

# Phylogenetic analysis of community assembly and structure over space and time

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Evolutionary ecologists are increasingly combining phylogenetic data with distributional and ecological data to assess how and why communities of species differ from random expectations for evolutionary and ecological relatedness. Of particular interest have been the roles of environmental filtering and competitive interactions, or alternatively neutral effects, in dictating community composition. Our goal is to place current research within a dynamic framework, specifically using recent phylogenetic studies from insular environments to provide an explicit spatial and temporal context. We compare communities over a range of evolutionary, ecological and geographic scales that differ in the extent to which speciation and adaptation contribute to community assembly and structure. This perspective allows insights into the processes that can generate community structure, as well as the evolutionary dynamics of community assembly.

## Bringing phylogeny into community ecology

Recent years have seen a growing interest in incorporating phylogenetic data into studies of community assembly and structure, ranging from the scale of individual guilds [1,2] to whole biomes [3]. The basic premise is that phylogenetic data provide a historical framework to quantify evolutionary and ecological patterns and infer evolutionary and ecological processes. There have now been multiple studies examining the tendency of species to either maintain or shift their niches, and the importance of such tendencies in dictating the phylogenetic composition of communities (e.g. Refs [4–10]). Despite the excitement and potential of this growing field, its importance in linking community ecology and evolutionary biology has yet to be fully realized. Speciation is of only extrinsic historical importance in most studies of community structure – it generates the regional pool of species from which a community is formed. But speciation can assume intrinsic importance within the community, and is indeed expected to do so across meaningful temporal and spatial scales [3,11]. Here we aim to place phylogenetic analysis of community assembly within a temporal scale, with the broader goal of understanding the relative importance of, and interplay between, environmental filtering, species interactions, immigration and speciation in community assembly. We focus on insular environments (islands, lakes, some mountaintops, fragmen-

ted landscapes, etc.), because their discrete nature makes them very accessible to such analyses. In addition, they can often provide a temporal reference, because islands and lakes generally have a well-defined geological (and hence chronological) record. We compare these results to other geographic settings, in each case examining the role of space and time in dictating community assembly and structure.

## Glossary

**Allopatry:** geographical separation between populations.

**Anagenesis:** evolutionary change in a single lineage through time.

**Character displacement:** divergence of a trait or traits in a region of range overlap between two otherwise similar species that can be the result of competition for resources or reinforcement.

**Cladogenesis:** the formation of independently evolving lineages from a single ancestral lineage through speciation.

**Community:** a group of populations that coexist in space and time and interact with one another directly or indirectly.

**Competitive interaction:** occurs when organisms of the same, or in this case different, species either utilize a common resource that is of limited supply (exploitation), or harm each other in the process of gaining a resource that is not limited (interference).

**Environmental filter:** the set of abiotic and biotic factors (excluding competitors) that an organism must tolerate in order to complete its life cycle. Also sometimes referred to as habitat filter.

**Facilitation:** species interactions that benefit at least one of the participants without causing harm to the other.

**Guild:** a set of organisms that use biotic or abiotic resources in a similar way.

**Habitat:** the locality or environment where a species lives.

**Metapopulation:** a group of spatially separated populations of the same species which interact at some level.

**Niche:** the requirements of a species to maintain positive population growth rates.

**$\alpha$  Niche:** the region of the realized niche of a species corresponding to species diversity at the local scale where interactions with other species can occur [63,64].

**$\beta$  Niche:** the region of the realized niche of a species corresponding to the different habitats where it is found [64,65].

**$\gamma$  Niche:** the geographical range of a species [44].

**Nurse plant:** a species that facilitates seed germination and seedling survival of another species by alleviating stressful environmental conditions.

**Phylogenetic clustering:** species co-occurring on a local scale are phylogenetically more closely related to each other than one would expect from a random sampling of species from the larger regional pool.

**Phylogenetic overdispersion:** species co-occurring on a local scale are phylogenetically more distantly related to each other than one would expect from a random sampling of species from the larger regional pool.

**Realized niche:** the region of its niche that a species is able to occupy in the presence of interspecific competition and natural enemies [66].

**Reinforcement:** evolution of trait divergence in areas of sympatry between two species resulting in increased probability for an individual mating with members of the same taxonomic group.

**Species assortment:** the process by which only species that are sufficiently dissimilar from one another are able to enter a community.

