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## Abstract

- Communities are located within a larger species pool of potential colonists. The study of community assembly considers the mechanisms by which local communities are formed from the species pool.
- Dispersal from the species pool, abiotic tolerance of colonists, and biotic interactions can all influence membership in local communities.
- Phenotypic similarities and differences of co-occurring species can be used (within limits) to make inferences about the role of alternative processes contributing to community assembly.

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- In many plant groups, close relatives tend to share similar phenotypic traits. Therefore, patterns of phylogenetic relatedness within a community can also be used to make inferences about community assembly mechanisms.
- As the community and the species pool can be defined at a number of different spatial and temporal scales, community assembly patterns often show strong scale dependence. In some cases, a single process can produce contrasting phenotypic patterns at different scales of analysis, while in other cases different processes may have stronger influences on community assembly at different scales.
- Species pools are shaped by dispersal of lineages among biogeographic regions, in situ speciation within regions, and extinction. The characteristics of the species pool often persist in local community patterns.
- Community assembly studies are often limited in the extent to which specific mechanisms can be inferred from community pattern. Future work should focus on improved models of competition and coexistence dynamics in community assembly as well as methods for considering multitrophic interactions.

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## Introduction

Community assembly is the study of the processes that shape the identity and abundance of species within ecological communities. Central to most studies of community assembly is the concept of a species pool that is larger in geographic scope than the local community under study. The species pool contains potential colonists of the community, and many studies in this area focus on developing an understanding of the role of dispersal, responses to abiotic conditions, and biotic interactions in shaping local assemblages. Thus, community assembly considers both the ecological interactions that shape local communities and the evolutionary and biogeographic processes that lead to variation in the diversity and composition of species pools across the globe.

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## A Brief History of the Development of Community Assembly Concepts

There are two persistent and central concepts in the study of community assembly. The first is the “species pool,” defined as the suite of possible colonists for a local site under study, and the second is the metaphor of a “filter” or a “sieve” that represents abiotic or biotic barriers to successful establishment at a local site. The two concepts can be traced back to two distinct sources: the study of species assemblages on oceanic islands and the study of succession following disturbance.

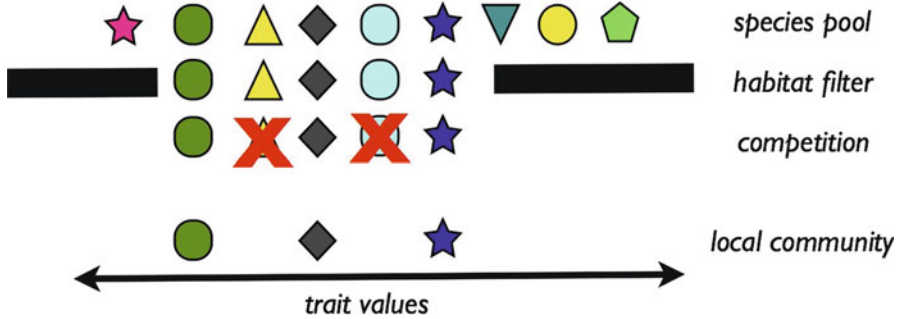
Perhaps the best-known precursor to community assembly theory is MacArthur and Wilson’s seminal theory of island biogeography, which describes the fate of an

oceanic island biota that is envisioned as receiving a supply of immigrants from a larger mainland species pool (MacArthur and Wilson 1967). The distance of the island from the mainland is predicted to influence the frequency with which new colonists arrive, and the size of the island influences the rate at which species go extinct on the island. Together these two properties predict the equilibrium number of species that the island will support at any point in time. Biotic interactions between species are implicit in island biogeography theory, as local extinction rates increase with species richness, though the primary focus of the theory is on the dynamics of dispersal to a community from a larger mainland species pool.

Following MacArthur and Wilson, the next step in the evolution of community assembly theory was Jared Diamond's study of bird communities on islands near New Guinea (Diamond 1975). Diamond was the first to use the concept of "assembly" in this context. In contrast to island biogeography, Diamond primarily focused on the role of biotic interactions in shaping local communities, and in particular he proposed "assembly rules" that captured the competitive exclusion of species that were too ecologically similar to co-occur. Diamond was criticized for lacking a proper null hypothesis for species differences when testing his assembly rules, as a null hypothesis is needed to permit the falsification of the hypothesis that competition shapes community assembly. If the process of competition is the only mechanism of community assembly that is considered, then there is no opportunity to allow for the role of other processes.

