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THE THEORY OF  
**ISLAND BIOGEOGRAPHY**  
Revisited

## Island Biogeography of Remote Archipelagoes

### INTERPLAY BETWEEN ECOLOGICAL AND EVOLUTIONARY PROCESSES

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THE EQUILIBRIUM THEORY OF ISLAND biogeography (ETIB) was developed around the concept of islands formed *de novo*, with species colonizing and over time reaching a balance between immigration and extinction (MacArthur and Wilson 1967, see Schoener chapter, this volume). A great challenge to the theory has been its application to remote oceanic islands—those that are formed from beneath the ocean surface and are beyond the normal limits of dispersal for a taxon, where immigration occurs relatively rarely and speciation relatively frequently. Here we examine the interaction between speciation and immigration in community assembly on remote islands. Perhaps the most significant finding is that lineages vary considerably in terms of how they colonize remote islands, and how they accumulate on those islands over time. In particular, in comparing lineages that have been in the Hawaiian archipelago for the lifespan of the current high islands (allowing island chronology to be used to assess community changes over time), some lineages seemingly accumulate species rapidly, often reaching numbers well beyond the putative equilibrium, before declining in number (see figures 13.4C and 13.4D below). Other lineages, especially those that are less diverse, appear to accumulate species more slowly, and some may not reach equilibrium within the time frame of existence of the high islands (approximately 5 my). These results have intriguing parallels to the ETIB, and lay a foundation for developing hypotheses to test the predictability of species accumulation, extinction, and invasion on remote islands.

#### Attributes of Remote Islands

Characteristics of communities on remote islands include (1) compositional disharmony as a result of differing abilities of lineages to disperse

over long distances, leading to attenuation in the number of organismal groups represented with increasing isolation; and (2) high levels of endemism associated with rare colonization events and adaptive radiation (see Carlquist 1974). In particular, when the isolation of an island is extreme, the frequency of colonization becomes sufficiently low to allow *in situ* evolution of new species to play a role in filling the available ecological space (MacArthur and Wilson 1967), often through adaptive radiation (see Schluter 2000). The isolation necessary for the rate of speciation to exceed immigration has been termed the “radiation zone” (MacArthur and Wilson 1967): “Near the outer limit of the dispersal range of a given taxon, speciation and exchange of newly formed autochthonous species within an archipelago can outrun immigration from outside the archipelago and lead to the accumulation of species on single islands” (p. 180). The physical separation required for this effect to be manifest is clearly dependent on dispersal abilities; for example the radiation zone for mammals is much nearer the source than for many insects.

For many isolated oceanic archipelagoes, the age of each island is often known with some precision. This knowledge, coupled with molecular tools that have allowed identification of the source and frequency of colonization, has provided a chronological framework within which to examine the interplay between migration and speciation in the formation of communities over time. The Hawaiian Islands are particularly amenable to such studies, in part because they are generally considered to be the most isolated archipelago in the world. In addition, the youth of the islands (current high islands formed 0.4–5.1 mya; Clague and Dalrymple [1987]) and their linear and chronological arrangement, provide a clear-cut framework for examining how communities have been formed over recent evolutionary time. Accordingly, much of our discussion will be focused specifically on the Hawaiian archipelago. Since the 1980s, molecular studies of a wide diversity of lineages from the Hawaiian Islands have allowed for a much better characterization of dispersal patterns and timing than was previously possible and in turn allow for biogeographic insights highly relevant to the ETIB, as discussed below.

We examine four aspects of remote islands relevant to the ETIB: (1) colonization, i.e., which species reach remote islands, and how and why; (2) changes that occur subsequent to colonization on remote islands, given that the much reduced rate of colonization allows evolutionary processes to come into play; (3) mechanisms by which species are added to communities on remote islands, and comparisons between outcomes from speciation and immigration; and, finally, (4) how communities are assembled over space and time on isolated archipelagoes, in particular

the interplay between ecological and evolutionary changes in dictating the composition of communities.

### Colonization of Remote Islands

To understand the formation of communities on remote islands, we must first recognize the context of species arrival. What are the characteristics of successful colonization—what species arrive, in what manner, and how frequently?

#### *Active versus Passive Dispersal*

[I]t can be expected that stepping stones are more important to species whose propagules tend to disperse actively or on floating "rafts," such as birds, mammals, and some plants and arthropods.

They are relatively less important to species whose propagules tend to be dispersed passively in the wind, such as most microorganisms and many higher plants and arthropods.

—MacArthur and Wilson 1967, pp. 132–33

A more general prediction based on this statement is that the likelihood of a species reaching a remote island, and its tendency to use intervening stepping stones, will be dictated by its propensity for active versus passive dispersal. Do recent empirical data support this prediction?

The different mechanisms and propensities for dispersal are likely to result in different biogeographic patterns, as evidenced by recent studies showing first that passively dispersive groups have colonized remote archipelagoes repeatedly and independently. For a number of these lineages, dispersal has been much reduced within each archipelago (see below), such that colonists are unlikely to use more proximate archipelagoes as stepping-stones to more remote archipelagoes. This may be simply because the chance of a highly dispersive mainland propagule reaching a remote archipelago is higher than the chance of arrival of a propagule from an intervening archipelago where evolution has resulted in reduction of dispersal ability. For example, the highly dispersive (by wind) spider genus *Tetragnatha* has colonized each of the different archipelagoes of Polynesia independently from different sources, with diversification within each archipelago from a single founder following reduction in dispersal abilities (Gillespie 2002). Drosophilid flies also seem to have colonized the different remote archipelagoes of Oceania independently (P. M. O'Grady, personal communication).

Among plants that are known for passive propagule dispersal, extensive within-archipelago diversification from a common founder is unusual. For example, significantly lower levels of endemism in Hawaiian ferns compared to angiosperms—both for the entire archipelago and for individual islands—probably reflects much greater passive-dispersal ability of spores compared to seeds in general (see Fosberg 1948; Driscoll and Barrington 2007). Passive transport of fern spores in the northern subtropical jet stream is consistent with phylogenetic data from multiple Hawaiian fern lineages (Geiger et al. 2007). Molecular phylogenetic evidence supports repeated colonization of the Hawaiian archipelago by most fern genera (e.g., *Asplenium* [Ranker et al. 1994, Schneider et al. 2004]; *Dryopteris* [Geiger and Ranker 2005]; *Polystichum* [Driscoll and Barrington 2007])). In such systems, the rate of colonization and occupancy of ecological space through dispersal may exceed or inhibit the rate of diversification (e.g., through outside gene flow) and thereby limit levels of endemism.

