders that are lacking from the native fauna of more remote Polynesian

islands. The Samoa fauna resembles that of Micronesia (51), and insects have not diversified as they have on the islands farther east. East of Samoa, representation of faunal groups becomes increasingly fragmentary. These archipelagoes are among the few areas on Earth that lack native species of ants (193). The disharmony is accentuated by the frequent diversification of species from single ancestors. The Society Islands (6000 km from Australia, 400 km from the nearest island group) have few insect genera and families, but show a fair degree of speciation in weevils (197), delphacids and issids (54), and other groups (23, 88). The yet more isolated Marquesas archipelago (7300 km from the nearest continent, now South America; 600 km from the nearest island group) exhibits pronounced disharmony and species-level endemism. The Hawaiian archipelago (4000 km from the nearest continent, North America; 3200 km from nearest island group) exhibits extreme disharmony: the native fauna is represented by only 50% of insect orders and 15% of known families (86), and exhibits extraordinarily high levels of endemism with numerous cases of adaptive radiation.

The accentuation of disharmony through speciation on isolated darwinian islands is well illustrated in the moth genus *Eudonia*, which is represented by only one species in central Polynesia and eastern Melanesia (the presumed source), but by 18 species in the Society Islands, 13 in the Marquesas, and over 100 species in the Hawaiian Islands. The microlepidopteran family Cosmopterigidae has only 180 species in North America (north of Mexico) and 388 in Australia, but has 85 endemic species in the Marquesas and over 350 in the Hawaiian Islands (126).

On fragment islands, disharmony results initially from sampling of the species represented on the landmass prior to fragmentation. This results in impoverishment, which may be accentuated by subsequent extinction, and/or failure of species to recolonize (146). Over time, and depending on isolation, disharmony on these islands will be exaggerated through evolutionary divergence on the island, or alternatively through extinction of ancestral taxa from the source. Islands near a source will have taxonomic representation similar, but not identical, to that of the mainland, with species showing relatively little divergence from continental relatives. In the California Channel Islands, for example, larger Lepidoptera are less diverse compared with their mainland counterparts than are smaller taxa perhaps because of the larger population size required to maintain populations of larger species (146). Such minimum area requirements may also be a function of trophic level; for example, they are greater for parasitoids than for herbivores (102).

Disharmony on fragment islands may be further augmented over evolutionary time. Island fragments that have been well isolated for greatly extended periods are characterized by relictual taxa as described above. For example, New Zealand has a number of ancient Gondwana lineages (70), as does the montane region of southern Africa (75). The peat bogs of central Europe are another ancient habitat that has become isolated and contains unique relict groups of species confined to these habitats since the early Holocene (170).

## SPECIES NUMBERS AND EQUILIBRIUM

The fact that larger islands tend to harbor a greater diversity of species has been known for a long time. However, the relationship between species diversity and area was not scrutinized until the 1960s with the development of the equilibrium theory of island biogeography (114). This theory relates species and area by the formula,  $S = cA^z$ , where  $S$  is species number,  $A$  is area,  $c$  is a constant measuring overall species richness, and  $z$  measures the extent to which increases in area have diminishing returns in terms of species number. Values of  $z$  tend to vary between 0.18 and 0.35; i.e., doubling the species number requires increasing the area by a factor of between 7 and 100. The premise of MacArthur & Wilson's arguments (114) is that the rate of immigration decreases with increasing distance from the source, while the rate of extinction decreases with increasing island size. The balance of these processes results in an equilibrium number of species on any one island. Once species are present, the chance of a new species arriving decreases with the number of resident species. Furthermore, the chance that a resident becomes extinct increases with the number of resident species. The predictions of the model are that (a) the number of species on an island should change little once the equilibrium is reached; (b) there should be continual turnover of species, with some becoming extinct and others immigrating; (c) small islands should support fewer species than large islands; and (d) species richness should decline with remoteness of the island because islands farther from the source will have lower rates of immigration.

The first and only rigorous test of the theory was performed by Simberloff & Wilson (165, 167) using mangrove islands off the Florida keys. They started by conducting a complete survey of the arthropod fauna of the islands on individual mangrove trees. They then eliminated all animal life from the islands and monitored recolonization. Species diversity first built up to numbers that exceeded the equilibrium value and then declined slightly to equilibrium. Thus, more species could be supported while most species were rare, but as populations approached their carrying capacity, competition and predation eliminated the "excess" species. This study supports the premise of an equilibrium number of species, as have several subsequent studies on other systems (e.g., 7, 101). However, a number of workers have brought into question specific aspects of the theory. For example, Toft & Schoener (181) found for spiders in the islands of the Bahamas that area can affect immigration (rather than extinction alone) and isolation can influence extinction (rather than immigration alone). In addition, extinction rates were positively related to species number and distance and negatively related to area (158). Another expectation from equilibrium theory is that turnover of species will be high and distributed evenly among species. However, studies on the arthropod fauna of *Spartina* grass (151) have shown that, although there is substantial turnover, it is not distributed evenly among species in the community. Likewise, among spiders in the Bahamas, turnover is highly heterogeneous and biased toward ephemeral

species (158), and even on the mangrove islands the high turnover noted originally does not hold over time (162).

Another aspect of the theory that has been questioned is the role of area per se in dictating species diversity. There are a number of parameters that have been proposed as the primary determinants in dictating species diversity, either in addition to, or instead of, area. We consider six such factors that have been suggested as playing a role in dictating species numbers on islands.

## Habitat Diversity

The habitat diversity hypothesis suggests that the number of species at equilibrium is more a function of the number of habitats than the size of the island per se, although the two are often highly correlated (188). Habitat diversity is clearly important. For example, atolls can certainly carry greater diversity when they are "raised" [e.g., Henderson Island (14)] but still carry much less diversity than high islands. In the Antilles, habitat diversity appears to be of primary importance for butterflies and other taxa that exhibit habitat specialization and large population size (152). Thus, it seems that both the biological features of the organisms and the geographic features of the islands mediate the relative contribution of island area and habitat diversity to variation in species richness. In a similar context, for moths on the California Channel Islands, species numbers are related more to the diversity of plants than island area (145). In the Seychelles, plant and structural diversity of the habitat appear to play a role in determining the diversity of spiders (124), although not that of ants (125).

## Climatic Conditions

Climatic regime, coupled with isolation, may be important in explaining diversity, particularly at higher latitudes (1). In islands of the southern ocean, the less-favorable environment (compared with lower latitudes) appears to have severely restricted the number of species (74). Here, both temperature and area can explain patterns of diversity for both introduced and indigenous species (31). Sadler (157) has compared north Atlantic and tropical Pacific islands and has shown that insect diversity is much higher in the latter. However, the difference here was attributed to time: During the Pleistocene, the polar regions were almost completely glaciated, and species diversity may not have reached equilibrium (see below).

## Island Age

In certain circumstances the diversity of species on a given island is a function of the geologic age of the island (30). For example, island age is associated with the diversity of *Scaptomyza* flies in Tristan de Cunha (189), beetles (16) and other arthropods (17) in the Azores, and *Rhyncogonus* weevils in the Hawaiian Islands (134). However, age was not important in explaining diversity of orthopteroids in the Galapagos (135). The role of age may be related to increased

habitat diversity with time, or alternatively, the attainment of equilibrium (see below).

## Extreme Isolation

On well-isolated darwinian islands, the MacArthur-Wilson model does not apply in the strict sense because immigration is no longer the major source of new species, although in these situations speciation may play a role equivalent to immigration (89, 114). A number of studies have examined species diversity using the model even on remote darwinian islands and have shown the predicted relationship between species number and area (12, 134, 138). The ability of local speciation to compensate for the deficiency in founder species is well illustrated in the Pyraloidea (Lepidoptera) of the Pacific islands in which species number is associated with island area, with little effect of distance from the source (126).

## Status of Knowledge

There are problems in estimating species numbers from the literature primarily due to incomplete knowledge (121). For Lepidoptera, for example, logplots of the number of species against the area of several Micronesian islands show little upward trend with increasing island size, which may be owing to lack of knowledge of the fauna on some of the larger islands (126). However, Baert & Jocqué (12) examined generalities among the spider faunas of tropical oceanic islands based mostly on published literature and were able to draw some tentative conclusions despite the fragmentary and often inaccurate nature of the available data (63). Nonetheless, there are still many arthropod groups on numerous islands for which there is insufficient knowledge to make conclusions based on numbers of known species.