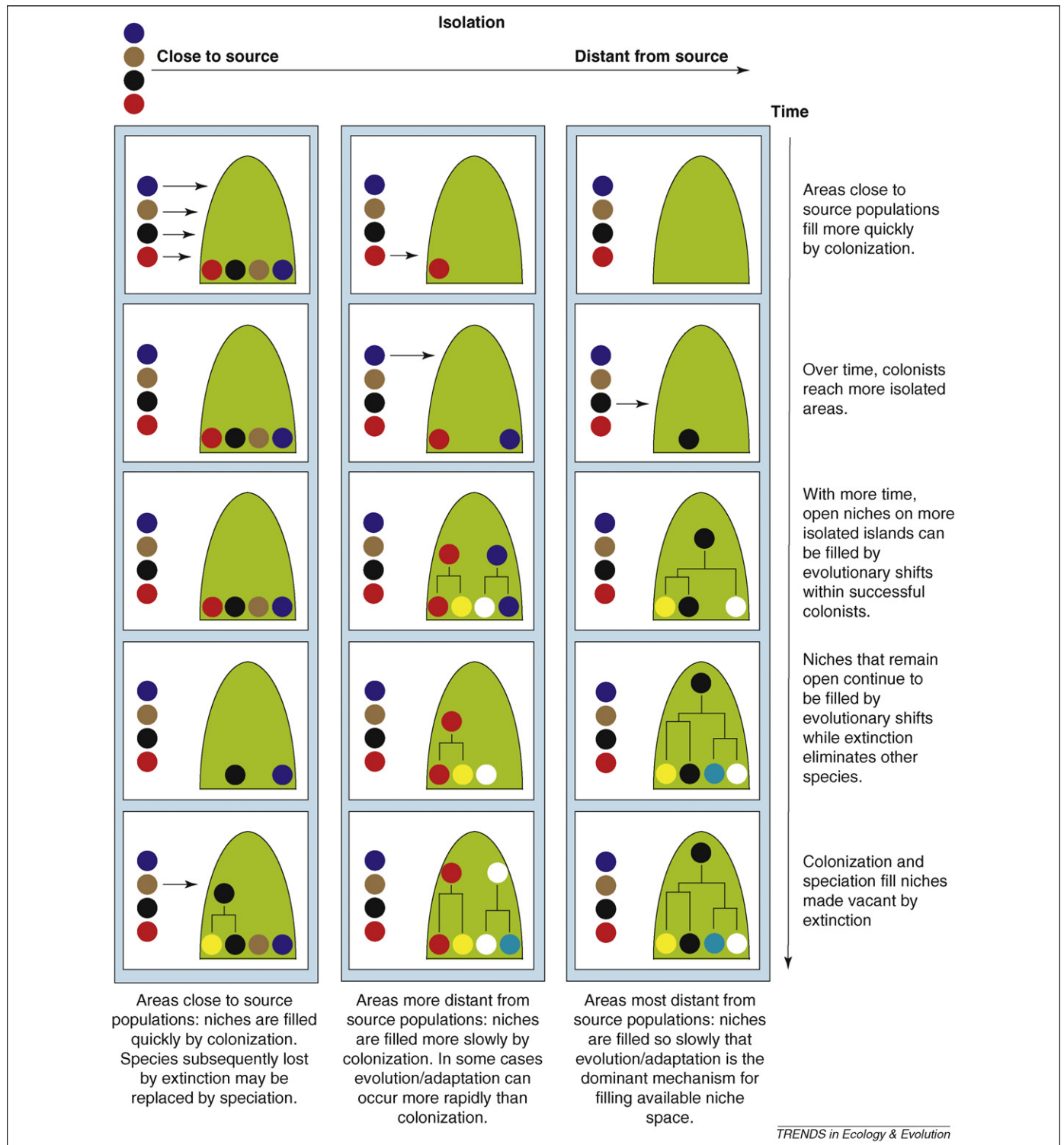
**Trait lability:** the probability of evolutionary change in a trait. Traits associated with niche that have high lability confer a high probability of adaptive change into a new niche. Traits associated with niche that have low lability confer a low probability of adaptive change into a new niche.

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### When are immigration and speciation important for community assembly?

The phylogenetic structure of a community is strongly dependent on the number and identity of available colonists (Figure 1). An unpopulated area in close proximity to a source of colonists will be colonized rapidly from that

source. Under this scenario where immigration is important, assembly patterns are largely stochastic and dictated by propagule pressure, although turnover eventually leads to a more deterministic set of members within a given community [12]. All else being equal, it is easier for a niche to be filled by colonization of ecologically preadapted organ-



**Figure 1.** Immigration, speciation and community assembly. Species can populate niches within an area by either colonization of preadapted species from outside the area, or evolutionary shifts within species already inhabiting the area. The relative importance of immigration and speciation is a function of both the isolation of the area from a source of colonizing species and of time. Three areas are shown with differing degrees of isolation from a source of colonizing species. For each of these a snapshot of species composition is given for five time points, showing the number of species in the area and the origin of each species. Species are represented by circles, with color indicating either origin from the source area (arrows show colonization) or origin by evolutionary shifts within the newly colonized area (phylogenetic trees show speciation). Time is represented as an evolutionary, rather than an absolute scale, as it will depend on the organisms in question and their rates of diversification.

isms than through adaptation of local forms. To this end, when a new habitat appears, organisms already adapted to that habitat can colonize the niche space more readily than taxa that are adjacent to, but not adapted to exploit, the new habitat. For example, many organisms that have diversified in the Andes of South America originated from climatically similar areas in North America [13]. In the same way, if environments remain largely unchanged, then organisms can persist for extended periods with little ecological change. Accordingly, lineages across mountaintops within Africa and Australia are characterized by remarkable niche conservatism despite large genetic distances [14,15].

Area and associated variables are well known to play a key role in dictating the number, and also identity, of colonists. Less well recognized in dictating patterns of species diversity is time, both in duration and temporal sequence [16,17]. Moreover, an increasing number of studies are showing that many, and perhaps most, communities are not at equilibrium [18,19]. This has implications, not only for understanding colonization and assembly dynamics but also for the related concept of species invasibility, as species have been found generally to invade communities without extinction or exclusion of native species, at least over ecological timescales [20].

Island biogeographic theory [21,22] predicts that, with a numerically large immigrant pool (due to geographic proximity to a source), immigration rates to unpopulated areas will be high, and one can expect immigration to dominate over speciation as the process that adds species locally. In more remote locales, immigration can be so low that speciation can play a role, the rate and extent of which also depends on the area of the isolated locale [23], topographic complexity and altitude [24,25] and temporal duration [23]. However, community composition at any point in time is the result of past immigration, speciation and extinction, together with associated interactions that vary according to the sequence of assembly [16] and/or disturbance [26]. Initial establishment in any community requires immigration, with the role of speciation potentially increasing over time. In a meta-analysis of arthropod phylogenetic data from the central and western Canary Islands [27], it was found that geologically younger islands show little evidence for cladogenetic evolution within islands. Endemic species on geologically younger islands were typically found to be the product of anagenetic evolution following colonization from neighboring islands. Thus immigration, not *in situ* cladogenetic speciation, is the key process in the initial stages of community assembly on the younger islands. On older islands, communities of endemic species are frequently found to be the product of cladogenetic speciation within islands. Island size also plays a role, and below a certain threshold size, there is little or no cladogenesis [28]. Moreover, taxa differ in rates of speciation and, for groups that form species very rapidly (e.g. some insects where sexual selection appears to drive speciation), *in situ* speciation can dominate even on the youngest islands (e.g. drosophilid flies and crickets in the Hawaiian Islands [29,30] and cichlid fish in the African rift lakes [31]).