Shortly following the publication of Diamond's work, and at least in part in response to it, null models were developed that offer a solution to this issue (Pielou and Routledge 1976; Connor and Simberloff 1979; Strong et al. 1979; Colwell and Winkler 1984). Central to the null model concept is the idea of a species pool that is used to create a null hypothesis for the assembly of communities within a region. The null model captures much of the ecology of the system, but removes the key process of interest, such as competitive interactions, from the model. Thus, a null model for assembly rules might simply contain the dispersal of species from the species pools into local communities, without any consideration of competitive interactions. Random samples from the species pool can then be used to generate a distribution under the null hypothesis describing what species assemblages should look like in the absence of competition. Since the original application of null models to island data, the approach has been developed extensively (Gotelli and Graves 1996) and still remains central to many studies of community assembly.

In addition to the concept of a species pool, another central idea in community assembly theory is the concept of a "filter" that allows some species to pass through while serving as a barrier to unsuitable species as they arrive and attempt to establish at a site. This concept is first seen in the study of succession following disturbance, when Nobel and Slatyer (1977) describe an "environmental sieve" during succession. This concept was used extensively throughout the development of plant community assembly studies, often in terms of a "filter" that only permitted particular phenotypes to establish and persist (van der Valk 1981; Woodward and Diamond 1991).



**Fig. 1** Basic conceptual model of community assembly in terms of species functional traits (phenotypes). Empirically, an ecologist can consider the local community in relation to the species pool of potential colonists. Habitat filtering is often hypothesized to limit the range of traits that can successfully survive and establish at a site, as well as sometimes shifting the mean value relative to the species pool. Competition, in its earliest forms in community assembly theory, was predicted to favor the coexistence of species that differed in resource use or requirements, reflected here in their functional traits. In the example here, competitive exclusion leads to a local community of species with trait values that are more dissimilar than species in the original species pool. Additional community assembly processes are not shown. (After Woodward and Diament (1991))

While some early community assembly studies focused on forbidden combinations of species, much of the later research quickly transitioned to a focus on patterns of phenotypic traits of community members rather than on species identity *per se*. In plant community ecology, the focus has often been on functional traits, which are defined as aspects of the plant phenotype that are indicative of variation in ecological strategies of resource use, growth, and distribution in relation to environmental conditions (Westoby and Wright 2006). Plant functional traits that are relevant to community assembly can be anatomical or morphological traits, such as specific leaf area ( $\text{m}^2 \text{g}^{-1}$  biomass), root depth, or seed size, or they can be ecophysiological measures that reflect the integrated activities of several related plant processes, such as maximum photosynthesis rate or photosynthetic water use efficiency ( $\text{mol CO}_2$  assimilated  $\text{mol}^{-1}$  water transpired). As these functional traits can be measured on most if not all plants within and across communities, they offer a phenotypic common currency that can be used to draw generalizations across species and to make inferences about the mechanisms that shape community patterns. For example, in studies of succession, environmental sieves or filters are often hypothesized to drive convergence or clustering in phenotypic traits (relative to a null model), whereas competition patterns of the sort originally proposed by Diamond are typically predicted to produce phenotypic overdispersion, where co-occurring species are more dissimilar in traits than expected (Fig. 1; Weiher and Keddy 1999). More recent community assembly studies have refined these predictions in a number of ways, as discussed in subsequent sections.

A number of methodological considerations arise when sampling and analyzing functional traits in a community assembly context. Functional traits may vary

across modules (e.g., branches, leaves) within an individual plant, individuals within species, and across species. Some of this variation is environmentally driven plasticity, which is often correlated across species. For example, leaves produced in full sun environments often have lower specific leaf area (thicker or more dense tissue) than leaves from the same plant grown in shaded environments. Functional traits may also change throughout the development of an individual organ (e.g., a leaf or a stem) and through the ontogeny of whole plant. In sampling plant functional traits, the convention has often been attempt to minimize the role of ontogenetic and environmentally driven plastic variation among individuals within a species by standardizing trait sampling to particular environmental conditions and ontogenetic stages (Cornelissen et al. 2003). For example, many leaf traits are typically sampled on fully expanded and hardened leaves growing in the outer canopy of adult trees. Sampling in this way then emphasizes the role of genetic differences among individuals in driving any intraspecific variation in traits.

In many plant community assembly analyses, trait values among individuals within species are averaged, and analyses conducted on species trait means. This is justifiable if intraspecific variation is modest relative to interspecific variation in traits. However, in some communities, particularly those with low species richness, intraspecific variation can be substantial relative to interspecific variation, and as such there is growing interest in incorporating intraspecific trait variation into community assembly analyses (Violle et al. 2012). One of the important considerations in these analyses is whether the trait values measured on each individual area direct measure of that individual's growth and function, mediating interactions with the environment and with other individuals, or whether the traits represent proxies for underlying life history strategies of the species. In the latter case, it may be more appropriate to focus on species means rather than the particular manifestation of a trait in one individual or one local environment. When the data is available, it is also possible to determine from a quantitative standpoint the importance of intraspecific variation. For example, Cornwell and Ackerly (2009) evaluated the shift in community level mean trait values across a gradient of soil water availability and found that incorporation of intraspecific variability led to a steeper shift across the gradient, but the difference was fairly modest due to the greater role of interspecific turnover. In addition to averaging individuals within species, some community assembly studies take the additional step of grouping species with similar functional traits into functional groups or functional types, such as "C<sub>4</sub> grasses" or "broadleaf evergreen trees," which can further simplify analyses.