In contrast, active dispersal (e.g., by birds) appears to be associated with less frequent or widespread island colonization and high levels of endemism, as in many flowering plants. Price and Wagner (2004) suggest that intermediate dispersal ability afforded by bird transport allows for plant colonization to occur across islands of an archipelago while maintaining a sufficient degree of isolation for diversification to occur. Indeed, the majority of Hawaiian angiosperm lineages have fruit or seed characteristics consistent with dispersal by birds (Carlquist 1974, Sakai et al. 1995) and those lineages are significantly more diverse than lineages with abiotic dispersal (Price and Wagner 2004); birds also appear to account for the majority of plant lineages (~90%) in the highly endemic flora of the Juan Fernandez Islands (Bernardello et al. 2006). In the genus *Cyrtandra* (Gesneriaceae), diversification on islands throughout the Pacific has been restricted to a fleshy-fruited and putatively bird-dispersed lineage within the genus, as in *Scaevola* (Howarth et al. 2003), with interisland dispersal events often associated with the origin of new species or major clades (Cronk et al. 2005). Likewise, crab spiders (Thomisidae), which are potentially bird-dispersed, are found throughout the Hawaiian, Society, and Marquesas islands, and are diverse within each archipelago, this entire lineage forming a tightly monophyletic clade (Garb and Gillespie 2006, 2009).

For taxa that undergo active dispersal, and in which the dispersal mechanism itself will not necessarily lead to loss of propagules from a remote island, it is unlikely that selection would act to dramatically reduce dispersal ability in the same manner as may occur in taxa that are passively dispersed (see below). However, selection may still reduce dispersal

ability among active dispersers if habitat space is highly confined in the island environment or a shift in ecology favors changes in propagule characteristics (see Carlquist 1974). Therefore, in general, stepping-stones may play a more prominent role in the biogeography of actively-dispersed taxa than of passively dispersed taxa that are subject to strong selection against dispersal ability in an insular setting.

#### *Niche Preemption*

*An island is closed to a particular species either when the species is excluded by competitors already in residence or else when its population size is held so low that extinction occurs much more frequently than immigration.*

—MacArthur and Wilson 1967, p. 121

Once a niche has been filled, it appears to be more difficult for closely related and putatively ecologically similar colonizers to enter, as suggested for plants in the Canary Islands: For the full suite of endemics in each of 20 plant genera that are highly diverse in the archipelago, Silvertown (2004) noted that each lineage is monophyletic; in contrast, he provided evidence for repeated colonization of the Canary Islands by 20 genera of low insular diversity. He interpreted that pattern as possible evidence for the importance of niche pre-emption by radiating lineages and consequent failure of later arriving close relatives to become established (see also Silvertown et al. 2005). Indeed, successful independent colonizations of Macaronesia by congeneric angiosperms have occurred only when different islands are involved or when the congeneric lineages are widely divergent and putatively distinct ecologically (Carine et al. 2004).

Similar conclusions could be drawn for the flora of the Hawaiian Islands, where, as noted above, molecular phylogenetic studies have shown that all endemic angiosperm species of most individual genera or groups of related genera constitute a single endemic clade, including numerous groups that were previously thought to stem from multiple introductions, such as the extraordinarily diverse lobeliads (Givnish et al. 2008). Hawaiian angiosperm genera with indigenous taxa that stem from multiple introductions include either only one or two species in each of two endemic lineages (*Rubus*, *Santalum*) or only a single species in two of three indigenous clades (*Scaevola*) (Howarth et al. 1997, Alice and Campbell 1999, Howarth et al. 2003, Harbaugh and Baldwin 2007).

Niche preemption also may contribute to the "progression rule" of Funk and Wagner (1995): In Hawaiian plants, rarity of back migration

to islands previously occupied by other members of a highly diversified island lineage and lack of diversity of such back-migrant lineages may reflect a degree of niche preemption by already present members of the same insular clade. The progression rule of successive dispersal from older to younger islands in the Hawaiian chain holds well for most well-resolved plant and animal lineages that appear to have arrived initially on older islands. In the silversword alliance, for example, no unequivocal instance of back migration has been documented (Baldwin and Robichaux 1995, B. G. Baldwin, unpublished); likewise in various spider (Hormiga et al. 2002, Gillespie 2004) and insect (Mendelson and Shaw 2005) lineages. In the lobeliad genus *Cyanea*, the only unequivocal younger to older island dispersal event (based on a cpDNA tree) involves a lineage that evidently had not previously colonized that island, instead initially dispersing east—past Oahu—from Kauai to Maui Nui and then west from Maui Nui to Oahu (Givnish et al. 1995). In the highly diverse *Schiedea*, Wagner et al.'s (2005) biogeographic hypothesis, based on molecular and morphological data, provides only one unequivocal example of a species recolonizing an ancestrally occupied island. Additional resolution of divergence times and better characterization of ecological traits of island lineages should allow for more rigorous evaluation of niche preemption within a phylogenetic context.

An example of possible niche preemption in the larger Pacific region is found in crab spiders (Thomisidae), where one lineage (apparently from the Americas) has diversified in the Hawaiian, Marquesas, and Society islands, while another (which appears to have arrived from Australasia) has diversified in the Australs (Garb and Gillespie 2006); there is no distributional overlap between the lineages. Given that these archipelagoes are separated by only ~500 km, and that molecular evidence suggests that crab spiders have been in each archipelago for ~5 million years, the lack of distributional overlap of the two lineages is likely due to priority effects (first to get there "wins") rather than lack of time for dispersal between archipelagoes.

The overall pattern of colonization of remote islands therefore has some elements of predictability, and some of stochasticity. Given propagule availability, the establishment of particular species is largely unpredictable; however, it appears that once the sweepstakes for a given niche have been "won," the chances of establishment by a distinct but closely related and ecologically similar species become considerably diminished (see also Losos et al. 1993). That interpretation is consistent with Darwin's (1859) naturalization hypothesis, of phylogenetic overdispersion in comparisons between native and invading species (see Strauss et al. 2006, Proches et al. 2008), although the causes of such overdispersion may

extend beyond niche considerations to community-level factors, such as sharing of enemies (e.g., herbivores or parasites) by closely related residents and invaders (but see Parker et al. 2006a,b, Riccardi and Ward 2006).

#### Change Subsequent to Colonization

Following successful establishment, island taxa can be expected to undergo ecological adjustment dictated by the abiotic and biotic environment. However, on remote islands, because of the paucity of successful colonizers and the associated abundance of "open" niches, successful colonists frequently have both time and opportunity to change, adapt, and often diversify to an unusual extent, with some widespread processes and patterns evident across distantly related taxa, as discussed below.