The shift in importance from immigration in younger communities to speciation in older communities can be

viewed as a shift toward equilibrium caused by changes in rates of immigration, speciation and extinction. If we make the simplifying assumptions that a given area has a maximum carrying capacity (in terms of species number), and abiotic conditions do not fluctuate significantly (in terms of allowing species existence), this equilibrium can again be considered in terms of island biogeographic theory [32]. As a community reaches carrying capacity, both the filling of still-vacant niche space, and the replacement of species lost through extinction, will increasingly be from within the membership of the community itself. Put another way, the immigration pool changes as a community assembles such that the community itself becomes an important component of this pool.

This discussion shows us that phylogenetic structure of communities is context dependent. The extent to which adaptation occurs within a community is dictated by an interplay between the number of propagules available to establish different niches within a community, the similarity and distance of the community to surrounding communities, the number of taxa already in the community (i.e. whether niches are already filled) and the area and time available for colonization and adaptation. The next question focuses on patterns of co-occurrence in a community, asking whether the history of initial community assembly affects patterns of either phylogenetic overdispersion or phylogenetic clustering.

### How are communities phylogenetically structured?

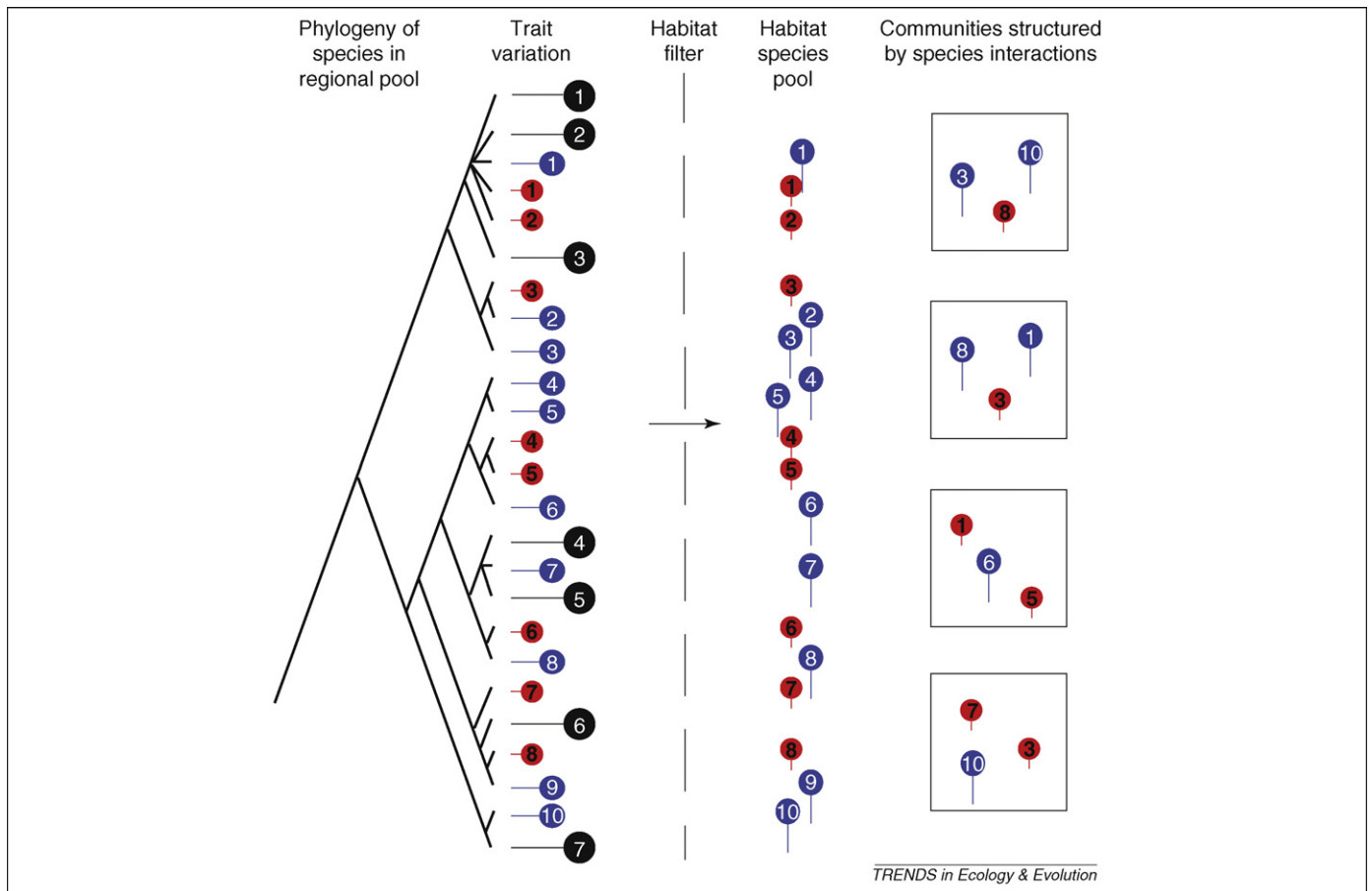
Many studies have now shown that patterns of co-occurrence can deviate from random expectations with regard to phylogenetic relatedness, either as phylogenetic overdispersion or phylogenetic clustering (Table 1). When species enter a community through immigration from a regional pool of species, community assembly can be largely neutral in that species have an equal chance of establishment or, alternatively, can be shaped by ecological processes. Here again, islands – and the temporal framework they provide – are beginning to allow examination of the contrasting neutral [21,33] versus competitive paradigms of community assembly. Under neutral models of community assembly such as MacArthur and Wilson's theory of island biogeography [21,22] as well as Hubbell's unified neutral theory of biodiversity and biogeography [33], species within a trophic level are competitively equivalent and become persistent through the stochastic dynamics of dispersal, within-island speciation and extinction via demographic drift. Colonization and persistence are therefore governed by dispersal ability and the species–area relationship such that times of colonization should fit a Poisson distribution after equilibrium has been reached between extinction and colonization/speciation. By contrast, models of competitive assembly (whether stochastic [34,35] or in accord with certain rules [36]) hold that established populations resist the advent of additional colonists in the context of limited ecological space. Therefore, competitive assembly predicts that the probability of colonization will drop immediately as species colonize and persist [35]. Current research is focused on the development of analytical tools to provide a statistical