## Equilibrium

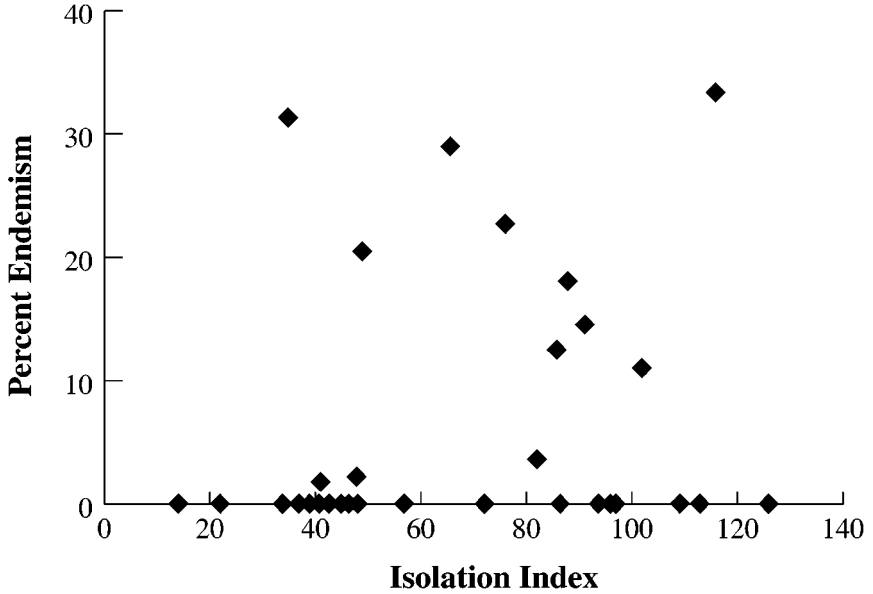
Species numbers on islands may differ from those expected based on their area if the system is not at equilibrium. Islands may not be at equilibrium for a number of reasons, including recent formation [e.g., Krakatau (178); Surtsey (109)], recent fragmentation, or recent human impacts (31, 145). The formation in 1963 of the darwinian island of Surtsey (33 km off the south coast of Iceland) has allowed species accumulation to be studied (109). Being young, only the simplest of communities are now developing, and it is likely that equilibrium numbers of species have not yet been reached. Krakatau in the Indian Ocean is another volcanic island that has never been attached to a continental landmass and is only 44 km from the nearest shores of Java and Sumatra (13 km from the nearest island, Sebesi). It is rather older than Surtsey, having undergone the last major eruption in 1883. However, even Krakatau is still in a dynamic state and is not considered to be at equilibrium (178). Likewise, fragment islands, such as those created through human impacts, will initially be "super-saturated" and will lose species until relaxation is complete (188).

## ISLAND DYNAMICS: COLONIZATION

Given a suitable abiotic environment, the success of any given natural colonization event will depend largely on the availability of ecological space. This effect is illustrated on isolated archipelagoes that are formed serially, some in a linear fashion, as they emanate from an oceanic hotspot (188), with most successful colonization occurring in the direction of the youngest islands. For example, in the Hawaiian Islands there is a general evolutionary progression down the island chain from older to younger islands (60, 155), a pattern first described for Hawaiian *Drosophila* in the seminal work of Carson (24). Other archipelagoes show temporal variation in island age, such as the Galapagos and the Canary Islands, although these are arranged as clusters rather than linear series. Yet on these islands the evolutionary progression of species also tends to be from older to younger islands, as illustrated by *Pimelia* and *Hegeter* beetles (93, 94) in the Canaries, and scarabs (89) and weevils (159) in the Galapagos. The heavily biased direction of colonization toward younger islands strongly suggests that once ecological space is "filled" on these islands, there is little further colonization. (It should be noted that processes governing colonization of recent invading species are different; these are discussed below.)

Because of the difference in availability of ecological space, natural colonization will play a much more important role on darwinian rather than on fragment islands, and indeed most studies of colonization have been conducted on darwinian islands. For example, studies on Krakatau (see above) suggest that early colonization may be fairly deterministic, whereas later colonization depends more on sequence of arrivals and intervals between arrivals (187). Over a longer time scale, the ability of organisms to colonize successfully dictates both the community composition of less remote islands and the extent of adaptive radiation in islands that are more remote.

Consideration of the numbers of butterfly species on different Pacific islands reveals a pattern that may reflect the ability of these insects to colonize remote islands. In the tropical Pacific, they comprise 285 species, of which 157 (55%) occur on the mainland as well (i.e., they have not speciated on the islands). One hundred are endemic to a single island/archipelago, and 28 are regional endemics (more than one archipelago, but not on the mainland) (4). Intra-island/archipelago speciation has been important only in New Caledonia, the Solomons and the Bismarcks, which contain 11, 35, and 36 island or archipelago endemics, respectively. All three of these islands/archipelagoes are fragments with relatively large land areas and proximity to continents. Therefore, butterflies may proliferate through processes leading to paleo-endemism as opposed to neo-endemism; there is no relationship between isolation and endemism (Figure 2). Adler and Dudley (4) argue that a possible explanation for the lack of neo-endemic butterflies on remote darwinian islands of the Pacific may be that larvae are evolutionarily constrained owing to requirements for specific host plants. However, this argument conflicts with the fact that other host plant specialists (such as moths and planthoppers) have radiated extensively even on the most isolated darwinian islands in the Pacific (8, 86, 154). An alternative argument may be that none of



**Figure 2** The relationship between isolation and endemism for butterflies in Caribbean and Pacific Islands (data from 4, 104a, 152, 188a). Island isolation was calculated by summing the square roots of the distances to the nearest equivalent or larger island, the nearest archipelago, and the nearest continent (see United Nations Environment Program <http://www.unep.ch/islands/>).

the islands of the Pacific are sufficiently isolated, relative to the superior dispersal abilities of some butterflies, to provide conditions necessary for adaptive radiation. This accords with observations of Gressitt (70), who reported a butterfly found in good condition on an oceanic vessel and considered that butterflies and other large insects, such as dragonflies and sphinx moths, may have a wider range of dispersal than most insect groups.

For most arthropods, the remote archipelagoes of the central Pacific, in particular the Hawaiian Islands, are within the radiation zone (defined above). It has been estimated that only 350–400 ancestral colonists have given rise to the 5382 naturally occurring described species of insects (of an estimated total of 10,000 including those undescribed) in the Hawaiian Islands (86), and “. . . perhaps only one successful colonization per 20,000 years” is necessary to account for the present fauna of the archipelago (199, p. 56).

On more remote islands, aerial colonization has been disproportionately important as the mode of colonization in the buildup of the insect fauna (135, 180). Long-term studies of insects over the ocean conducted by the Bishop Museum from 1957 to 1970 showed a good correlation (with some exceptions) between the proportions of different insect groups trapped in aerial nets and those that make up the faunas of oceanic islands (82).

## ISLAND DYNAMICS: SPECIES CHANGE SUBSEQUENT TO COLONIZATION

When an organism colonizes an island, its establishment depends on the suitability of the environment and the availability of ecological space, as described above. What happens to a population subsequent to successful colonization?

### Ecological Change

There is abundant evidence for ecological release and range expansion during the initial establishment of species in new habitats, coupled with range fragmentation and restriction with time since colonization (113). Many recent examples of this phenomenon come from the literature on biological invasions (49). However, similar expansion may occur when species first become established on a darwinian island. For example, in the apparently recent (post-glaciation) colonization of the islands of the north Atlantic, the ecological range of insects is much broader than on mainland Europe (34), a pattern that could be attributed to ecological release upon colonization. In the future, these species may undergo range reduction or fragmentation.

Regular cycles of distributional change following colonization of islands have been proposed several times in the literature, starting with Wilson's (191) "taxon cycle" for Melanesian ants. Wilson proposed that widespread, dispersive populations (Stage I) give rise to many more restricted and specialized populations (Stage II) or species (Stage III). Stage I species are "generalists" and dominate in marginal habitats. They are largely trail-making ants that nest in the soil. At Stage II the ants have moved into the forest and specialize on specific substrates. Stage III species show development of the process of becoming local endemics. The concept of the taxon cycle has been adapted for carabid beetles in the related "taxon pulse" hypothesis of Erwin (50). Gagne (62) proposed that a colonizing species of the genus *Sarona* (Miridae) in the Hawaiian Islands first utilized several families of host plants and spread through the archipelago but then gradually became specialized on host species within different families of host plants.

However, more recent studies have suggested a different pattern of speciation for *Sarona*: Phylogenetic analysis of extant species suggests that, rather than generalist species giving rise to specialist species, specialist phytophagous species have given rise to a diverse array of specialist species, resulting in a group that exploits a broad array of hosts (10). There are now many additional studies using extant species that show no evidence for taxon cycles or that show evidence contradicting the idea. For example, speciation of specialist species through host switching to form new specialist species seems to underlie diversification in the genus *Cyrtolepis* (Miridae) (61) and perhaps *Nesosydne* (Delphacidae) (154). Direct cladistic tests of the taxon cycle using a lineage of carabid beetles did not support the existence of unidirectional shifts toward range restriction and specialization through the phylogeny of a lineage (107). Together, these studies question the generality of the taxon cycle.

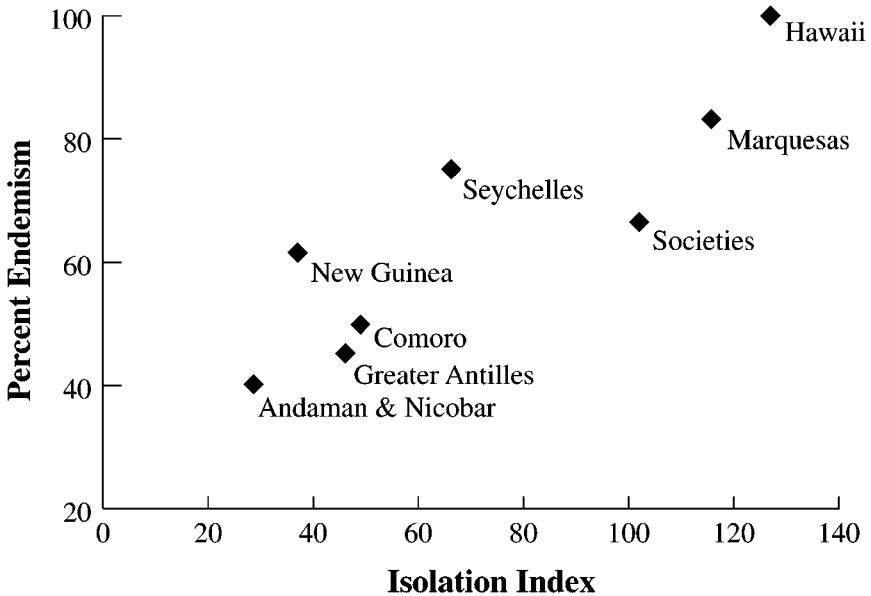
The inconclusive and conflicting results from studies of taxon cycles may be a problem of scale: Stage I is effectively equivalent to ecological release, which is a population-level phenomenon experienced by populations of a species that colonize new areas. It may not be maintained as populations differentiate to form species. In other words, although a population may have behaved as a generalist subsequent to initial colonization of an island and may have given rise to more specialized descendant populations and species, the initial taxon that underwent ecological release may then no longer exist in its (transient) generalist ecological state.