#### *Loss of Dispersal Ability*

*[C]onspicuous is the tendency to lose dispersal power [which can occur through the development of] flightlessness . . . increase in fruit size. . . . A second means by which dispersal power is apt to be reduced is the tendency of evolving isolates to vacate the marginal habitats that are the best staging ground for . . . arriving propagules.*

—MacArthur and Wilson 1967, pp. 157–58

Reduction or change in dispersal abilities subsequent to colonization of oceanic islands was initially discussed by Darwin (1859), who wrote

In some cases we might easily put down to disuse modifications of structure which are wholly, or mainly, due to natural selection. Mr. Wollaston has discovered the remarkable fact that 200 beetles, out of the 550 species inhabiting Madeira, are so far deficient in wings that they cannot fly; and that of the twenty-nine endemic genera, no less than twenty-three genera have all their species in this condition! Several facts, namely, that beetles in many parts of the world are very frequently blown to sea and perish; that the beetles in Madeira, as observed by Mr. Wollaston, lie much concealed, until the wind lulls and the sun shines; that the proportion of wingless beetles is larger on the exposed Dezertas than in Madeira itself; and especially the extraordinary fact, so strongly insisted on by Mr. Wollaston, of the almost entire absence of certain large groups of beetles, elsewhere excessively numerous, and which groups have habits of life almost necessitating frequent flight;—these several considerations have made me believe that the wingless condition of so many Madeira

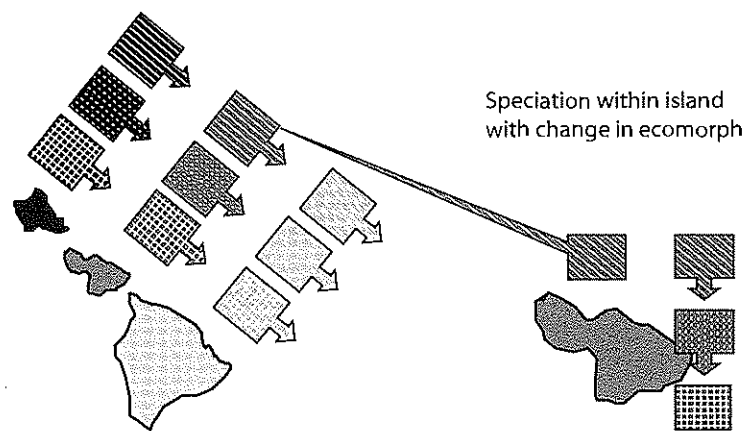
beetles is mainly due to the action of natural selection, but combined probably with disuse. For during thousands of successive generations each individual beetle which flew least, either from its wings having been ever so little less perfectly developed or from indolent habit, will have had the best chance of surviving from not being blown out to sea; and, on the other hand, those beetles which most readily took to flight will oftenest have been blown to sea and thus have been destroyed.

The above ideas have largely been substantiated, with some caveats, by more recent research, and have been discussed extensively by Carlquist (1966, 1974, 1980). At least among many taxa that are passively dispersed by wind, if dispersal ability is not reduced there is a high chance of being transported off the island and lost at sea or, within an island, being transported beyond the bounds of the narrow, stable habitats to which insular organisms often become adapted. As discussed above, these arguments do not apply as much to taxa that undergo active dispersal. Recent work continues to lend support to the arguments for loss of dispersal power among passive dispersers on remote islands (Gillespie et al. 2008). This single tendency has clearly played a major role in subsequent adaptive radiation, although selection leading to reduced dispersal ability may have diverse explanations in animals and plants (Carlquist 1966, 1974, 1980).

#### *Ecological Release*

Ecological release is a commonly documented pattern among island colonists that enter a community with a smaller fauna (MacArthur and Wilson 1967, p. 105). On very remote islands, because of the paucity of successful colonizers and the associated abundance of "open" niches, successful colonists frequently have both time and opportunity to change, adapt, and often diversify to an unusual extent (see Schluter 2000; Nosil and Reimchen 2005). Roughgarden (1972) stated that "[t]he process of faunal buildup on an island is a race between a widening of the offspring phenotype distribution of the first species there and dispersion to the island by members of some other ecologically differentiated species. If the widening of the offspring phenotype distribution, and hence the niche width, is sufficiently slow, vacant regions exist on the resource axis, which facilitate establishment of emigrants from elsewhere" (p. 117). In this scenario, ecological release, by filling the niche space, impedes faunal buildup. However, evidence also shows that broad ecological release may serve as a precursor to adaptive radiation, at least in some situations (Simpson 1953, Schluter 2000). Diamond (1970) showed that, under species-poor conditions, much of an island can become occupied by taxa

Colonization/speciation between islands without change in ecomorph



Speciation within island with change in ecomorph

Figure 13.1. Schematic representation of the two mechanisms by which species on the Hawaiian archipelago can occupy a niche on a new island as it arises. Left. Species colonize down the chain of islands (represented by shades of gray), in the direction of open ecological space, and occupy the niche (represented by different patterns) to which they were already adapted on the older island. Right. Species colonize open ecological space on an island by speciation and an adaptive shift from one niche that allows occupation of the “new” niche.

that are relatively maladapted, at least initially, setting the stage for selection on subsequent generations of phenotypes that may lead to evolutionary specialization. During the course of adaptive radiation, at least in archipelago situations, both colonization and evolution are clearly involved in adding new species to a community (figure 13.1). Therefore, expanding on the arguments of Roughgarden (1972), in situations where colonization is extremely rare, the “race” may be between repeated colonization of different preadapted species as opposed to evolution within a single colonist lineage that expands its ecological range and subsequently specializes on a suite of different resources.

Some radiations show repeated episodes of phenotype expansion (with or without speciation), while others show a single episode of phenotype expansion at the base of the radiation, with further speciation accompanied by little ecological change. Clear examples of the latter situation have been documented in insects (plant hoppers in the genus *Nesosydne*, Delphacidae) in which extensive ecological shifts have occurred early in the radiation, with relatively minor changes subsequently (Roderick

1997). A number of flowering plant radiations show a similar pattern of early radiation into distinct ecological settings, followed by allopatric divergence in similar habitats on different islands (e.g., *Schiedea*; Sakai et al. 2006). Other flowering plant lineages undergo less frequent inter-island dispersal, with independent ecological radiation into diverse habitats on each island (e.g., the Hawaiian silversword alliance; Baldwin and Robichaux 1995) (figure 13.2). Both patterns have been commonly resolved within the same major radiation in each of several endemic Canarian angiosperm clades (e.g., woody *Sonchus* [Kim et al. 1996]; *Pericallis* [Panero et al. 1999]; *Sideritis* [Barber et al. 2000]; *Crambe* [Francisco-Ortega et al. 2002]; *Aeonium* and relatives [Mort et al. 2002]; *Lotus*, [Ilan et al. 2004]; *Bystropogon* [Trusty et al. 2005]). Note that the Canaries, although relatively close to a continent compared to Hawaii, are effectively remote for many taxa because the nearby (desertic) regions of Africa are climatically distinct from most of the islands. Other Canarian plant lineages display principally one pattern, of primarily allopatric divergence across similar habitats on different islands (e.g., *Argyranthemum* [Francisco-Ortega et al. 1996]) or of adaptive radiation across different habitats on the same island (e.g., *Micromeria* [Meimberg et al. 2006]), as in the Hawaiian silversword alliance (Baldwin and Robichaux 1995).