**Table 1. Studies of community phylogenetic structure showing the variation in observed pattern and inferred process**

Taxonomic scale	Geographic/ecological scale	Phylogenetic pattern	Phenotypic pattern	Conclusions	Refs
Angiosperms	Borneo: 0.16 ha plots within 150 ha	Clustered	Not assessed	Environmental filtering suggested to be of most importance.	[40]
Angiosperms	Equatorial Guinea: 1 ha plots within 2500 ha	Unstructured within plant lineages; clustered across all Angiosperms	Not assessed	Environmental filtering, particularly by altitude among divergent evolutionary lineages. Neutral mechanisms or lack of phylogenetic resolution to detect phylogenetic overdispersion within specific clades.	[67]
Plants	South America: 0.1 ha plots across South America	Individual plots exhibit clustering, overdispersion and random phylogenetic structure.	Not assessed	Overdispersion by ancestral montane environments filtering for ancestral lineages, clustering by either dispersal limitation or filtering for derived lineages.	[68]
Angiosperms	Panama: plots of various size within 50 ha of forest	Unstructured across the entire plot; clustering and overdispersion within habitats	Not assessed	Strength of phylogenetic pattern influenced by null model. Variation in phylogenetic structure requires more information on species traits.	[41]
Oak trees	Florida: 0.1 ha plots within three state preserves of size 921–2083 ha	Overdispersed	Clustered and overdispersed	Traits important for habitat specialization show evolutionary convergence; traits important for coexistence are evolutionarily conserved.	[8]
Trees	Florida: 0.1 ha plots	Clustered	Clustered	Shift from phylogenetic overdispersion to clustering at broader phylogenetic scale consistent with increasing trait conservatism at broader phylogenetic scale.	[39]
Woody plants	Eastern Iberia: nine sites of size 900–70 000 ha varying in fire frequency	Clustered within high-fire-frequency plots, overdispersed within low-fire-frequency plots	Conservative evolution of seed fire tolerance; phenotypic clustering	Fire is a strong environmental filter selecting for related fire-tolerant species. In the absence of fire, competitive interactions select for less-related species.	[69]
Schoenoid sedges	South Africa: 11 vegetation surveys using 5 × 10 m plots in the Cape Floristic Region	Overdispersion within a lineage, but unstructured at a broader phylogenetic scale	Trait conservatism and phenotypic overdispersion	Interspecific competition suggested to be of importance, but analysis of more niche-associated traits might implicate habitat filtering.	[70]
Angiosperms	Zapotitlán Valley, Mexico: four 1000 m transects in each of three plant communities	Overdispersed	Conserved evolution of regeneration niche	Plant communities where facilitative interactions are important among distantly related species can generate patterns of phylogenetic overdispersion.	[71]
Plants	Plot sizes of several square meters	Communities range from highly clustered to highly dispersed.	Conserved evolution of 16 functional traits	Evolutionary divergence of traits promotes coexistence of closely related species.	[72]
<i>Ceanothus</i>	California: occurrence data for 51 sites	Overdispersed	$\alpha$ Niche evolutionarily conserved; $\beta$ niche evolutionarily labile	Co-occurrence facilitated by $\alpha$ niche differences between species-reducing competitive interaction.	[7]
Wood warblers	North America: >4000 39.4 km transects	Overdispersed	Overdispersion of foraging strategy	Phylogenetic niche (terrestrial versus arboreal foraging) conservatism limits co-occurrence of closely related species.	[9]
<i>Anolis</i> lizards	Soraa, Biosphere Preserve Sierra del Rosario, Cuba	Unstructured	Niche is not conserved	Phylogenetic niche lability promotes coexistence of both species irrespective of phylogenetic relatedness.	[73]
Dusky salamanders	Eastern North America	Overdispersed	Conserved evolution of ecomorphological traits	Long-term stability of species communities facilitated by early evolution of niche differences.	[74]

Sunfish	Wisconsin: 890 lakes	Unstructured across all lakes, but some environmental variables generate phylogenetic clustering. Statistically removing environmental effects resulted in phylogenetic overdispersion.	Not assessed	Environmental filtering and competitive interactions are both contributing to community structure.	[75]
Dytiscid beetles	Alberta, Canada: 53 lakes	Clustered	Body size evolutionarily conserved	Habitat use is a highly conserved trait; environmental filtering is suggested to be more important than competition. Pattern might be influenced by intraguild predation.	[76]
<i>Dactylogyrus</i> parasites	Czech Republic: 328 fish from two localities on the Morava river basin	Clustered	Trait conservatism and phenotypic clustering	Competitive interactions among species are of less importance than environmental filtering.	[77]
Mammals	595 island assemblages	Most assemblages unstructured, but evidence for both overdispersion and clustering within some taxonomic groups	Not assessed	Island attributes such as elevation, size and origin suggested to contribute to patterns of phylogenetic structure.	[78]
Mammals	142 continental assemblages	Consistent tendency for overdispersion	Not assessed	Competition of close relatives with conserved traits of habitat filtering for distant relatives with convergent traits is important.	[79]
Bacteria	Freshwater mesocosms differing in primary productivity	Clustered when considering all bacteria or only subgroups	Not assessed	Decreased relatedness at higher-productivity levels might indicate that low-productivity environments are more stressful.	[80]
Bacteria	Virginia and Delaware: five surface or water-table soil samples	Clustered within three water-table communities; unstructured or overdispersed in each of the surface samples	Not assessed	Increased carbon availability could perhaps be relaxing habitat filtering, leading to reduced phylogenetic clustering.	[80]
Ammonia-oxidizing bacteria	Costa Rica: soils from five different land-use types	Clustering, overdispersion or no structure depending upon soil type	Not assessed	Habitat filtering possibly becomes more important as ammonia levels increase.	[80]
Ammonia-oxidizing and -denitrifying bacteria	Chesapeake Bay: sediment samples differing in salinity and nitrogen	Clustered	Not assessed	Lack of expected overdispersion could be due to conserved evolution of genes analyzed, or the assumption of conservative niche might be violated.	[80]