## Evolutionary Change

On fragment islands the fundamental evolutionary process is relictualization, or the formation of paleo-endemics (36). The key element here is that, because the islands are ecologically "filled," with time relictualization can result in large genetic distances between fragments of great age coupled with high levels of endemism. This is readily seen on ancient islands such as New Zealand and Madagascar. In New Zealand, 90% of terrestrial arthropods are endemic, with high generic-level endemism [paleo-endemism, over 43% in beetles (99), and similarly high in other insect (52) groups]. As mentioned above, habitat islands such as the tepuis of South America (147) and the mountaintops of northeastern Australia (90), can show a similar phenomenon, although the insect fauna of these mountain masses is largely unknown. At slightly lower latitudes, however, where glaciation, with the encompassing of refugia, has alternated with the opening of ecological space during interglacial periods, conditions may promote the formation of paleo-endemics during glacials and neo-endemics during interglacials. Studies on the sky islands, a series of isolated mountaintops in western North America, suggest that diversification in grasshoppers is associated with glaciation, with just a few taxa being confined to refugia during glacial maxima (100). Interglacials may then have allowed range expansion, speciation, and coexistence of multiple close relatives on one mountain.

On darwinian islands accumulation of neo-endemics will depend on the rate of speciation relative to the frequency of island colonization: If colonization is sufficiently infrequent, then neo-endemics may form, often prolifically, as a consequence of in situ evolutionary diversification and adaptation to different ecological roles (36). This phenomenon is known as adaptive radiation (65). Spiders in the genus *Tetragnatha* are known throughout the islands of the world and have undergone adaptive radiation only on the most remote islands [e.g., the Hawaiian Islands (64, 67)]. Figure 3 shows the relationship between isolation and endemism for this genus in the Pacific. Overall, among the arthropods in the Hawaiian Islands, 98% are neo-endemics (122). About 50% of the Canary Islands invertebrates are neo-endemics (93). Using beetles, the rate of formation of neo-endemics in three remote darwinian islands is compared in Table 2.

**FLIGHTLESSNESS** Considering islands in the broadest sense, as defined above, one of the most recurrent evolutionary themes in more isolated situations is



**Figure 3** The relationship between isolation and endemism for spiders in the genus *Tetragnatha* (R. Gillespie, unpublished data). Isolation index calculated as above.

flightlessness or loss of dispersal ability. This is particularly striking because most colonists of remote islands are highly dispersive. Working on Campbell Island, Gressitt and colleagues (71) showed that 40% of 183 indigenous insects show some degree of wing reduction. On Tristan de Cunha there are 20 endemic beetle species, all but two of which have reduced wings (190). In the Hawaiian Islands, 10 of the 11 orders of alate species that colonized the islands have evolved flightless species, the exception being odonates (84). Because most of the flightless continental species have failed to colonize remote islands, flightlessness must have evolved independently in each lineage; indeed, it appears to have evolved multiple times within many lineages.

Most discussion of loss of dispersal ability in island taxa has been based on the incidence of morphologically determined flightlessness rather than observations of dispersal. However, loss or reduction of dispersal ability (with which flightlessness is associated) may be considerably more common on islands than flightlessness itself. For example, in New Zealand 94% of Lepidoptera have limited powers of dispersal (45). Moreover, species on islands are characterized by small ranges (87). Thus, whether resident insects have wings, there appears to be considerably less dispersal among native species on these remote islands. In Hawaiian spiders, for example, dispersal seems to be much reduced in endemic species (63), although they may still have the physiological ability to disperse.

Why does loss of dispersal ability evolve so frequently in isolated environments? A number of environmental parameters have been linked to flightlessness, some

**TABLE 2** Comparison of formation of neo-endemic Coleoptera on the Galapagos, Canary, and Hawaiian islands

	Likely number of colonists	Number of endemic species
Galapagos islands (135)		
<i>Pterostichus</i>	1	20
<i>Physorinus</i>	1	7
<i>Stomion</i>	1	9
<i>Ammophorus</i>	2	12
<i>Blapstinus</i>	3	16
<i>Galapaganus</i>	2-3	6
<i>Pseudopentarthrum</i>	1	6
Canary islands (93)		
<i>Calathus</i>	3	24
<i>Cardiophorus</i>	1?	31
<i>Attalus</i>	1?	51
<i>Tarphius</i>	1	30
<i>Hegeter</i>	1?	23
<i>Neostes</i>	1?	20
<i>Laparocerus</i>	1?	66
<i>Acalles</i>	1?	18
Hawaiian islands (127a); (108)		
<i>Mecyclothorax</i>	1	86
<i>Metromenus</i> (subg.)	1	73
<i>Blackburnia</i> (subg.)	1	51
<i>Proterhinus</i>	1	174
<i>Oodemus</i>	1	62
<i>Rhyncogonus</i>	1	34
<i>Mirosternus</i>	1	71
<i>Xyletobius</i>	1	72
<i>Eupetinus</i>	1	144
<i>Nesopeplus</i>	1	31
<i>Nesopetinus</i>	1	25
<i>Plagithmysus</i>	1	138
<i>Diestota</i>	1	30
<i>Oligota</i>	1	29
<i>Cis</i>	1	34
<i>Eopenthes</i>	1	33
<i>Aeletes</i>	1	35
<i>Dromaeolus</i>	1	33

of which (e.g., habitat persistence, latitude) may not be related to habitat isolation per se, while others (e.g., altitude, dissimilarity of the habitat from the matrix) clearly are (156). Darwin (38) suggested that, for beetles in Madeira, the evolution of flightlessness on the island is a consequence of selection for individuals that disperse least, perhaps because of the high risk of mortality over the ocean. A much larger proportion of insects trapped off the coast were winged species. However, few Lepidoptera or ichneumonid Hymenoptera were caught, which suggests that these insects may restrict their flying to calm conditions and thereby avoid being blown out to sea. A similar situation has been found in aerial samples from the Canary Islands, with proportionally larger samples of introduced insects and underrepresentation of beetles (9). However, there are several endemic insects in which selection pressures for retention of flight outweigh the disadvantages and that do participate in aerial dispersal. In sum, it seems that, unless there is a strong counter pressure, on remote islands selection will result in reduction of dispersal abilities among arthropods relative to the ancestral colonists, either because of the lack of advantage or the disadvantage of dispersal relative to other components of fitness.

**INNOVATIONS** The known disharmony of islands appears to be associated with selection for some unusual traits in island groups. For example, the absence of native social insects such as ants in some of the more remote islands of the Pacific may have been largely responsible for the adaptive shift to predation in some terrestrial insect groups and the diversity of non-social predatory arthropods on these islands (192). One of the most striking innovations is the evolution of ambush predatory behavior in a lineage of Hawaiian moth caterpillars in the genus *Eupithecia* (123). Another innovation in the Hawaiian Islands has been the development of odonates with terrestrial larvae (199), associated with the paucity of lakes in the upland yet moist forests of the islands. Similarly, in the Subantarctic islands, the unusual habitat of cryptogram herbivory in beetles is considered to be a result of the disharmony of the flora (29).

## PROCESSES OF SPECIES FORMATION

### Paleo-Endemism

The formation of paleo-endemics is clearly an important process on fragment islands, particularly those that are older. Because it is difficult to study, the process of relictualization is not well understood. The dolichopodid fly genus *Parentia* includes species from Australia, New Zealand, and New Caledonia, with most of the diversification in the more ancestral taxa of the genus, suggesting that the speciation in this lineage is associated with the ancient separation of Gondwana and subsequent relictualization (15). Similarly, fragmentation of the southwest Pacific island arc seems to underlie the pattern of endemic clades of cicadas in the Indo-Pacific (39). In the Caribbean, which contains both fragment and darwinian islands,

diversification of beetles appears to have occurred through relictualization and speciation in isolation without any habitat shifts (58, 105). Even on islands close to the mainland, endemic taxa have arisen, closely related to mainland species, through modification of the mainland ancestor or because of adaptation in the isolated population to conditions on the island (145).

On mountaintops within continents, a similar pattern of relictualization has been shown for beetles in North America (128) and northern Australia (11). The species formed may be of recent origin. Phylogeographic studies indicate intriguing patterns of recent relictualization and rapid divergence in spiders (116) and grasshoppers (100) in the North American mountain sky islands. However, additional patterns have been superimposed, apparently owing to the events of recent glaciations (see above).

### Neo-Endemism and Adaptive Radiation

The formation of neo-endemics is characteristic of darwinian islands but also may occur if ecological niche space opens up on fragment islands. Neo-endemism is most conspicuous among species that have undergone adaptive radiation. The most spectacular examples of adaptive radiation are in the Hawaiian Islands (155). However, other examples of adaptive radiation are known from the remote oceanic islands of the southern Pacific, including the Marquesas (R. Gillespie, unpublished data), Society Islands [e.g., carabid beetles (141)], and Rapa Island (133) in French Polynesia, and to a lesser extent the Galapagos Islands (135). Adaptive radiation has also been documented for a number of lineages in the Canary Islands of the Atlantic (93). Peck (135, p. 111) notes that "very isolated, single, high islands are initially colonized by few insect species, and . . . these often produce large (seemingly monophyletic) species swarms on a single island. . . ." A number of mechanisms have been proposed to underlie diversification in adaptive radiations (65), and are described below. It should be noted that these mechanisms are not mutually exclusive, and several may be involved in diversification within any given lineage.