Insular adaptive radiation involves filling ecological space with limited underlying genetic diversity. A lineage is therefore constrained by the variation available for selection to act on in adaptation to a given environment. Accordingly, some niches likely remain unfilled. Also, although a given niche (e.g., “under bark,” “under leaf”) in different sites (e.g., different islands) may be filled by different taxa within a lineage, and not necessarily by closest relatives, those different species may use the niche in an almost identical manner (see below).

#### Species Addition on Remote Islands

The most pronounced difference between very isolated islands and those closer to a source is the relative contribution of evolutionary processes compared to immigration of colonists in adding species. Heaney (2000) argued that, because the interaction between speciation and colonization is complex on remote islands (the rate of the former being dictated by a fine balance with the magnitude of the latter), speciation cannot be considered simply as additive to colonization. However, the primary difference with more remote islands is that different niches within the environment will tend to remain relatively “open” for long periods, and consequently

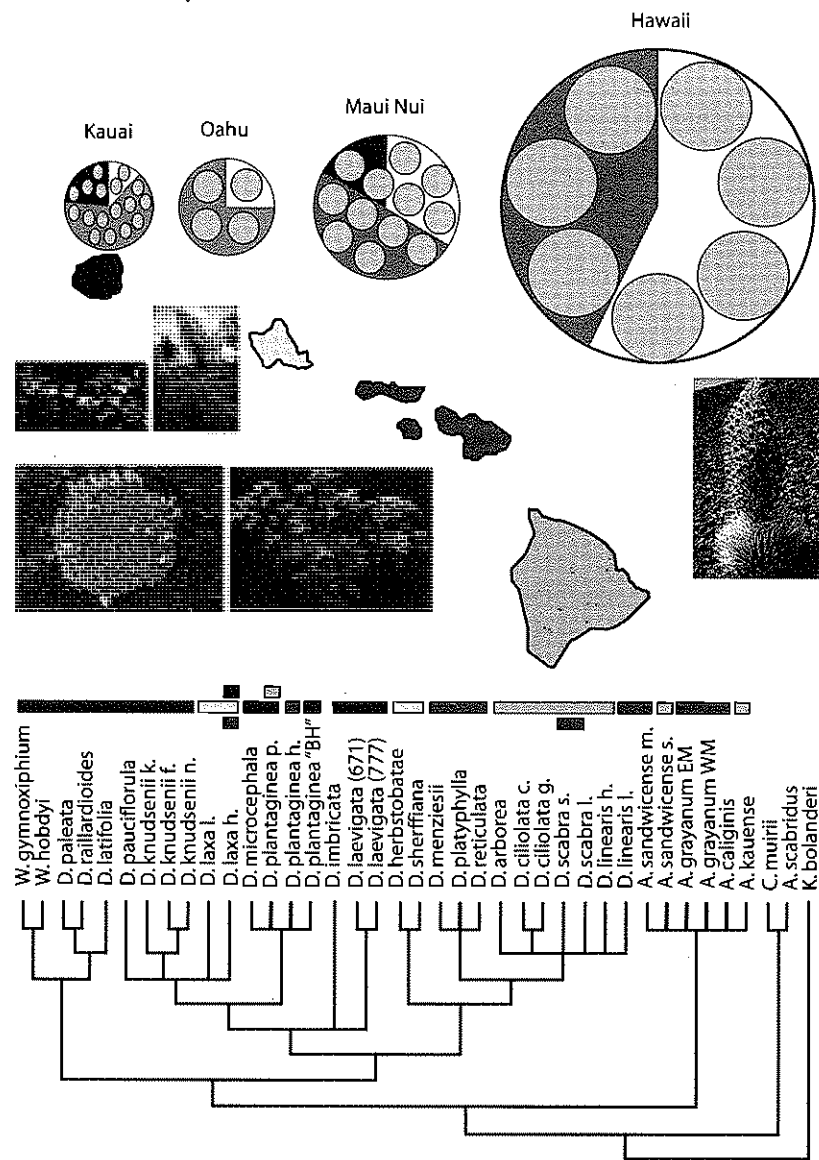


Figure 13.2. Habitat diversity in the Hawaiian silversword alliance (*Argyroxiphium*, *Dubautia*, and *Wilkesia*) across islands. As illustrated, species diversity (per unit area) is greatest on the oldest high island, Kauai, and least on the youngest island, Hawaii. The proportion of species found in mesic to wet habitats (including bogs) is greatest on Kauai (where such habitat is relatively extensive—and highly dissected) and least on Hawaii (where low and high elevation dry

may be filled by evolution as readily as (or more readily than) by dispersal, depending on the relative rates of these two processes.

Losos and Schluter (2000) showed that, for lizards in the Caribbean, speciation can serve as a surrogate for colonization in terms of contributing species to a system. Moreover, lizards on these islands are known to exhibit discrete ecological affinities, represented by “ecomorphs” or taxa whose appearance is determined by ecology (Williams 1972). Similar, and highly deterministic, sets of ecomorphs have evolved, almost always independently, on each island. That such evolution of similar forms can occur may be explained again by the relative roles of colonization and speciation in the context of ecological range shifts (Roughgarden 1972).

The relative rates of colonization versus adaptive differentiation will vary across and within lineages. In damselflies, for example, the rate of migration between islands, though uncommon, is likely sufficient to preclude niche shifts in the earliest colonizers (Jordan et al. 2005). In the case of host-associated insects on remote islands (Gagne 1997, Roderick 1997, Farrell and Sequeira 2004), the very few initial colonists may undergo major host shifts at the outset of the radiation, though once these shifts have occurred, subsequent differentiation within the archipelago is limited almost entirely to shifts between closely related hosts.

In assessing the parallels between colonization and speciation in forming communities, we must consider the sequence of events following colonization of remote islands. The Hawaiian Islands are particularly

habitats are more extensive relative to mesic and wet habitats than on the older islands). Size of pies is proportional to area of island(s). Portions of the pie indicate the habitats in which the plants occur: dry, i.e., dry forest, scrub, or barrens (no shading); bogs (heavy shading); and other wet habitats, i.e., mesic to wet forest or scrub (light shading). Circles within the pies represent species that occur in each habitat/island, with bars on the cladogram color-coded according to island: black, Kauai; white, Oahu; dark gray, Maui Nui; and light gray, Hawaii. [Note: Some species that occur predominantly in mesic to wet forest or scrub on Oahu and Hawaii also are known from bogs or bog edges there (not shown); *Anisocarpus scabridus*, *Carlquistia muirii*, and *Kyhosia bolanderi* are continental tarweeds.] Data are from Baldwin and Robichaux (1995) and B. G. Baldwin (unpubl.). Photos: *D. latifolia* (liana), by B. G. Baldwin (left, top); *W. gymnoxiphium* (semelparous rosette plant), by G. D. Carr (second from left, top); *D. waialealae* (cushion plant), by K. Wood (left, bottom); *D. scabra* subsp. *scabra* (mat plant), by B. G. Baldwin (second from left, bottom); *A. sandwicense* subsp. *macrocephalum* (semelparous rosette plant), by D. W. Kyhos (far right).