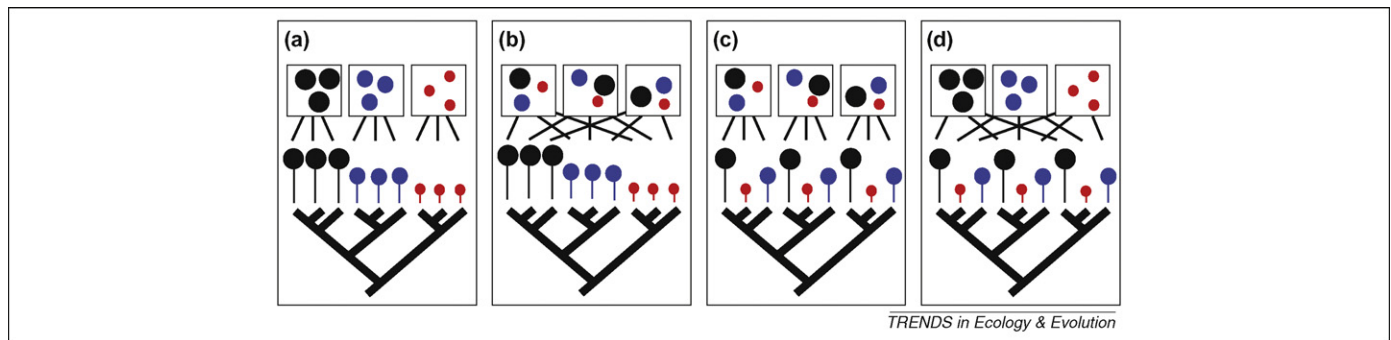
**Figure 2.** Community assembly by environmental filtering and interspecific competition. For a given habitat, the pool of species able to colonize that habitat is the subset of a regional species pool, constrained to those species possessing the necessary traits to complete their life cycle within that habitat. The four squares represent geographically discrete but identical habitats that have each been colonized from a regional pool of species. Within the regional pool of species, each species can occupy one of three possible niches. The species traits associated with niche are represented by three different circles (small = red; medium = blue; large = black). Establishment of the seven large black species is precluded by the environmental filter. From among the habitat species pool (blue and red numbered circles), the final species composition of each of the four habitats is dictated by interactions among species. Redrawn and modified with permission from Ref. [44].

foundation for addressing these questions using chronologically arranged islands [37].

Assuming ecological nonequivalence, much research has focused on the phylogenetic consequences of two contrasting processes underlying community assembly, competitive interaction and environmental filtering (Figure 2) [1]. Other processes can also result in phylogenetic structuring within communities (Box 1), but these have been less explored [38]. Before considering temporal data, we will first review some key studies. Within oak tree communities in Florida (Figure 3), Cavender-Bares *et al.* [8] assessed whether the phylogenetic distance between pairs of species correlated with their co-occurrence, and found that oaks are locally phylogenetically overdispersed, with co-occurring species more distantly related than expected by chance. To evaluate whether these patterns were due to species interactions or environmental filtering, niche-associated traits were also measured. This showed that convergent evolution of traits was important for niche occupancy, suggesting that environmental filtering was relatively more important than species interactions. However, when taxonomic scale was increased to incorporate other tree groups in the analysis, the pattern of phylogenetic overdispersion among oaks [8] gave way to an overall pattern of phylogenetic clustering [39]. Phylogenetic clus-

#### Box 1. Processes other than competitive interaction and environmental filtering can also lead to phylogenetic structure within communities

Phylogenetic clustering in dytiscid beetles is more apparent in communities of smaller-bodied species, and it has been suggested this could be a result of predation by larger-bodied dytiscid species where body size is a phylogenetically conserved trait [76]. The diversity of smaller dytiscid species was found to increase in the absence of larger species, leading to phylogenetic clustering. Predation can also cause the reverse effect. In mimicry complexes of *Heliconius* butterflies, distantly related species cluster in morphological and ecological space [82], the result being phylogenetic overdispersion and phenotypic clustering. Phylogenetic overdispersion in angiosperm communities of Mexico is explained by facilitation, where nurse plant species facilitate distantly related species [71]. It has recently been suggested that pollinator facilitation can lead to patterns of phylogenetic clustering or overdispersion, depending upon whether pollinator traits are evolutionarily conserved or labile [62]. Likewise, stochastic disturbance might influence phylogenetic structure and, in woody plant communities of eastern Iberia, fire has been shown to generate phylogenetic clustering [69]. Speciation can also have consequences for phylogenetic community structure. If most speciation occurs in allopatry, then a suitable null expectation would be that co-occurrence of closely related species would be less than that of distantly related species [38].



**Figure 3.** Environmental filters, interspecific competition, trait lability and the structure of communities. Species composition within and among communities can be influenced by environmental filtering, interspecific interactions and the potential for evolutionary change of traits associated with niche occupancy. (a) Both phylogenetic and phenotypic clustering in three communities (squares) consistent with the existence of both the conserved evolution of traits associated with niche occupancy (represented by circle size and color) and strong environmental filtering. Such a pattern is observed in the Gigasporaceae and Glomeraceae lineages of Arbuscular mycorrhizal fungi on *Plantago lanceolata* [81]. (b) Both phylogenetic and phenotypic overdispersion consistent with conserved evolution of traits associated with niche occupancy, and greater importance for species interactions over environmental filtering in determining species composition. Such a pattern is inferred for wood warblers in North America [9]. (c) Phylogenetic clustering and phenotypic overdispersion consistent with evolutionary change in traits associated with niche occupancy and adaptive radiation as observed among *Anolis* lizards on different Caribbean islands [53]. (d) Phylogenetic overdispersion and phenotypic clustering consistent with evolutionary change in traits associated with niche occupancy and strong environmental filtering, as observed in Floridian oak communities [8]. Modified with permission from Ref. [8].