**GEOGRAPHICAL ISOLATION AND FOUNDER EVENTS** Speciation through geographical isolation and/or founder events can take place on islands relatively close to the source, provided gene flow is reduced sufficiently to allow population divergence through genetic drift [(196), see above]. This mechanism of species formation has been proposed for many such islands. It may also underlie the radiation of *Drosophila* (Drosophilidae) in the Caribbean (81) and butterflies in the genus *Gonepteryx* (Pieridae) in the Canary Islands (20), where a single endemic species occurs on each of the major islands. A similar process may have caused the pattern of single island endemism found on more remote archipelagoes. In the Hawaiian Islands, for example, a number of lineages, including spiders [*Labulla*, Linyphiidae (67)], grasshoppers [*Banza*, Tettigoniidae (173)], and moths [*Eupithecia*, Geometridae (123)], seem to have differentiated in this manner. Among

cave species, colonization and subsequent isolation in the different lava tubes on the same island may have allowed the formation of new species. For example, new species have formed among isolates of the planthopper *Oliarus polyphemus* (Cixiidae) in different lava tube systems (80).

There has been much written on the importance of founder events in initiating rapid species formation (28, 119). Relative to the ancestral population, selective pressures experienced by the colonists are probably different, and the environment of the small area they occupy may be more homogeneous. More importantly, allele frequencies at some loci will differ from those of the parent population because of accidents of sampling (175). These ecological and genetic conditions may lead to significant adaptive character change mediated by selection (26). The best known studies implicating founder events in speciation have been conducted in the Hawaiian Islands and particularly for the large radiation of *Drosophila*. Volcanic activity may have allowed multiple opportunities for isolation and founder events both within and between islands (25) thereby promoting diversification of species. However, it is likely that this mechanism operates in conjunction with ecological shifts (see below). Geographic isolation appears also to have played a prominent role in the diversification of beetles in the Canary Islands (48, 93) and psocids (179) and pipunculids (40), in addition to *Drosophila* (97), in the Hawaiian Islands.

**BEHAVIORAL ISOLATION** Sexual selection is frequently implicated in the acceleration of species formation. Based on the premise that founder events play an important role in speciation, Kaneshiro (96) proposed a model implicating sexual selection in driving species proliferation in the Hawaiian *Drosophila*: A newly founded population, released from interaction with related species, acquires simpler sexual behavior, with more intraspecific variability. Intrasexual selection may then operate to cause divergence of the sibling species during isolation as a result of a shift in the distribution of mating preferences during the founder/flush cycle (27). Sexual selection has also been implicated in the evolution of Hawaiian crickets in the genus *Laupala* (Gryllidae), although in this case founder events may not have played a major role (130, 161).

**ECOLOGICAL ISOLATION** Ecological segregation has been demonstrated in numerous cases where members of an adaptive radiation occur sympatrically (65). However, the relative importance of allopatric, parapatric, and sympatric speciation in leading to the co-occurrence of closely related species is not clear. Allopatry appears to be involved in the initial diversification of beetles in the Canary Islands. In the laurel forests of these islands, there are a number of species of close relatives that live in sympatry, including members of the beetle genus *Calathus* (48). Speciation in *Calathus* appears to have occurred through isolation of marginal populations and specialization and may be associated with volcanic activity (93). A similar process may underlie diversification in tenebrionid beetles in the genus *Pimelia*, which shows extensive within-island speciation based on habitat associations (92).

In the Hawaiian Islands differentiation among marginal isolates may have played a role in species formation within the large radiation of Hawaiian carabid beetles (106, 108). A similar mechanism has been proposed for Hawaiian moths (126). Adaptive shifts to new breeding sites, perhaps coupled with initial isolation and founder events (see above), appear also to have played an important role in the diversification of the Hawaiian *Drosophila* (35, 95).

Parapatric divergence through adaptive shifts has probably been most clearly documented for cave faunas. This process has been implicated in the formation of lava tube cave endemics from surface relatives on the different Hawaiian Islands (80, 83, 85). In Jamaica (136), the Galapagos Islands (137), and the Canary Islands (6), switches to caves by spiders and insects have occurred repeatedly in a similar manner to that in the Hawaiian Islands.

Sympatric speciation based on ecological shifts has only recently been examined on islands. This mode of speciation may explain the phylogeny and biogeography of a lineage of weevils in the genus *Dusmoecetes* in the Marion Islands of the Subantarctic (30). In a radiation of Hawaiian *Tetragnatha* spiders, species on any one island are often most closely related to each other, with multiple close relatives in sympatry. However, although this pattern could be explained by sympatric speciation, initial divergence may have occurred in allopatry, with acceleration of ecological distinction when sibling species are reunited (64).

In sum, whatever the mechanism allowing initial divergence of populations, ecological segregation plays a primary role in allowing coexistence of close relatives of an adaptive radiation.

**SPECIATION ASSOCIATED WITH HOSTS** Host switching is a form of ecological shift and can result in speciation if, following a switch to a new host, the individuals concerned become sufficiently isolated and divergent from the species on the original host. Among Hawaiian insects, speciation in the genus *Sarona* (Miridae) appears to be largely mediated by host switching (10). Similarly, in Hawaiian *Prognathogryllus* (Gryllidae) crickets, changes in host associations, coupled with geographical isolation, may underlie species formation (160). Speciation through host shifts may occur rapidly. For example, the *blackburni* group of *Omiodes* (*Hedylepta*; Pyralidae) moths in the Hawaiian Islands consists of seven species, two feeding on palms, one occasionally straying to banana, and five known only from banana. Banana was introduced to these islands by Polynesians around 1000 years ago, when the native *Pritchardia* palms were much more widely distributed; thus it seems that the banana feeders have become distinct species within the last 1000 years (200).

Another mechanism through which herbivorous arthropods can diversify and shift ecological affinity is by means of cospeciation and tracking the ecological shifts of the host. Species may shift habitat with their host, as has been suggested for *Nysius* (Lygaeidae) bugs and their allies in the Hawaiian Islands (183). A lineage of *Nesosydne* (Delphacidae) planthoppers associated with plants in the Hawaiian silversword alliance (Asteraceae) are highly host specific, with each

species feeding on one or a few closely related hosts (154). The data suggest that planthoppers and their hosts share parallel phylogenies. However, it is not yet clear whether any reciprocal adaptation might be involved. A similar scenario may explain diversification of psyllids (Hemiptera) in Macronesia (139). Taken together, the data indicate that host-associated divergence, whether through host-shifts or host-tracking, may occur both rapidly and locally, potentially creating conditions for sympatric speciation.

## PROCESSES OF COMMUNITY FORMATION

The process of colonization and development of community equilibrium has been studied in detail. In the classic experiments on mangrove islets in the Florida keys (165, 167; see above), one of the most important conclusions was that more highly coadapted sets of species find themselves by chance on an island and tend to persist as sets. Community formation can be therefore somewhat deterministic, even though there is a strong stochastic element to colonization (188).

The deterministic nature of community formation is even more striking on islands that are well isolated, where species composition of a community results largely from speciation as opposed to immigration. In a radiation of Hawaiian *Tetragnatha* spiders, similar sets of ecological forms ('ecomorphs') appear to have evolved independently on each of the different islands, which suggests convergence of the same set of ecomorph types on each island (64). Further studies are required to establish the ubiquity of this phenomenon and determine the evolutionary underpinnings that have led to independent evolution of similar communities.

## CONSERVATION ISSUES: ISLAND INVASIONS

Islands in general are well known for elevated levels of extinction (118). Of the known extinctions of insect species since the 1600s, 10 have been on continents and 51 on islands (76). The Hawaiian Islands have been recorded as having lost more arthropod species than has the entire continental United States (46), and the number of species listed as candidates for listing as endangered (184) is twice that of the highest number in any state of the continental United States (77). However, given the fragmentary knowledge of arthropods, these numbers can only be used as an imprecise reflection of the difference between islands and continents.

Conservation concerns on island fragments are rather different from those on darwinian islands, although the problem of small population size may be common to both. However, in terms of what is being protected, in conserving the biota of fragment islands (mostly paleo-endemics), one is maintaining patterns of diversity, or "islands as museums," whereas in conserving the biota of darwinian islands (neo-endemics), one is maintaining the result of the special process of evolution, or "islands as laboratories" (37, p. 488). In addition, the relative importance of various impacts may differ.

## Small Population Sizes

Species on islands tend to have a limited geographic distribution (164). The naturally small population sizes may mean that most of these populations will not suffer high levels of inbreeding depression (63). However, they are vulnerable to extinction as a result of demographic accidents. In the tropical islands of the Pacific, extinction has been much higher than on the islands of the north Atlantic, where ranges are much broader (157). Species with naturally small population sizes are also more vulnerable to habitat modification simply because loss of even a small amount of habitat for a geographically restricted species could reduce numbers below sustainable levels.

## Alien Species Invasion

One of the most severe impacts affecting many island systems comes from nonnative species. For insects, extinctions attributed to alien species invasion have been noted on Guam (127) and the Galapagos (110). However, alien species appear to have taken a much greater toll on the native biota of the Hawaiian Islands (87). The number of organisms that have been purposely or accidentally introduced into the Hawaiian Islands and have become established now totals 3046 arthropods, 20 reptiles, 46 land birds, 19 mammals, and 927 plants (122). Besides merely counting the number of alien species, determining whether a species is native remains a major challenge for conservation biologists working on island systems. This problem is especially difficult in tropical areas where knowledge of the native, as well as the potential pool of nonnative, species is frequently sparse, fragmentary, and often unreliable. The factors accounting for the diversity of introduced versus indigenous species are different, so the two cannot be lumped together either for conservation purposes or to understand ecological or evolutionary processes (31).