useful for studying this process, as the chronology of the islands allows examination of communities as they have developed on an evolutionary time scale. Among spiders in the genus *Tetragnatha*, taxa in the spiny-leg (cursorial, no webs) clade exhibit discrete ecomorphs, defined on the basis of their color and habitat use: green (associated with leaves), maroon (moss), large brown (tree trunks), and small brown (twigs) (Gillespie 2004). Among these spiders, the island chronology (comparing oldest through youngest islands) has been used to illustrate the stages of adaptive radiation: Communities on the youngest island are comprised largely of populations that descended from spiders on the older island(s). Each of the older islands contains similar numbers and ecological sets (one representative of each ecomorph) of species. However, the second youngest island (East Maui) contains a larger number of species, including multiple members of the same ecomorph, some of which appear to have arisen by colonization from an older island, others by *in situ* speciation. Thus it appears that, at least initially, subsequent to successful occupation of any given land mass, there may be no absolute limit to the number of species that can form (figure 13.3). This outcome is comparable to what has been observed in the development of arthropod communities through immigration on mangrove islets off Florida, where substantial overshoot in species numbers was found prior to equilibrium (Simberloff 1976), and was interpreted as a consequence of the small population sizes of species in the early stages of community development. The *Tetragnatha* finding also lends support to the idea that—at least in the context of community assembly—speciation can serve as a surrogate for immigration on isolated islands.

### Community Assembly

#### *Species Accumulation—Pattern and Process*

A number of studies have examined the relationship between island area and/or age and species diversity for plants and animals (Peck et al. 1999, Emerson and Kolm 2005) with mixed conclusions in terms of underlying processes, although some general patterns are emerging (Whittaker et al. 2008, and this volume). Lineages that have diversified throughout the history of the modern high islands of the Hawaiian chain generally show a pattern of older-to-younger island dispersal (see Funk and Wagner 1995) and offer an excellent opportunity to examine the effects of both island age and island area on species accumulation. Here, we examined how species diversity changes with island area and time for different Hawaiian groups of animals and plants (figure 13.4). To detect the signa-

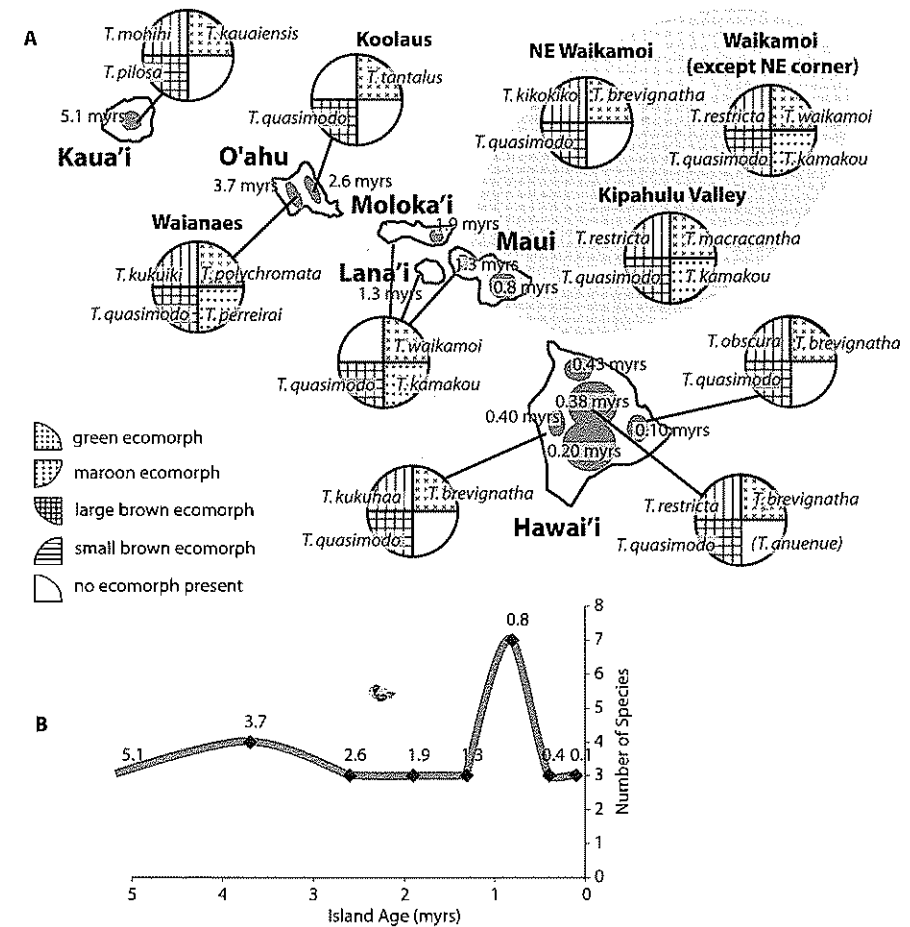


Figure 13.3. Map of the Hawaiian Islands showing how ecomorph diversity of spiny leg *Tetragnatha* changes with island age. A. Ecomorphs in different habitats (Gillespie 2004) on a given volcano (note: Kauai is made up of a single volcano; Oahu, two; Molokai and Lanai, one each; Maui, two; and Hawaii, five). Volcanoes are represented by gray circles, with age indicated in millions of years (myrs). Each section of a pie represents a different ecomorph (green, maroon, large brown, and small brown) whenever a morph is present at a site. Never are two species that share the same ecomorph found in the same locality. B. Number of species on each island against island age (simple scatterplot connected by smoothed line), showing the surprisingly large number of species on East Maui.