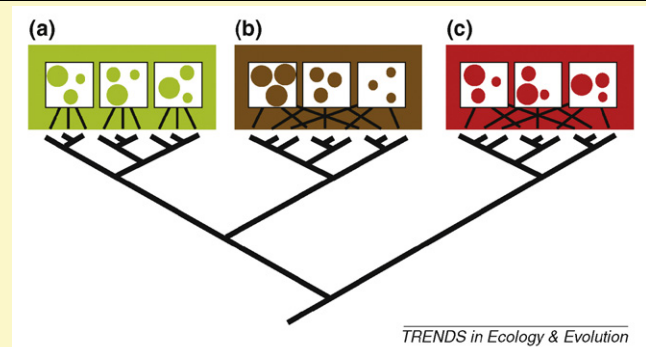
tering was also observed within sampling plots in a Bornean rain forest with a broad taxonomic sampling of 324 species [40]. Under the assumption that niche is a phylogenetically conserved trait, this pattern of phylogenetic clustering was explained by environmental filtering at the local scale due to ecological differences among sampling plots [40]. However, recent investigation of a neotropical forest tree community has shown that choice of a null model might in itself influence conclusions of community structure and that mean community phylogenetic structure might not differ from null expectations [41].

Based on this discussion, we can see that assessment of phylogenetic structure of communities is sensitive to choice of both null model as well as taxonomic, geographic and ecological scales [39,42] (Box 2). Analyses of angiosperm phylogenetic community structure, in particular forest tree communities, have received the most attention to date (Table 1) and illustrate the scale dependency.

Evolutionary relatedness and species co-occurrence have also been explored for North American wood warblers [9] (Figure 3) to determine whether local co-occurrence might be explained more simply as a result of phenomena

## Box 2. Phylogenetic and phenotypic community structure are scale dependent

Conclusions about the processes important for community assembly and structure are dependent upon phylogenetic, geographic and ecological scale. Phylogenetic clustering of Bornean rain forest trees within sampling plots has been suggested to be the result of environmental filtering [40], where phylogenetic clustering is associated with habitat differences among sampling plots. This pattern is consistent with the global phylogenetic pattern of Figure 1, where different habitats are represented by green (a), brown (b) and red rectangles (c). However, at the scale of individual habitats, competitive interactions among Bornean tree species might dominate, leading to phylogenetic and phenotypic overdispersion, as in the red habitat of Figure 1c. Similar to the pattern inferred for Bornean rain forest trees, British meadow plants exhibit phylogenetically conservative evolution of  $\beta$  niche traits leading to phylogenetic and phenotypic clustering within different habitats, as in the global phylogenetic pattern of Figure 1. However, the evolutionary lability of  $\alpha$  niche traits results in phenotypic overdispersion within communities but not necessarily phylogenetic overdispersion. Island communities of *Anolis* lizards in the Caribbean exhibit phylogenetic clustering and phenotypic overdispersion [53]. This pattern is consistent with the three communities (Caribbean islands) within the green habitat (*Anolis*  $\gamma$  niche) in Figure 1a, where species character traits represent  $\alpha$  niche. However, at the scale of an individual island or phylogenetic clade, *Anolis* communities are phylogenetically and phenotypically overdispersed [54], as in the red habitat of Figure 1c, where the three communities represent differences in  $\beta$  niche. Among wood warblers of North America, phylogenetic overdispersion is concluded to be due to competitive exclusion resulting from the conservative evolution of niche [9], as in the red habitat of Figure 1c. Niche has been coarsely divided into terrestrial foraging or arboreal foraging, but environmental filtering might also be important if there has been convergent evolution of niche traits within these foraging types, as in the brown habitat of Figure 1b.



**Figure 1.** Nine communities (squares) are clustered into three distinct habitat types represented by three differently colored rectangles. The three habitats can represent differences between  $\alpha$ ,  $\beta$  or  $\gamma$  niche of member species. Species are represented by circles and traits associated with habitat occupancy are represented by circle color. Species traits associated with niche occupancy within habitats are represented by circle size. At the scale of the entire phylogenetic tree the three habitats are both phylogenetically clustered, with conserved evolution of traits associated with habitat occupancy. At the lower scale of within an individual habitat or individual phylogenetic clade, community structure can differ from other habitats and clades and from the global pattern. (a) Communities within the green habitat are phylogenetically clustered and phenotypically overdispersed with convergent evolution of niche-associated traits. (b) Communities within the brown habitat are phylogenetically overdispersed and phenotypically clustered with convergent evolution of niche-associated traits. (c) Communities within the red habitat are phylogenetically and phenotypically overdispersed with conserved evolution of niche-associated traits. Redrawn and modified with permission from Ref. [39].

happening at a larger spatial scale. As in the Florida oaks, most species pairs that were broadly sympatric within a region were seldom found to co-occur at local sites, and in general closely related species pairs never exhibited high local co-occurrence. Complementing this, a hierarchical analysis found that local co-occurrence was positively related to time since divergence, highlighting the temporal component to patterns of species co-occurrence. These results have been interpreted as a signature of competitive exclusion being more relaxed for more distantly related taxa given a conservatively evolving niche [9]. However, in this study, niche could only be broadly defined, and so might give a misleading view of the pervasiveness of niche conservatism in evolutionary ecological analyses. Without directly quantifying whether traits associated within each warbler foraging niche are evolutionarily conservative or convergent, it becomes difficult to distinguish between the importance of competitive interaction or environmental filtering in explaining patterns of phylogenetic overdispersion (Box 2).

The message from these studies is that phylogenetic structure clearly has both spatial and temporal components. A common spatial pattern is regional phylogenetic clustering (due to environmental filtering) and local overdispersion (due to competitive interactions). In the context of insular environments, this phenomenon has a parallel temporal component: when remote islands are initially colonized, taxa will tend to be phylogenetically clustered (colonization limited to groups that share common traits of dispersal and survival in the new environment) with local overdispersion between close relatives potentially becoming more important over time as communities are filled.