**MODIFICATIONS OF SUCCESSFUL INVADERS** The Hawaiian Islands provide an ideal situation for examining the early effects of invasion because so many species have been introduced to the islands in small numbers. What has happened, in terms of host and habitat associations for example, to species that have been accidentally or deliberately introduced to the archipelago? It is widely cited that the worst kind of introduction to an isolated archipelago is that of a generalist predator or competitor capable of exploiting a broad array of habitats and hence causing widespread devastation of the native biota (142). However, most introductions of generalist predators have been accidental or occurred before protocols were established for the purposeful introduction of nonnative species. The introduction of highly specialized species for biocontrol purposes has generally been believed to be safe in that they are unlikely to go beyond the confines of their unique host or habitat (59). However, although preliminary, evidence is accumulating to suggest that even specialized species can expand their range when faced with novel conditions in the Hawaiian Islands and may do so quite dramatically. A. Asquith & E. Miramontes (unpublished manuscript) have documented new host records for numerous species introduced for biological control and shown that several such

species exploit native hosts. However, it seems that most of the recent purposeful introductions have had less impact on the native biota than some of the earlier introductions.

**IMPACT OF SPECIES INVASIONS** The impact of alien species is often thought to be more severe on islands. However, rather than being tied to the level of disharmony of the island biota (163), the impact of invasions of alien species may depend on the island type and isolation. For example, much of the fauna of fragment islands, however remote, initially evolved within a species-rich continent and may not be as vulnerable to aggressive alien species as are species on remote darwinian islands in which the biota evolved in isolation. In the latter case, the impact of nonnative species may be due to the novelty of perturbations imposed by the nonnative species (63). Introduced arthropods can impact both vertebrates and invertebrates. For example, in the Hawaiian Islands, there is evidence that introduced mosquitoes, (*Culex quinquefasciatus*), and malaria from introduced birds have combined to cause the extinction and/or endangerment of many endemic forest birds (184). There are many more examples that illustrate the impact of alien arthropods on native arthropods on islands. Introduced social Hymenoptera, ants in particular, have been widely implicated in causing severe adverse effects on the native arthropod fauna on various Pacific islands (91, 110, 112). The insect fauna of the more remote islands of the Pacific (east of Samoa) evolved in the absence of ants, but a total of over 40 species of ants have become naturalized in these islands, mostly in the past century (193). The impact of these introductions has been especially severe in the Hawaiian Islands (110). In particular, *Pheidole megacephala* was already linked to the extirpation of lowland native arthropods in the early 1900s (140), with additional extinctions of native arthropods since then being attributed to this species as well as to *Linepithema humile* and *Anoplolepis longipes* (32, 66, 199).

## CONCLUSIONS

Islands have intrigued biologists for centuries. Not only are they discrete units within which the biota can be quantified and compared, but the interaction of isolation and time has allowed the development of uniquely derived faunas, comprising neo-endemics in the case of darwinian islands and paleo-endemics in the case of fragment islands. Understanding of the interplay between time and isolation in the development of these distinctive sets of biota is still limited. Even more limited is our knowledge of the nebulous concept of "vacant niche space," which seems to play a critical role in fostering colonization and diversification. There is much to be learned from the natural patterns of diversification on islands. At the same time, the current rate of anthropogenically induced habitat degradation and homogenization of species threatens the biota of the world, and particularly that of islands. Research is critically needed on islands to mitigate the impact of

alien species and to determine the identity and distribution of native and alien species. The challenge, initiated by Darwin and Wallace, of understanding evolutionary processes so well illustrated on islands, has therefore become a race against time. Evolutionary biologists must work closely with conservation biologists if this challenge is to be met.

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## LITERATURE CITED

1. Abbott I. 1974. Numbers of plant, insect, and land bird species on nineteen remote islands in the Southern Hemisphere. *Biol. J. Linn. Soc.* 6:143–52
2. Abensperg-Traun M. 2000. In defence of small habitat islands: termites (Isoptera) in the Western Australian central wheat-belt, and the importance of dispersal power in species occurrence. *Pac. Conserv. Biol.* 6:31–39
3. Adamson AM. 1939. Review of the fauna of the Marquesas Islands and discussion of its origin. *Bishop Mus. Bull.* 159:1–93
4. Adler GH, Dudley R. 1994. Butterfly biogeography and endemism on tropical Pacific Islands. *Biol. J. Linn. Soc.* 52:151–62
5. Andriamampianina L, Kremen C, Vane-Wright D, Lees D, Razafimahatratra V. 2000. Taxic richness patterns and conservation evaluation of Madagascan tiger beetles (Coleoptera: Cicindelidae). *J. Insect Conserv.* 4:109–28
6. Arnedo MA, Ribera C. 1999. Radiation of the genus *Dysdera* (Araneae, Dysderidae) in the Canary Islands: the island of Tenerife. *J. Arachnol.* 27:604–62
7. Ås S, Bengtsson J, Ebenhard T. 1997. Archipelagoes and theories of insularity. *Ecol. Bull.* 46:88–116
8. Asche M. 1997. A review of the systematics of Hawaiian planthoppers (Hemiptera: Fulgoroidea). *Pac. Sci.* 51:366–76
9. Ashmole NP, Ashmole MJ. 1988. Insect dispersal on Tenerife, Canary Islands: high altitude fallout and seaward drift. *Arct. Alp. Res.* 20:1–12
10. Asquith A. 1995. Evolution of *Sarona* (Heteroptera, Miridae). See Ref. 185, pp. 90–120
11. Baehr M. 1992. An introduction to the biogeography of the Carabidae of montane refugia in northern Australia (Coleoptera: Carabidae). See Ref. 128, pp. 67–78
12. Baert L, Jocqué R. 1993. A tentative analysis of the spider fauna of some tropical oceanic islands. *Mem. Qld. Mus.* 33:447–54
13. Barr TC, Holsinger JR. 1985. Speciation in cave faunas. *Annu. Rev. Ecol. Syst.* 16:313–37
14. Benton TG. 1995. Biodiversity and biogeography of Henderson Island's

- insects. *Biol. J. Linn. Soc.* 56:245–59
15. Bickel DJ. 1996. Restricted and wide-spread taxa in the Pacific: biogeographic processes in the fly family Dolichopodidae (Diptera). See Ref. 98, pp. 331–46
  16. Borges PAV. 1992. Biogeography of the Azorean Coleoptera. *Bol. Mus. Munic. Funchal* 44:5–76
  17. Borges PAV, Brown VK. 1999. Effect of island geological age on the arthropod species richness of Azorean pastures. *Biol. J. Linn. Soc.* 66:373–410
  18. Browne DJ, Peck SB, Ivie MA. 1993. The longhorn beetles (Coleoptera Cerambycidae) of the Bahama Islands with an analysis of species-area relationships, distribution patterns, origin of the fauna and an annotated species list. *Trop. Zool.* 6:27–53
  19. Browne J. 1983. *The Secular Ark: Studies in the History of Biogeography*. New Haven: Yale Univ. Press
  20. Brunton CFA, Hurst GDD. 1998. Mitochondrial DNA phylogeny of Brimstone butterflies (genus *Gonepteryx*) from the Canary Islands and Madeira. *Biol. J. Linn. Soc.* 63:69–79
  21. Buckley TR, Simon C, Shimodaira H, Chambers GK. 2001. Evaluating hypotheses on the origin and evolution of the New Zealand alpine cicadas (*Maoricicada*) using multiple-comparison tests of tree topology. *Mol. Biol. Evol.* 18:223–34
  22. Burgess ND, Clarke GP, Rodgers WA. 1998. Coastal forests of eastern Africa: status, endemism patterns and their potential causes. *Biol. J. Linn. Soc.* 64:337–67
  23. Buxton PA. 1935. Summary. In *Insects of Samoa and Other Samoan Terrestrial Arthropoda*, ed. BMN History, pp. 33–104. London/Beccles: Clowes
  24. Carson HL. 1987. Tracing ancestry with chromosomal sequences. *Trends Ecol. Evol.* 2:203–7
  25. Carson HL. 1990. Extinction and recolonization of local populations on a growing shield volcano. *Proc. Natl. Acad. Sci. USA* 87:7055–57
  26. Carson HL. 1990. Increased genetic variance after a population bottleneck. *Trends Ecol. Evol.* 5:228–30
  27. Carson HL, Kaneshiro KY. 1976. *Drosophila* of Hawaii: systematics and ecological genetics. *Annu. Rev. Ecol. Syst.* 7:311–45
  28. Carson HL, Templeton AR. 1984. Genetic revolutions in relation to speciation phenomena: the founding of new populations. *Annu. Rev. Ecol. Syst.* 15:97–131
  29. Chown SL. 1989. Habitat use and diet as biogeographic indicators for subantarctic Ectemnorhini (Coleoptera: Curculionidae). *Antarct. Sci.* 1:23–30
  30. Chown SL. 1990. Possible effects of Quaternary climate change on the composition of insect communities of the South Indian Ocean Province Islands. *S. Afr. J. Sci.* 86:386–91
  31. Chown SL, Gremmen NJM, Gaston KJ. 1998. Ecological biogeography of southern ocean islands: species-area relationships, human impact, and conservation. *Am. Nat.* 152:562–75
  32. Cole FR, Medeiros AC, Loope LL, Zuehlke WW. 1992. Effects of the Argentine ant on arthropod fauna of Hawaiian high-elevation shrubland. *Ecology* 73:1313–22
  33. Collins NM, Thomas JA. 1991. *The Conservation of Insects and Their Habitat*. London: Academic
  34. Coope GR. 1986. The invasion and colonisation of the north Atlantic islands: a palaeoecological solution to a biogeographic problem. *Phil. Trans. R. Soc. London Ser. B* 314:619–35
  35. Craddock EM, Kambysellis MP. 1997. Adaptive radiation in the Hawaiian *Drosophila* (Diptera: Drosophilidae): ecological and reproductive character analyses. *Pac. Sci.* 51:475–89
  36. Cronk QCB. 1992. Relict floras of the