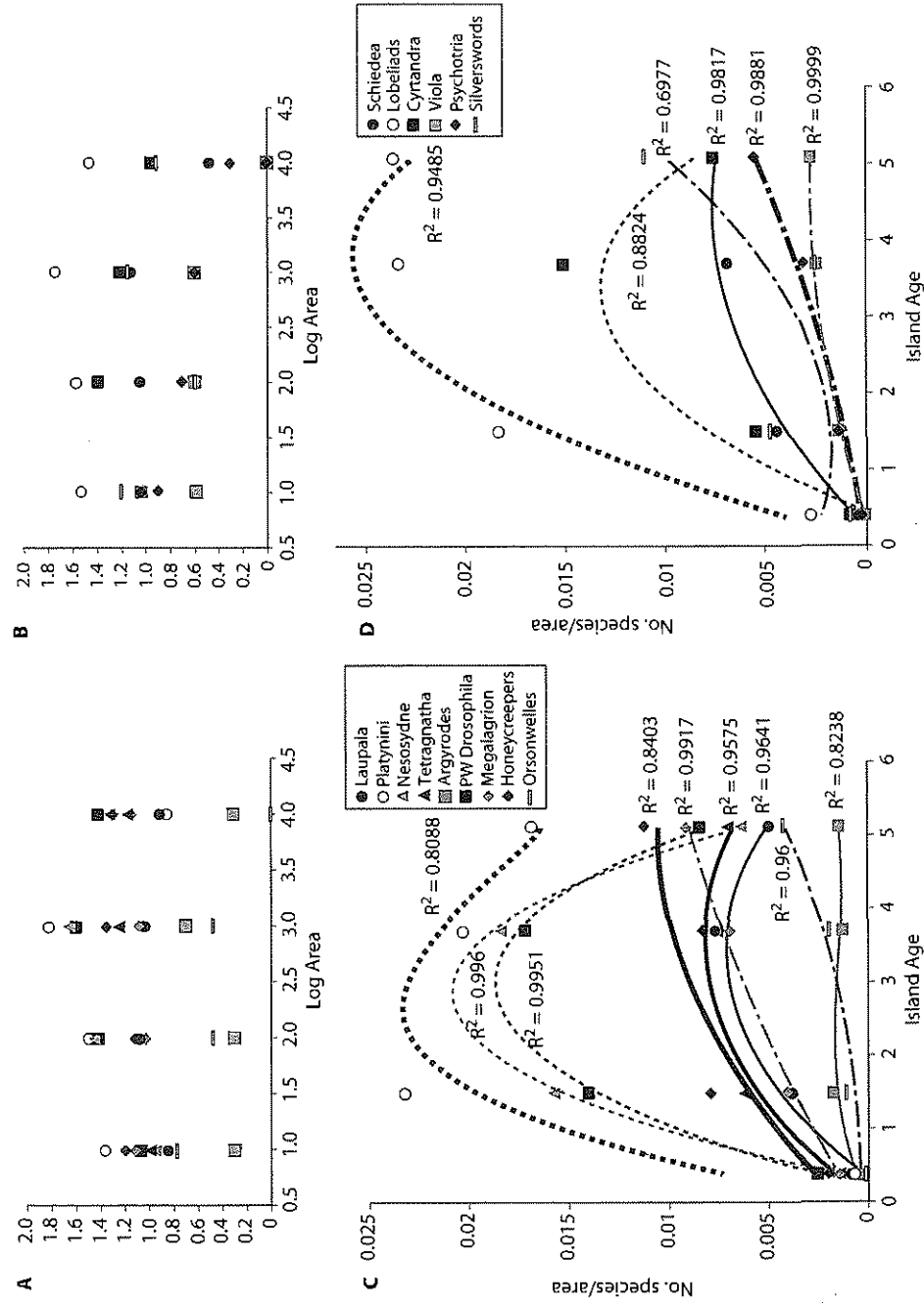


Figure 13.4. Relationships of species numbers in the Hawaiian Islands with area of an island and time, as inferred from island age (for island ages, see Figure 13.3). The analysis is limited to groups that are estimated, based mainly on molecular data, to have been in the Hawaiian Islands at least since Kauai was the youngest island in the chain; this allows us to use the chronology of the islands to help infer process. A. Species-area relationships for different groups of arthropods. Data are for honeycreepers (Olson and James 1991, James and Olson 1991), *Megalagrion* damselflies (Jordan et al. 2003), picture-wing (PW) *Drosophila* flies (Carrson 1983), *Nesosydne* planthoppers (Nishida 2002), *Laupala* crickets (Shaw 2000, Nishida 2002), and Platynine beetles (Liebherr and Zimmerman 2000), and for *Tetragnatha* (Gillespie 2004), *Orsonwelles* (Hormiga et al. 2003), and *Argyrodés* (Gillespie and Rivera 2007) spiders. There is no general picture of a relationship between species numbers and area. B. Species-area relationships for different groups of plants. Data are for lobeliads, *Viola*, *Cyrtandra*, the silversword alliance, *Psychotria*, and *Schiedeia* (Lammers 1999, 2004, 2005, 2007; Baldwin and Robichaux 1995; Givnish et al. 1995, 2008; Wagner et al. 1999a, b, 2001, 2005; Wagner and Lorence 2000; Ballard and Sytsma 2000; Nepokroeff et al. 2003; Baldwin and Carr 2005; Cronk et al. 2005; Lorence and Perlman 2007; Havran et al. 2008; Baldwin, unpubl.). Here again, there is no general picture of a relationship between species numbers and area. C. Detailed examination of the relationship between numbers of species per unit area and time (island age) for the same groups of arthropods. Quadratic functions fitted to each data set independently, with  $r^2$  values shown for each. All groups have the fewest number of species per unit area on Hawaii, the youngest island. The most species-rich lineages show a very high peak of diversity on islands of intermediate age (dashed lines); in most other lineages, numbers appear to level off towards the older islands (solid line), while in two (*Orsonwelles* spiders, *Megalagrion* damselflies), diversity increases constantly to the oldest island (dash-dot line). D. The same analysis for plants. Again, all groups have the fewest species on Hawaii, and the most diverse lineages have a high peak in diversity on Oahu (dashed lines). In one lineage (*Schiedeia*), numbers level off towards the older islands (solid line), while diversity in the remaining lineages increases to the oldest island without evidence of any equilibrium having been achieved.

ture of time, we included only those groups that are estimated to have been in the Hawaiian Islands for at least as long as the current main islands have been in existence (otherwise the effects of island age will be confounded by recency of colonization). As can be seen (figures 13.4A and 13.4B), the relationship between species number and island area is not clear. However, when the number of species per unit area is examined over time (figures 13.4C and 13.4D), a pattern emerges. Considering only the current high islands (not the series of atolls and other islets—the remnants of previous high islands, which lie to the northwest of the main chain), in the animal groups examined (figure 13.4C), species diversification appears to occur at different rates, with the most species-rich groups examined being platynine beetles, picture-wing *Drosophila* flies, and plant hoppers. In each of these species-rich lineages, diversity per unit area is very high on islands of intermediate age, and drops off on the oldest islands. Most of the somewhat less species-rich lineages (honeycreepers, *Tetragnatha* spiders, *Argyrodes* spiders, *Laupala* crickets) show a more gradual increase to their highest diversity per unit area on islands of intermediate age, diversity appearing to level off toward the older islands. However, two lineages, *Megalagrion* damselflies and *Orsonwelles* spiders, show a steady increase in numbers per unit area from the youngest to the oldest islands, suggesting that equilibrium has not been reached in these groups.

The signature across different plant groups is remarkably similar. The two most species-rich Hawaiian plant lineages, *Cyrtandra* and the lobeliads, reach their highest diversity per unit area on one of the oldest islands (Oahu, Kauai) and may represent examples of ecological saturation (perhaps somewhat delayed relative to animal lineages) and subsequent diversity loss on the oldest island, at least in the case of *Cyrtandra* (figure 4D). In less species-rich groups (e.g., the silversword alliance, *Psychotria*, *Schiedea*, *Viola*), the highest number of species per unit area is often found on the older islands, although here diversity appears to level off in some groups (*Schiedea*, *Viola*) while the other lineages show a steady increase in diversity toward the older islands. Again, it appears that equilibrium has not been reached in these plant lineages, even on the oldest islands.