### Why are communities phylogenetically structured?

Depending upon the spatial and temporal scale, patterns of both phylogenetic overdispersion and clustering can be consistent with either environmental filtering or competitive interaction selecting for species composition within a community (Figure 3). To understand the relative importance of environmental filtering and competitive interaction requires an evolutionary analysis of traits that are important for niche occupancy. If traits associated with niche exhibit phylogenetic conservatism, then closely related species are likely to be ecologically similar. However, distantly related species can be ecologically similar if trait lability has resulted in convergent evolution. For example, in analyses of niche structure of British meadow plant communities [10,43,44], niche has been characterized at three hierarchical scales of  $\alpha$ ,  $\beta$  and  $\gamma$  niche to assess whether traits that correspond to  $\alpha$  niche (varying within a habitat) evolve as slowly as has been reported for  $\beta$  niche traits (varying among habitats) [1,39,45–49]. Correlation between  $\alpha$  niche and phylogenetic distance was found to be low and nonsignificant, suggesting that traits associated with  $\alpha$  niche are not affected by phylogenetic conservatism [43,44], as has been reported for traits associated with  $\beta$  niche. Under these conditions, local communities will reflect environmental filtering for phylogenetically related species. However, strong environmental filtering does not obviate a role for competition and other species inter-

### Box 3. Mechanisms promoting species coexistence

When taxa with similar resource utilization occur in both allopatry and sympatry, competition in sympatry resulting from niche overlap can promote niche divergence, facilitating species coexistence [83,84]. However, two different processes can be invoked to explain greater divergence in sympatry than in allopatry: either ecological character displacement [85], in which functionally similar species evolve in different directions, or species assortment, in which only taxa with preexisting differences in niche can successfully colonize the same habitat and coexist. Character displacement is consistent with trait lability and competition-driven niche segregation promoting coexistence, whereas species assortment suggests trait conservatism and competitive exclusion. A molecular phylogenetic approach has the potential to assess the relative roles of both ecological character displacement and species assortment. Although only few in number, these studies provide evidence for the importance of both processes (see Ref. [86] for a recent review).

Besides ecological character displacement and species assortment, other conditions can also facilitate coexistence. In the absence of limiting resources, perhaps the existence of particular demographic features within one or more species, such as a metapopulation structure, might permit coexistence with niche overlap [87]. The application of molecular phylogenetic methodology, both among and within species, can help to reveal the relative importance of trait divergence and demographic explanations for species coexistence. Within the beetle genus *Aphanarthrum* (Coleoptera: Scolytidae) on the Canary Islands, a four-gene phylogeographic analysis has uncovered the evolutionary origin of two sympatric and ecologically indistinguishable species on the island of La Palma, *A. subglabrum* and *A. glabrum nudum* [88]. Analyses point to reproductive character displacement more consistent with reinforcement theory [89] than ecological character displacement, resulting in the coexistence of two ecologically indistinguishable but reproductively isolated taxa. A metapopulation structure for these species, due to patchy host plant distribution or lack of resource limitation, remains a testable hypothesis for their coexistence. It is interesting to note that the few studies of morphological patterns of character divergence among other beetles [90–93] have also been shown to reflect possibly reproductive rather than ecological character displacement [86], supporting a neutral ecological model of coexistence. Neutral models of community assembly [33,41] predict a minor role for niche segregation for coexistence, and insect communities deserve further investigation to evaluate such models.

actions (Box 3) in refining the membership of a community of species through evolutionary change among  $\alpha$  niche traits.

If greater  $\alpha$  than  $\beta$  niche trait lability facilitates phylogenetic clustering, then this should be a general phenomenon [44]. This is not reflected in analyses of other plant communities that, although also suggesting the evolutionary lability of  $\alpha$  niche traits, are less conclusive regarding the conservative evolutionary nature of  $\beta$  and  $\gamma$  niche traits [43]. Analyses of niche evolution in the plant genus *Ceanothus* have employed a modification of the method of phylogenetic independent contrasts [50], the divergence order test [7], to assess whether  $\alpha$  niche traits (leaf area) evolved before or after  $\beta$  niche traits (climatic distributions). In contrast to the analyses of British meadow plants,  $\alpha$  niche traits in *Ceanothus* exhibited less lability than  $\beta$  niche traits. Although this result has been described as at odds with the hypothesis of  $\alpha$  niche being more labile than  $\beta$  niche [43], it does explain the pattern of phylogenetic overdispersion observed within this group [7]. Because evolutionary change along the  $\beta$  axis (habitat) for *Ceanothus* appears to occur more readily than along the  $\alpha$  axis (niche), taxa are phylogenetically overdispersed



within a given area, because close relatives tend to be in different habitats.

An important caveat to these studies is that niche dynamics are dependent upon the spatial, temporal, environmental and phylogenetic scale of investigation [51]. At the extremes, strictly allopatric divergence into different habitats might be a case of a shift in  $\beta$  niche affinity. However, allopatric divergence need not necessarily lead to a shift in habitat affinity if similar habitats are disjunct. For example, Peterson *et al.* [52] found that sister taxa on opposite sides of the Isthmus of Tehuantepec inhabit climatic regimes that are more similar than expected by chance. Likewise, modification in microhabitat within the same habitat might be a case of a shift in  $\alpha$  niche affinity; however, if the habitat of an organism is defined by the biotic community, such as occurs in parasites or plant-associated insects, distinguishing between  $\alpha$  and  $\beta$  niche shifts becomes more difficult. However, in each case, the goal is generally to understand the relative lability of different traits in allowing organisms to exploit different habitats, or to exploit different microhabitats within a habitat. Here again, comparison of islands and continents is enlightening, as it allows assessment of general conditions and time frame under which organisms might evolve within versus between habitats.

Greater Antillean *Anolis* lizards in particular offer important insights into the role of  $\alpha$  niche and  $\beta$  niche, the phylogenetic structure of communities and the relevance of scale (Box 2). Anoles on different islands have undergone repeated evolution of similar ecomorphs (Figure 3), leading to communities of four or more species differing in  $\alpha$  niche traits (microhabitat specialization, such as tree-canopy dwelling or trunk-ground dwelling) [53]. Although similar evolutionary changes along the  $\alpha$  axis (niche) have occurred among islands, most speciation within islands has involved diversification within ecomorphs along the  $\beta$  niche axis (habitat) associated with allopatrically distributed macrohabitat types [54]. Thus, when one compares communities among islands within the archipelago, anoles appear to be phylogenetically clustered and phenotypically overdispersed, with evolutionary convergence of  $\alpha$  niche traits. However, comparing habitats within individual islands, anoles can appear both phylogenetically and phenotypically overdispersed with conservative evolution of  $\alpha$  niche traits.