- Atlantic islands: patterns assessed. *Biol. J. Linn. Soc* 46:91–103
37. Cronk QCB. 1997. Islands: stability, diversity, and conservation. *Biodivers. Conserv.* 6:477–93
  38. Darwin C. 1859. *The Origin of Species by Means of Natural Selection*. Harmondsworth, UK: Penguin Classics. 460 pp.
  39. de Boer AJ, Duffels JP. 1996. Biogeography of Indo-Pacific cicadas east of Wallace's Line. See Ref. 98, pp. 297–330
  40. DeMeyer M. 1996. Cladistic and biogeographic analyses of Hawaiian Pipunculidae (Diptera) revisited. *Cladistics* 12:291–303
  41. Diamond JM. 1975. The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. *Biol. Conserv.* 7:129–46
  42. Didham RK, Ghazoul J, Stork NE, Davis AJ. 1996. Insects in fragmented forests: a functional approach. *Trends Ecol. Evol.* 11:255–60
  43. Donnelly TW. 1988. Geological constraints on Caribbean biogeography. See Ref. 105, pp. 15–37
  44. Dover JW. 1991. The conservation of insects on arable farmland. See Ref. 33, pp. 294–318
  45. Dugdale JS. 1989. New Zealand Lepidoptera: basic biogeography. *NZ J. Zool.* 16:679–87
  46. Dunlop BN. 1989. Endangered and threatened wildlife and plants; animal notice of review. *Fed. Regist.* 54:554–79
  47. Emberson RM. 1995. The Chatham Islands beetle fauna and the age of separation of the Chatham Islands from New Zealand. *NZ Entomol.* 18:1–7
  48. Emerson BC, Oromi P, Hewitt GM. 1999. MtDNA phylogeography and recent intra-island diversification among Canary Island *Calathus* beetles. *Mol. Phylogenet. Evol.* 13:149–58
  49. Enserink M. 1999. Biological invaders sweep in. *Science* 285:834–36
  50. Erwin TL. 1979. Thoughts on the evolutionary history of ground beetles: hypotheses generated from comparative faunal analyses of lowland forest sites in temperate and tropical regions. In *Carabid Beetles: Their Evolution, Natural History and Classification*, ed. TL Erwin, GE Ball, DR Whitehead, AL Halpern. The Hague: DW Junk. 635 pp.
  51. Esaki T. 1950. *A zoogeographical consideration of the insect fauna in the Pacific islands*. Presented at 8th Int. Congr. Entomol., Stockholm
  52. Eyles AC, Carvalho JCM. 1995. Further endemic new genera and species of Mirinae (Hemiptera; Miridae) from New Zealand. *NZ J. Zool.* 22:49–90
  53. Faeth SH, Kane TC. 1978. Urban biogeography: city parks as islands for Diptera and Coleoptera. *Oecologia* 32: 127–33
  54. Fennah RG. 1958. Fulgoroidea of south-eastern Polynesia. *Trans. R. Entomol. Soc. London* 110:117–220
  55. Fisher BL. 1997. Biogeography and ecology of the ant fauna of Madagascar (Hymenoptera: Formicidae). *J. Nat. Hist.* 31:269–302
  56. Fisher BL, Girman D. 2000. Biogeography of ants in eastern Madagascar. See Ref. 111, pp. 1–10
  57. Fleming CA. 1975. Adaptive radiation in New Zealand cicadas. *Proc. Am. Phil. Soc.* 119:298–306
  58. Freitag R. 1992. Biogeography of West Indian tiger beetles (Coleoptera: Cicindelidae). See Ref. 128, pp. 123–58
  59. Funasaki GY, Lai PY, Nakahara LM, Beardsley JW, Ota AK. 1988. A review of biological control introductions in Hawaii: 1890 to 1985. *Proc. Hawaii. Entomol. Soc.* 28:105–60
  60. Funk DJ, Futuyma DJ, Ortí G, Meyer A. 1995. A history of host associations and evolutionary diversification for *Ophraella* (Coleoptera: Chrysomelidae): new evidence from mitochondrial DNA. *Evolution* 49:1008–17

61. Gagne WC. 1969. New species and a revised key to the Hawaiian *Cyrtopeltis* Fieb. with notes on *Cyrtopeltis* (*Engytatus*) *hawaiiensis* Kirkaldy (Heteroptera: Miridae). *Proc. Hawaii. Entomol. Soci.* 20:35–44
62. Gagne WC. 1997. *Insular Evolution, Speciation, and Revision of the Hawaiian Genus Nesiomiris* (Hemiptera: Miridae). Honolulu: Bishop Mus. Press
63. Gillespie RG. 1999. Naiveté and novel perturbations: conservation of native spiders on an oceanic island system. *J. Insect Conserv.* 3:263–72
64. Gillespie RG, Croom HB, Hasty GL. 1997. Phylogenetic relationships and adaptive shifts among major clades of *Tetragnatha* spiders (Araneae: Tetragnathidae) in Hawaii. *Pac. Sci.* 51:380–94
65. Gillespie RG, Howarth FG, Roderick GK. 2001. Adaptive radiation. In *Encyclopedia of Biodiversity*, ed. SA Levin, pp. 25–44. New York: Academic
66. Gillespie RG, Reimer N. 1993. The effect of alien predatory ants (Hymenoptera, Formicidae) on Hawaiian endemic spiders (Araneae, Tetragnathidae). *Pac. Sci.* 47:21–33
67. Gillespie RG, Rivera MA, Garb JE. 1998. Sun, surf and spiders: taxonomy and phylogeography of Hawaiian Araneae. In *Proc. 17th Eur. Coll. Arachnol., Edinburgh 1997*, pp. 41–51. Burnham Beeches, Bucks: Br. Arachnol. Soc.
68. Gotelli NJ, Kelley WG. 1993. A general model of metapopulation dynamics. *Oikos* 68:36–44
69. Gressitt JL. 1954. Introduction. In *Insects of Micronesia*, ed. JL Gressitt, 1:1–257. Honolulu: Bishop Mus. Press
70. Gressitt JL. 1961. Problems in the zoogeography of Pacific and Antarctic insects. *Pac. Insects Monogr.* 2:1–94
71. Gressitt JL. 1970. Subantarctic entomology and biogeography. *Pac. Insects Monogr.* 23:295–374
72. Gressitt JL. 1982. Pacific-Asian biogeography with examples from the Coleoptera. *Entomol. Gen.* 8:1–11
73. Gressitt JL, Quate LW. 1958. Zoogeography and evolution of Pacific insects. *Bull. Entomol. Soc. Am.* 4:124–26
74. Gressitt JL, Weber NA. 1960. Bibliographic introduction to Antarctic-Subantarctic entomology. *Pac. Insects* 1:441–80
75. Griswold CE. 2000. “Afromontane” spider families in Madagascar (Araneae, Araneomorphae: Cyatholipidae, Phyxellidae, Zorocratidae). See Ref. 111, pp. 345–54
76. Groombridge B, ed. 1992. *Global Biodiversity: Status of the Earth's Living Resources*. London: Chapman & Hall
77. Hafernik JE. 1992. Threats to invertebrate biodiversity: implications for conservation strategies. In *Conservation Biology: The Theory and Practice of Nature Conservation, Preservation and Management*, ed. PL Fiedler, SK Jain, pp. 171–95. New York: Chapman & Hall
78. Harrison D, Murphy DD, Ehrlich PR. 1988. Distribution of the Bay Checkerspot butterfly, *Euphydryas editha bayensis*: evidence for a metapopulation model. *Am. Nat.* 132:360–82
79. Hart DD, Horwitz RJ. 1991. Habitat diversity and the species-area relationship: alternative models and tests. In *Habitat Structure: The Physical Arrangement of Objects in Space*, ed. DS Bell, ED McCoy, HR Mushinsky, pp. 47–68. London: Chapman & Hall
80. Hoch H, Howarth FG. 1999. Multiple cave invasions by species of the planthopper genus *Oliarus* in Hawaii (Homoptera: Fulgoroidea: Cixiidae). *Zool. J. Linn. Soc.* 127:453–75
81. Hollocher H. 1996. Island hopping in *Drosophila*: patterns and processes. *Phil. Trans. R. Soc. London Ser. B* 351:735–43
82. Holzapfel EP, Clagg HB, Goff ML. 1978. Trapping of airborne insects on