Although it would be premature to infer causal relationships as to the ecological mechanisms underlying these patterns, it is worth noting the analogy with the study of mangrove islands by Simberloff and Wilson (1969a,b), who found that on all islands but the most distant (where immigration was very low), species number rose above the predefaunation number, then fell and oscillated about that number. Correspondingly, the Hawaiian data often show an overshoot, though the effect is more pronounced in some of the large (high speciation rate) lineages. Simberloff and Wilson explained this effect as being due to the small population

sizes in the early stages of colonization allowing more species to coexist. Whether analogous processes (small population sizes or small ranges allowing more species to occur within a given island) may explain the effect in the Hawaiian lineages requires further study. It is also worth pointing out that, among the Hawaiian lineages that seem not to have reached equilibrium even on the oldest island, interactions between conspecifics, and for angiosperms between plants and pollinators, may be less important generally than in at least some of the radiations that appear to have approached or reached peak diversity during the history of the modern high islands of the Hawaiian chain (Baldwin and Robichaux 1995, Hormiga et al. 2003, Jordan et al. 2003). The implications of these findings to the attainment of species equilibrium are discussed in the next section.

### Equilibrium

The ETIB, in its basic form, predicts that more isolated islands will have fewer species because the immigration curve will be lower. According to MacArthur and Wilson: "The island will equilibrate at fewer species . . . [w]here the degree of isolation from the source regions that supply the species is increased, reducing immigration." (1967, pp. 22–23; reviewed in Schoener, this volume, Lomolino et al. 2005). However, no effect of isolation on the slope of the species-area relationship was found in a global analysis of birds (Kalmar and Currie 2007). Power (1972), who constructed a path diagram to model the regulation of numbers of plant and bird species on the Californian Channel Islands, also found that isolation had little effect on island plant species diversity, although Moran (1996) found that the Guadalupe Island flora has much lower species diversity by area (and much higher single-island endemism) than floras of the other, far less remote California islands.

The issue of whether remote islands support fewer species seems to hinge in part on when (and whether) equilibrium is achieved. One explanation for the reduced number of species often found on remote islands is that these islands are less likely to be at species equilibrium because of their very slow rate of acquisition of diversity through immigration + speciation compared to rates of immigration to islands near major source areas (Schoener, this volume). This nonequilibrium explanation, also noted by MacArthur and Wilson (1967, pp. 22–23), suggests that, given enough time, remote islands may be expected to attain a level of diversity comparable to otherwise similar near-source islands, although rates of island erosion and subsidence with accompanying loss of island area may be sufficiently high to prevent diversity from ever reaching such a high level. At the same time, the effect of isolation in reducing immigration might be diminished in an archipelago, where

colonization between islands (coupled with speciation) would be expected to elevate species numbers, reducing (or even negating) the effect of isolation predicted in the basic formulation of the ETIB (MacArthur and Wilson 1967).

Recent findings on the number of invasive species are relevant to this discussion: Using estimated values of prehuman diversity (Burney et al. 2001, James 2004, James and Olson 2005, Paxinos and al. 2002), Sax et al. (2002) have shown that the number of bird species currently found on remote oceanic islands (native plus introduced) is no higher than the number that was there prior to human occupation. At the same time, the number of species of plants (native plus introduced) is almost double the number prior to human occupation. This finding suggests that communities may be saturated for birds, but not for plants, assuming in part that lag in time-to-extinction is no greater for plants than for birds (Sax et al. 2007). Indeed, when put in the context of the discussion above, the result is consistent with the idea that birds (and various other animal groups) may have reached equilibrium prior to arrival of Polynesians, but many plant groups had not.

#### *Random versus Deterministic Changes*

The ETIB is neutral in that it assumes that all species are equal in their probabilities of immigrating onto an island or of going extinct once there, and predicts only a diversity equilibrium, not a taxonomic equilibrium (i.e., no effect of species identity; see Hubbell, this volume). At the same time, studies have shown a degree of predictability in species composition on islands, implying a role for niche assembly in conjunction with some level of stochasticity (Roughgarden and Diamond 1986). Overall, ecological studies indicate that community formation is somewhat deterministic, even though there is a strong stochastic element to colonization. Wilson (1969) and Simberloff and Wilson (1970) termed the initial, relatively stable number of species, the "noninteractive equilibrium," and suggested that as immigrant taxa become increasingly "co-adapted," a nonrandom "interactive equilibrium" is established.

The situation on remote islands where evolutionary processes dominate in the assembly of diversity shows some intriguing parallels to those islands on which ecological processes dominate. For the Hawaiian *Tetragnatha* spiders mentioned above (Gillespie 2004), one could view the initial stages of community assembly as a "race" between *in situ* adaptive radiation producing closely related species occupying different ecomorph niches versus between-island colonization in which species pre-adapted to each of the niches arrive from elsewhere and subsequently

speciate in allopatry without change in ecomorph. The phylogenetic results support a neutral model inasmuch as niche filling appears to be largely stochastic, likely dictated by the chance arrival of propagules: Whichever spider arrives first is the one that fills that niche space; but the identity of the first taxon to arrive is unpredictable, so the niche may be filled by an ancestor from another island moving into the same niche on the new island, or by adaptation and speciation from an ancestor (either on the same or a different island) occupying another niche. Moreover, it appears that a given area can initially support a large number of species while any one is rare: Before the numbers of any one species have increased beyond a critical threshold, competition is likely minimal, with little impediment to the addition of more species. However, competition likely does play a role, as species of the same ecomorph have never been found to co-occur; rather, they are separated by tight geographic (parapatric) boundaries. This particular situation may be the result of the circumstances through which a niche is filled that may be peculiar to remote islands: Because all species in the radiation are very closely related, any species of the same ecomorph is, from a niche perspective (as mentioned above), ecologically identical. An analogous situation in less remote locales is likely to allow for more distributional overlap, between less closely related and less ecologically similar species.

On the older Hawaiian Islands, almost every community is represented by a single species of each ecomorph of *Tetragnatha* spiders, suggesting that deterministic processes play a part in the equilibrium species composition. These findings implicate competitive exclusion of similar ecomorphs in the "final" species composition. In other words, the community may undergo "fine-tuning" following initial species proliferation as a result of inter- and intraspecific competition for resources (Arthur 1987). This ecological/evolutionary "jostling" may result in a predictable community structure, with single representatives filling a given niche in any one community. A similar scenario has been proposed to explain diversification in a radiation of weevils in an isolated subantarctic archipelago (Chown 1990). Indeed, such a scenario may provide a mechanistic basis for the species accumulation curves (figures 13.4C and 13.4D), and why such curves might differ between taxonomic groups.