The Greater Antillean anole example provides a clear demonstration of how  $\alpha$  and  $\beta$  niche trait lability, together with the potential for species addition by both immigration (i.e. the size of the regional pool) and speciation, jointly contribute to phylogenetic structuring within communities. Further insights into the interplay between  $\alpha$  and  $\beta$  niche trait lability in the evolution of communities can be recognized from studies of other radiations. For example, major ecological ( $\alpha$  and  $\beta$  niche) shifts tend to accompany the initiation of species radiations (e.g. Refs [55,56]). Subsequent diversification generally occurs within the ecological domains established (e.g. within plant families in Hawaiian planthoppers [55]), although shifts can be in either  $\alpha$  niche traits (e.g. Hawaiian spiders [57,58]) or  $\beta$  niche traits (e.g. Hawaiian silverswords [59,60]). Thus, given time and opportunity, many traits can display lability;

but when time and opportunity are more limited, certain traits will display greater lability than others, and the extent to which this occurs in  $\alpha$  versus  $\beta$  niche traits will then depend on the taxa and the environment.

### Is community assembly a predictable process?

The theory of island biogeography [21,22] assumes that immigration is essentially neutral with respect to the identity of the colonists. However, experiments have shown that, although a community can support more species in the early phase of assembly while most species are rare (termed the noninteractive phase) [12,61], as population sizes increase, and competition likely becomes stronger, the species number drops (interactive equilibrium), with more highly coadapted sets of species tending to persist. This result suggests that community assembly is somewhat deterministic, even though there is a strong stochastic element to colonization.

The temporal framework of some oceanic islands has been used to investigate the evolutionary dynamics of community assembly in a radiation of spiders in the 'spiny leg' lineage of the genus *Tetragnatha* in the Hawaiian Islands [58]. These spiders display four distinct ecomorphs, one of each occurring in most habitats throughout the main archipelago. Molecular phylogenetic analyses suggest that ecomorphs are not monophyletic groups, but instead represent multiple independent origins of the same ecomorph. Importantly, community assembly is a product of

#### Box 4. Microbial experimental approaches to community assembly

The potential for experimental analysis of community assembly theory has recently been capitalized upon using both fungal and bacterial systems. Arbuscular mycorrhizal fungi (AMF) have been used to investigate the influence of phylogenetic relatedness on community assembly of fungi on the roots of *Plantago lanceolata* [81]. Most AMF belong to three taxonomic families in which niche-associated traits are phylogenetically conserved. Members of the family Gigasporaceae typically utilize hyphae located outside of the plant root, whereas the majority of the fungal biomass in the Glomeraceae is found in hyphae growing inside the root. Members of the Acaulosporaceae produce low biomass both inside and outside the root. Experimental communities were constructed with eight AMF species, manipulating phylogenetic relatedness to range from across all three families to all species being members of the same family. Results from these experiments indicate that phylogenetic trait conservatism can promote coexistence through reduced competition. One year after the experiments were set up it was found that species richness was highest in those communities assembled from all three families, compared to those assembled from one or two families.

Recent experiments using the bacteria *Pseudomonas fluorescens* have demonstrated the importance of immigration history in dictating the eventual composition of diversity within a community [16]. It was found that predictable patterns of diversification into vacant niche space could be disrupted by the immigration of a particular niche specialist within a specific window of time. In the same way arrival order has been shown to disrupt diversification [16], it is almost certain that successful membership of a community through colonization can also be contingent upon the existing species composition of that community. Experimental microbial systems such as the AMF of *P. lanceolata* [81] might provide insights to the exact nature of this by the manipulation of species colonization times. Understanding the processes underlying general phylogenetic patterns within bacterial communities [80] might also profit from experimental approaches.

both dispersal and intra-island speciation, with niches being filled apparently by the first appropriate ecomorph to arrive, either by adaptive speciation from another ecomorph on the same island or by colonization by an ecomorph from another island. The pattern of community assembly here, in which chance dictates the phylogenetic identity of a taxon filling a niche (even though the resulting set of ecomorphs is the same), and with more species being supported on an island when any one is rare, shows interesting parallels to patterns found on islands closer to a source of migrants, despite the very different time scales involved [12]. This suggests the possibility of some universal principles of community assembly. However, all biological systems have both general and special properties, reflecting unique histories of individual species and location [11], and much work is needed to understand the relative roles of these for community assembly and structure [38,62]. For example, the role of order of arrival is poorly understood in natural systems. Experimental microbial microcosms have recently demonstrated the importance of colonization history and associated interactions in dictating community composition, with the effect most marked in smaller ecosystems, thought to be due to greater priority effects [59] (Box 4). A particular challenge is to apply the knowledge gained from these rich microbial systems to a more general appreciation of colonization and adaptive diversification in dictating community assembly patterns.

## Conclusions

The incorporation of phylogenetics into community ecology has allowed key insights into the assembly and structure of communities. Here we have used insular environments to provide a temporal context for understanding the role of spatial and temporal scale in dictating pattern. Although much remains to be understood, we can draw some preliminary conclusions. Spatial (isolation) and time (for adaptation) interact to dictate first whether a niche is more likely to be filled by immigrants or through adaptation and diversification of existing taxa. When immigration plays the dominant role compared to speciation in community assembly, environmental filtering and competitive interaction generate patterns of phylogenetic structure that are conditional upon the evolutionary lability of traits important for niche occupancy. Studies suggest that the same might be true for communities in which speciation plays the key role in community assembly. In both cases, some patterns of species coexistence do not appear to differ from chance expectations (i.e. can be predicted based simply on availability of colonists), and the challenge remains to provide null models that clearly differentiate structured and unstructured communities. A fuller understanding of the processes and patterns of community assembly will require research to assess the temporal sequence and spatial scale of evolutionary shifts in species traits associated with niche occupancy. Much research to date has focused on communities in which members belong to the same guild or closely related guilds. Further research is needed to assess biotic interactions both between and within guilds, such as predators and parasites, and their role in structuring communities. Phylogenetic analyses

spanning the full breadth of community membership can provide the historical framework required to determine what general rules apply to community assembly and structure. These kinds of studies are feasible on islands, which therefore offer considerable untapped potential for our general understanding of community assembly.

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