- ships on the Pacific, part 9. *Pac. Insects* 19:65–90
83. Howarth FG. 1981. Community structure and niche differentiation in Hawaiian lava tubes. In *Island Ecosystems; Biological Organization in Selected Hawaiian Communities*, ed. D Mueller-Dombois, KW Bridges, HL Carson, pp. 318–36. New York: Academic
84. Howarth FG. 1990. Hawaiian terrestrial arthropods: an overview. *Bishop Mus. Occas. Pap.* 30:4–26
85. Howarth FG. 1993. High stress subterranean habitats and evolutionary change in cave-inhabiting arthropods. *Am. Nat.* 142:565–77
86. Howarth FG, Mull WP. 1992. *Hawaiian Insects and Their Kin*. Honolulu: Univ. Hawaii Press. 160 pp.
87. Howarth FG, Ramsay GW. 1991. The conservation of island insects and their habitats. See Ref. 33, pp. 71–107
88. Iyengar MOT. 1960. A review of the mosquito fauna of the South Pacific (Diptera: Culicidae). *S. Pac. Comm. Tech. Pap.* 130:1–102
89. Johnson KP, Adler FR, Cherry JL. 2000. Genetic and phylogenetic consequences of island biogeography. *Evolution* 54:387–96
90. Joseph L, Moritz C, Hugall A. 1995. Molecular data support vicariance as a source of diversity in rainforests. *Proc. R. Soc. London Ser. B.* 260:177–82
91. Jourdan H. 1997. Threats on Pacific Islands: the spread of the tramp ant *Wasmannia auropunctata* (Hymenoptera: Formicidae). *Pac. Conserv. Biol.* 3:61–64
92. Juan C, Ibrahim KM, Oromi P, Hewitt GM. 1996. Mitochondrial DNA sequence variation and phylogeography of *Pimelia* darkling beetles on the island of Tenerife (Canary Islands). *Heredity* 77:589–98
93. Juan C, Ibrahim KM, Oromi P, Hewitt GM. 2000. Colonization and diversification: towards a phylogeographic synthesis for the Canary Islands. *Trends Ecol. Evol.* 15:104–9
94. Juan C, Oromi P, Hewitt GM. 1995. Mitochondrial DNA phylogeny and sequential colonization of Canary Islands by darkling beetles of the genus *Pimelia* (Tenebrionidae). *Proc. R. Soc. London Ser. B* 261:173–80
95. Kambysellis MP, Craddock EM. 1997. Ecological and reproductive shifts in the diversification of the endemic Hawaiian *Drosophila*. In *Molecular Evolution and Adaptive Radiation*, ed. TJ Givnish, KJ Sytsma, pp. 475–509. New York: Cambridge Univ. Press
96. Kaneshiro KY. 1983. Sexual selection and direction of evolution in the biosystematics of the Hawaiian Drosophilidae. *Annu. Rev. Entomol.* 28:161–78
97. Kaneshiro KY, Boake CRB. 1987. Sexual selection and speciation: issues raised by Hawaiian *Drosophila*. *Trends Ecol. Evol.* 2:207–12
98. Keast A, Miller SE, eds. 1996. *The Origin and Evolution of Pacific Island Biotas, New Guinea to Eastern Polynesia: Patterns and Processes*. Amsterdam: SPB Academic
99. Klimaszewski J. 1997. Biodiversity of New Zealand beetles (Insecta, Coleoptera). *Mem. Mus. Vic.* 56:659–66
100. Knowles LL. 2000. Tests of Pleistocene speciation in montane grasshoppers (genus *Melanoplus*) from the sky islands of Western North America. *Evolution* 54:1337–48
101. Kotze DJ, Niemela J, Nieminen M. 2000. Colonization success of carabid beetles on Baltic islands. *J. Biogeogr.* 27:807–19
102. Kruess A, Tscharrntke T. 2000. Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia* 122:129–37
103. Krüger O, McGavin GC. 2000. Macroecology of local insect communities. *Acta Oecol.* 21:21–8

104. Kuusela K. 1979. Early summer ecology and community structure of macrozoobenthos on stones. *Acta Univer. Ouluensis Ser. A Sci. Rerum Nat.* 87:1–130
- 104a. Lewis OT, Wilson RJ, Harper MC. 1998. Endemic butterflies of Grande Comore: habitat preferences and conservation priorities. *Biol. Conserv.* 85:113–21
105. Liebherr JK, ed. 1988. *Zoogeography of Caribbean Insects*. Ithaca: Comstock. 285 pp.
106. Liebherr JK. 1997. Dispersal and vicariance in Hawaiian platynine carabid beetles (Coleoptera). *Pac. Sci.* 51:424–39
107. Liebherr JK, Hajek AE. 1990. A cladistic test of the taxon cycle and taxon pulse hypotheses. *Cladistics* 6:39–59
108. Liebherr JK, Zimmerman EC. 2000. *Hawaiian Carabidae (Coleoptera), part 1: Introduction and Tribe Platynini*. Honolulu: Univ. Hawaii Press. 494 pp.
109. Lindroth CH, Andersen H, Bødvarsson H, Richter SH. 1973. Surtsey Island: the development of a new fauna, 1963–1970, terrestrial invertebrates. *Entomol. Scand. Suppl.* 5:1–280
110. Loope LL, Hamann O, Stone CP. 1988. Comparative conservation biology of oceanic archipelagoes. *Bioscience* 38:272–82
111. Lourenço WR, Goodman SM, eds. 2000. *Diversity and Endemism in Madagascar*. Paris: ORSTOM
112. Lubin YD. 1984. Changes in the native fauna of the Galapagos Islands following invasion by the little red fire ant *Wasmannia auropunctata*. *Biol. J. Linn. Soc.* 21:229–42
113. MacArthur RH. 1972. *Geographical Ecology; Patterns in the Distribution of Species*. New York: Harper & Row
114. MacArthur RH, Wilson EO. 1967. *The Theory of Island Biogeography*. Princeton: Princeton Univ. Press
115. Mackerras IM. 1950. The zoogeography of the Diptera. *Aust. J. Sci.* 12:157–61
116. Masta SE. 2000. Phylogeography of the jumping spider *Habronattus pugilis* (Araneae: Salticidae): recent vicariance of sky island populations? *Evolution* 54:1699–711
117. Matyot P. 1998. The orthopteroids of the Seychelles: a threatened island fauna. *J. Insect Conser.* 2:235–46
118. Mawdsley NA, Stork NE. 1995. Species extinction in insects. In *Insects in a Changing Environment*, ed. R Harrington, NE Stork, pp. 321–69. London: Academic
119. Mayr E. 1954. Change in genetic environment and evolution. In *Evolution as a Process*, ed. JS Huxley, AC Hardy, EB Ford, pp. 156–80. London: Allen & Unwin
120. Mildenhall DC. 1980. New Zealand Late Cretaceous and Cenozoic plant biogeography: a contribution. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 31:197–233
121. Miller SE. 1996. Biogeography of Pacific insects and other terrestrial invertebrates: a status report. See Ref. 98, pp. 463–75
122. Miller SE, Eldredge LG. 1996. Numbers of Hawaiian species: supplement 1. *Bishop Mus. Occas. Pap.* 45:8–17
123. Montgomerly SL. 1982. Biogeography of the moth genus *Eupithecia* in Oceania and the evolution of ambush predation in Hawaiian caterpillars (Lepidoptera: Geometridae). *Entomol. Gen.* 8:27–34
124. Mühlenberg M, Leipold D, Mader HJ, Steinhauer B. 1977. Island ecology of arthropods. I. Diversity, niches, and resources on some Seychelles Islands. *Oecologia* 29:117–34
125. Mühlenberg M, Leipold D, Mader HJ, Steinhauer B. 1977. Island ecology of arthropods. II. Niches and relative abundances of Seychelles ants (Formicidae) in different habitats. *Oecologia* 29:135–44
126. Munroe E. 1996. Distributional patterns of Lepidoptera in the Pacific Islands. See Ref. 98, pp. 275–95

127. Nafus DM. 1993. Extinction, biological control, and conservation on islands. In *Perspectives on Insect Conservation*, ed. KJ Gaston, TR New, MJ Samways, pp. 139–54. Andover: Intercept
- 127a. Nishida GM. 1992. *Hawaiian Terrestrial Arthropod Checklist*. Honolulu: Bishop Mus. Press. 287 pp.
128. Noonan GR. 1992. Biogeographic patterns of the montane Carabidae of North America north of Mexico (Coleoptera: Carabidae). In *The Biogeography of Ground Beetles of Mountains and Islands*, ed. GR Noonan, GE Ball, NE Stork, pp. 1–41. Andover, UK: Intercept
129. Opler PA. 1974. Oaks as evolutionary islands for leaf-mining insects. *Am. Sci.* 62:67–73
130. Otte D. 1989. Speciation in Hawaiian crickets. In *Speciation and Its Consequences*, ed. D Otte, JA Endler, pp. 482–526. Sunderland, MA: Sinauer
131. Owen J, Owen DF. 1975. Suburban gardens: England's most important nature reserve? *Environ. Conserv.* 2:53–59
132. Patterson BD. 1987. The principle of nested subsets and its implications for biological conservation. *Conserv. Biol.* 1:323–34
133. Paulay G. 1985. Adaptive radiation on an isolated oceanic island: the Cryptorhynchinae (Curculionidae) of Rapa revisited. *Biol. J. Linn. Soc.* 26:95–187
134. Paulay G. 1994. Biodiversity on oceanic islands: its origin and extinction. *Am. Zool.* 34:134–44
135. Peck SB. 1996. Origin and development of an insect fauna on a remote archipelago: the Galapagos Islands, Ecuador. See Ref. 98, pp. 91–122
136. Peck SB. 1999. Historical biogeography of Jamaica: evidence from cave invertebrates. *Can. J. Zool.* 77:368–80
137. Peck SB, Finston T. 1993. Galapagos Island troglobites: the questions of tropical troglobites, parapatric distributions with eyed-sister-species, and their origin by parapatric speciation. *Mem. Biospeol.* 20:19–37
138. Peck SB, Wigfull P, Nishida G. 1999. Physical correlates of insular species diversity: the insects of the Hawaiian Islands. *Ann. Entomol. Soc. Am.* 92:529–36
139. Percy D. 2001. *The evolution of psyllid host relationships in Macronesia*. PhD dissertation. Univ. Glasgow, Glasgow
140. Perkins RCL. 1913. Introduction. In *Fauna Hawaiiensis*, ed. D Sharp, pp. xv–ccxxviii. Cambridge: Cambridge Univ. Press
141. Perrault GG. 1992. Endemism and biogeography among Tahitian *Mecyclothorax* species (Coleoptera: Carabidae: Psyllidini). See Ref. 128, pp. 201–15
142. Pimm SL. 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities*. Chicago: Univ. Chicago Press
143. Polhemus DA. 1996. Island arcs and their influence on Indo-Pacific biogeography. See Ref. 98, pp. 51–66
144. Porembski S, Barthlott W. 2000. *Inselbergs: Biotic Diversity of Isolated Rock Outcrops in Tropical and Temperate Regions*. Berlin: Springer
145. Powell JA. 1994. Biogeography of Lepidoptera on the California Channel Islands. In *The Fourth California Islands Symposium: Update on the Status of Resources*, ed. WL Halvorson, GJ Maender, pp. 449–64. Santa Barbara: St. Barbara Mus. Nat. Hist.
146. Powell JA, Wagner DL. 1993. The microlepidoptera fauna of Santa Cruz Island is less depauperate than that of butterflies and larger moths. In *Third California Islands Symposium: Recent Advances in Research on the California Islands*, ed. FG Hochberg, pp. 189–98. Santa Barbara: St. Barbara Mus. Nat. Hist.
147. Prance GT. 1996. Islands in Amazonia. *Phil. Trans. R. Soc. London Ser. B* 351:823–33