Why do some taxa show predictable and deterministic patterns of differentiation, while no such effect has been found in other groups? As described above, some lineages tend to undergo repeated ecological release upon colonization of islands, which may be conducive to repeated evolution of specialists for a given set of resources, as found in Caribbean lizards (Losos et al. 1998) and Hawaiian spiders (Gillespie 2004). But this begs the question, why do some taxa tend to expand their ecological

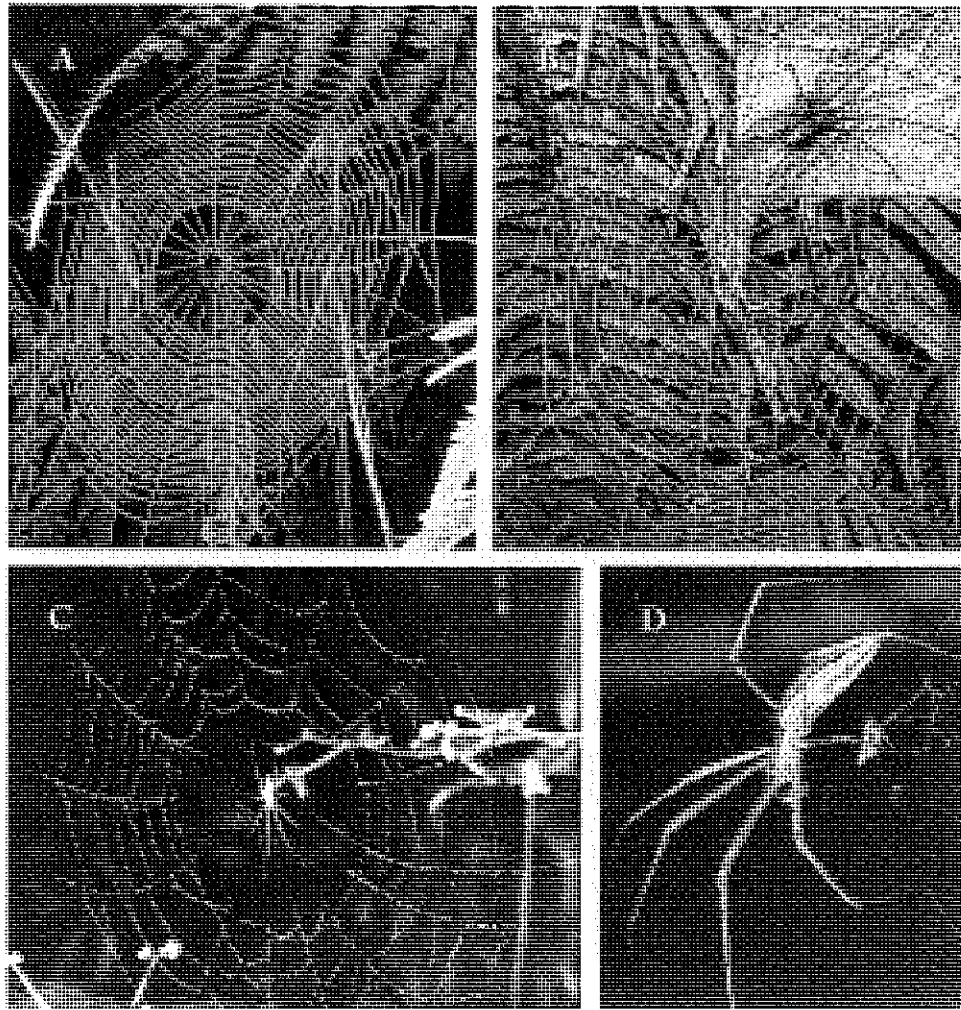


Figure 13.5. Ecological plasticity in web structures of the spider *Tetragnatha stelarobusta*. A. Typical web spun by *T. stelarobusta* (D) in sites where it co-occurs with *T. eurychasma* (web shown in B, spider inset). At these sites, the web of *T. stelarobusta* (A) has tightly spun spirals while that of *T. eurychasma* (B) has large spaces between the spirals (Blackledge and Gillespie 2004). C. Typical web spun by *T. stelarobusta* at another site where *T. eurychasma* does not occur. This observation suggests that *T. stelarobusta* may change the form of its web according to the presence of congeners in a community. Photos A, B, and D by T. A. Blackledge; C by R. G. Gillespie.

amplitude while others do not? Part of the explanation for the apparent inability to utilize newly available resources may lie in the degree of initial pre-adaptation to the new resource and differences in ecological, behavioral, and/or genetic plasticity: The pattern of ancestral plasticity can determine which behavioral/ecological phenotypes are expressed in a given environment, and, therefore, which phenotypes have the potential to evolve in response to selection (West-Eberhard 2003). Indeed, such plasticity is evident in Hawaiian spiny-leg *Tetragnatha* spiders; when a given ecomorph is “missing” from a community, one species may display polymorphism (likely developmental in this case) such as to effectively fill the niche of the ecomorph that is absent (R. Carter, unpublished). Similar ecological plasticity is found in web-building representatives from the same radiation (figure 13.5). Current research is focused on quantifying the nature of the polymorphic species, and their relationship to those that are specialized for a given ecomorph.

### Conclusions

We have discussed the application of ideas of the ETIB to remote archipelagoes, which have often been considered enigmatic in the context of community assembly (Webb et al. 2002). We focused in particular on the Hawaiian Islands, where the data indicate some striking parallels in the pattern of species accumulation between near-source and remote islands, with (1) often a strongly stochastic element involved in the phylogenetic identity of a taxon colonizing available niche space, and (2) some groups showing an increase in species number beyond an apparent equilibrium, prior to falling to a sometimes predictable set of “coadapted” species (Wilson 1969, Simberloff and Wilson 1970). Overall, it appears that colonization of an island may be dictated by propagule pressure and ecological opportunity: Niches are filled by the interplay between colonization of species from the same niche in another region (e.g., on another island) or by adaptive shifts from another niche on the same island. However, at least in the Hawaiian Islands, the subsequent development of the community may be dictated by an interaction between (1) the rate of speciation; and (2) the degree of ecological/behavioral plasticity.

For the Hawaiian taxa examined here (both plants and animals), some clear correlates with different patterns of diversity are evident: (1) Large overall species diversity correlates with a high peak in diversity on islands of intermediate age prior to reduced diversity on the oldest island, (2) most lineages with lower overall species diversity show a steady increase towards an apparent equilibrium on the older islands, and (3) lineages in which sister-species are largely allopatric (or microallopatric)

often show a steady increase in species numbers to the oldest island with no indication of having reached a diversity equilibrium.

These observations indicate that research on remote islands must continue to recognize the evolutionary and ecological differences among lineages (e.g., Givnish et al. 2008), rather than searching for general patterns across taxa, and must incorporate hypothesized mechanisms underlying these differences in order to derive more concrete inferences on processes dictating community assembly.

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