148. Price PW. 1984. Communities of specialists: vacant niches in ecological and evolutionary time. In *Ecological Communities: Conceptual Issues and the Evidence*, ed. DR Strong, D Simberloff, LG Abele, AB Thistle, pp. 510–23. Princeton: Princeton Univ. Press
149. Rahn ME, Rust RW. 2000. Nested Coleoptera and Orthoptera on sand dunes in the Basin and Range Province of western North America. *J. Insect Conserv.* 4:33–43
150. Resh VH, De Szalay FA. 1995. Streams and rivers of Oceania. In *River and Stream Ecosystems*, ed. CE Cushing, KW Cummins, GW Minshall, pp. 717–36. Amsterdam: Elsevier
151. Rey JR. 1985. Insular ecology of salt marsh arthropods: species level patterns. *J. Biogeogr.* 12:97–107
152. Ricklefs RE, Lovette IJ. 1999. The roles of island area per se and habitat diversity in the species-area relationships of four Lesser Antillean faunal groups. *J. Anim. Ecol.* 68:1142–60
153. Deleted in proof.
154. Roderick GK. 1997. Herbivorous insects and the Hawaiian silversword alliance: coevolution or cospeciation? *Pac. Sci.* 51:440–49
155. Roderick GK, Gillespie RG. 1998. Speciation and phylogeography of Hawaiian terrestrial arthropods. *Mol. Ecol.* 7:519–31
156. Roff DA. 1990. The evolution of flightlessness in insects. *Ecol. Monogr.* 60:389–421
157. Sadler JP. 1999. Biodiversity on oceanic islands: a palaeoecological assessment. *J. Biogeogr.* 26:75–87
158. Schoener DW, Spiller DA. 1987. High population persistence in a system with high turnover. *Nature* 330:474–77
159. Sequiera AS, Lanteri AA, Scatagliini MA Confalonieri VA, Farrell BD. 2000. Are flightless *Galapaganus* weevils older than the Galapagos Islands they inhabit? *Heredity* 85:20–29
160. Shaw KL. 1995. Biogeographic patterns of two independent Hawaiian cricket radiations (*Laupala* and *Prognathogryllus*). See Ref. 185, pp. 39–56
161. Shaw KL. 1996. Sequential radiations and patterns of speciation in the Hawaiian cricket genus *Laupala* inferred from DNA sequences. *Evolution* 50:237–55
162. Simberloff D. 1976. Species turnover and equilibrium island biogeography. *Science* 194:572–78
163. Simberloff D. 1995. Why do introduced species appear to devastate islands more than mainland areas? *Pac. Sci.* 49:87–97
164. Simberloff D. 2000. Extinction-proneness of island species: causes and management implications. *Raffles Bull. Zool.* 48:1–9
165. Simberloff D, Wilson EO. 1969. Experimental zoogeography of islands: defaunation and monitoring techniques. *Ecology* 50:267–78
166. Simberloff D, Wilson EO. 1969. Experimental zoogeography of islands: the colonization of empty islands *Ecology* 50:278–96
167. Simberloff D, Wilson EO. 1970. Experimental zoogeography of islands: a two-year record of colonization. *Ecology* 51:934–37
168. Simon C. 1987. Hawaiian evolutionary biology: an introduction. *Trends Ecol. Evol.* 2:175–78
169. Spencer-Smith D, Ramos SJ, McKenzie F, Munroe E, Miller LD. 1988. Biogeographical affinities of the butterflies of a “forgotten” island: Mona (Puerto Rico). *Bull. Allyn Mus.* 121:1–35
170. Spitzer K, Bezdek A, Jaros J. 1999. Ecological succession of a relict Central European peat bog and variability of its insect biodiversity. *J. Insect Conserv.* 3:97–106
171. Stevens G. 1990. Geological evolution and biotic links in the Mesozoic and Cenozoic of the Southwest Pacific. *Acta XX Congr. Inter. Ornithol.* 1:361–82
172. Storey M, Mahoney JJ, Saunders AD,

- Duncan RA, Kelley SP, Coffin MF. 1995. Timing of hot spot-related volcanism and the breakup of Madagascar and India. *Science* 267:852–55
173. Strazanac J. 1996. *Systematics and acoustics of Hawaiian genus Banza (Orthoptera: Tettigoniidae)*. PhD dissertation. Univ. Hawaii, Honolulu
174. Svensson BW. 1999. Environmental heterogeneity in space and time: patch use, recruitment and dynamics of a rock pool population of a gyrenid beetle. *Oikos* 84:227–38
175. Templeton AR. 1980. The theory of speciation via the founder principle. *Genetics* 91:1011–38
176. Thomas CD, Harrison S. 1992. Spatial dynamics of a patchily distributed butterfly species. *J. Anim. Ecol.* 1:437–46
177. Thomas MB, Wratten SD, Sotherton NW. 1992. Creation of “island” habitats in farmland to manipulate populations of beneficial arthropods: predator densities and species composition. *J. Appl. Ecol.* 29:524–31
178. Thornton I. 1996. *Krakatau: The Destruction and Reassembly of an Island Ecosystem*. Cambridge, MA: Harvard Univ. Press
179. Thornton IWB. 1984. Psocoptera of the Hawaiian Islands Part III. The endemic Ptycta complex (Psocidae): systematics, distribution and evolution. *Int. J. Entomol.* 26:1–128
180. Thornton IWB. 1996. The origins and development of island biotas as illustrated by Krakatau. See Ref. 98, pp. 67–90
181. Toft CA, Schoener TW. 1983. Abundance and diversity of orb spiders on 106 Bahamian islands: biogeography at an intermediate trophic level. *Oikos* 41:411–26
182. Trewick SA. 2000. Molecular evidence for dispersal rather than vicariance as the origin of flightless insect species on the Chatham Islands, New Zealand. *J. Biogeogr.* 27:1189–200
183. Usinger RL. 1941. Problems of insect speciation in the Hawaiian Islands. *Am. Nat.* 75:251–63
184. van Riper III C, van Riper SG, Goff ML, Laird M. 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56:327–44
185. Wagner WL, Funk VA, eds. 1995. *Hawaiian Biogeography, Evolution on a Hot Spot Archipelago*. Washington, DC: Smithsonian Inst. Press
186. Wallace AR. 1902. *Island Life*. London: MacMillan. 526 pp.
187. Ward SA, Thornton IWB. 2000. Chance and determinism in the development of isolated communities. *Global Ecol. Biogeogr.* 9:7–18
188. Whittaker RJ. 1998. *Island Biogeography: Ecology, Evolution, and Conservation*. Oxford: Oxford Univ. Press
- 188a. Wiemers M. 1995. The butterflies of the Canary Islands: a survey on their distribution, biology and ecology (Lepidoptera: Papilionoidea and Hesperioidea). *Linn. Belg.* 15:63–87
189. Williamson M. 1983. A century of islands: from Darwin to the Hawaiian Drosophilidae. *Biol. J. Linn. Soc.* 20:3–10
190. Williamson MH. 1981. *Island Populations*. Oxford: Oxford Univ. Press. 286 pp.
191. Wilson EO. 1961. The nature of the taxon cycle in the Melanesian ant fauna. *Am. Nat.* 95:169–93
192. Wilson EO. 1996. Hawaii: a world without social insects. Bishop Mus. Occas. Pap. 45:3–7
193. Wilson EO, Taylor RW. 1967. *The Ants of Polynesia (Hymenoptera, Formicidae)*. Honolulu: Entomol. Dept., Bishop Mus.
194. Wilson EO, Willis EO. 1975. Applied biogeography. In *Ecology and Evolution of Communities*, ed. ML Cody, JM Diamond, pp. 522–34. Cambridge, MA: Belknap

195. Wool D, Inbar M. 1998. Colonization of ecological islands: galling aphid populations (Sternorrhyncha: Aphidoidea: Pemphigidae) on recovering *Pistacia* trees after destruction by fire. *Eur. J. Entomol.* 95:41–53
196. Wright S. 1978. *Variability within and among Natural Populations*. Chicago: Univ. Chicago Press
197. Zimmerman EC 1936. Cryptorrhynchi-  
nae of the Society Islands. *Bishop Mus. Occas. Pap.* 12:1–48
198. Zimmerman EC. 1942. Distribution and origin of some eastern oceanic insects. *Am. Nat.* 76:280–307
199. Zimmerman EC. 1948. *Introduction*. Honolulu: Univ. Hawaii Press. 206 pp.
200. Zimmerman EC. 1960. Possible evidence of rapid evolution in Hawaiian moths. *Evolution* 14:137–38



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## ERRATA

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