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## Dispersal

Dispersal refers to the movement of an individual organism during its lifetime, from its place of birth to the location where it produces offspring. As plants are sessile organisms, in most species, dispersal only occurs once during the life cycle at the seed stage. Once a plant germinates, it occupies a single location for the rest of its life. In addition to this mechanism, a small number of species are able to disperse via

vegetative fragmentation, where disarticulated modules of a plant are able to initiate new roots after being transported to a new location. Dispersal is a key component of the community assembly process, as a plant must arrive at a location first before it can become a member of the community. The various mechanisms of propagule dispersal, together with the sessile habit, have many important consequences for plant population and community ecology. Four critical aspects of the dispersal process are considered here: dispersal mechanisms, dispersal distances, seed dormancy, and the role of dispersal limitation in shaping community assembly.

Seed dispersal is accomplished by a wide variety of different mechanisms, including gravity (i.e., large seeds that fall directly below the adult), ballistic mechanisms that eject a seed a short distance, floating on water, movement by wind, and dispersal by animals (either attached to the outside on fur or feathers or ingested and carried internally until deposited after a short time). The importance of these mechanisms for community ecology is that they are often undirected relative to the sites where a plant may be best suited to grow (unlike many animals, which can search for appropriate habitats). For example, many early successional plants are wind dispersed and produce numerous small seeds; this increases the likelihood that at least a few seeds will land in recently disturbed sites by chance, but wind dispersal will not generally be targeted at disturbed sites. Animal-mediated dispersal may be more directed, as when many seeds are deposited below perch trees where birds rest after eating. However, seeds are often dispersed more or less randomly with respect to the distribution of environments or communities where a particular species is most likely to germinate and successfully establish.

Most seeds travel only a short distance. In wind-dispersed species, tree height, seed size, and dispersal structures (wings, hairs, etc.) all influence dispersal distances, but even for tall trees with small seeds, most seeds travel less than 1 km. Thus, on short timescales, community assembly may be dispersal limited, in the sense that new species would arrive from external seed sources only infrequently and in small numbers. However, while most seeds travel short distances, plants have a remarkable ability to achieve rare, long-distance dispersal events. The best evidence for these events comes from remote oceanic islands, such as Hawaii, where the entire native flora is descended from hundreds of independent colonization events, in which seeds traveled thousands of miles across open water at some point over the past 5–10 million years. The recovery of Northern Hemisphere vegetation following widespread glaciation also demonstrates the importance of long-distance dispersal. Following past glacial epochs, species moved north in Europe and North America far faster than would be predicted based on the more common, short-distance seed dispersal from adult plants (Clark et al. 1998).

At the landscape scale, seed dormancy can be thought of as an important component of dispersal. Opportunities for germination and establishment may only occur infrequently, especially for species that colonize after disturbances such as wildfire or treefalls or in highly variable environments such as deserts where periods of sufficient rainfall for germination and establishment are sporadic and unpredictable. For these species, dormancy represents dispersal in time, allowing a seed to persist in a particular spot until suitable conditions occur.

Thus, while dispersal is undirected in space, the combination of dormancy and specific germination cues (discussed in the next section) allows some species to disperse in time so seedlings can occupy suitable environments for establishment and growth. Many examples have been documented of viable seeds germinating after hundreds or even thousands of years of dormancy. However, it is likely that most seeds in natural populations germinate from the seed bank within a few years, before they are lost to burial, predation or fungal attack.

What are the consequences of dispersal for community assembly? On the one hand, over short timescales most plants move short distances, and arrival of new species in a community may be infrequent. On the other hand, over longer timescales (e.g., thousands of years), many plants have a remarkable capacity for long-distance dispersal, and the history of vegetation response to climate change demonstrates that the composition of plant communities is highly dynamic. As a practical matter, many studies of community assembly assume that the plant species in a regional species pool (on the scale of tens to hundreds of kilometers) have the capacity to disperse anywhere within that region, given a reasonable amount of time. To the extent that is true, then community assembly patterns reflect local abiotic and biotic interactions that determine the composition and abundance of co-occurring species. However, it is difficult to establish the exact temporal and spatial scales at which the assumption of unlimited dispersal is a reasonable approximation; at local scales, over short durations, and at biogeographic scales over longer time periods, dispersal may be a critical process that explains patterns of species distributions and community composition.

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## Abiotic Filtering

One of the central metaphors in community assembly is that of a habitat filter, where the abiotic environment “filters out” species by limiting establishment or survival at particular sites. As plant dispersal is often relatively undirected, seeds may often arrive at locations where conditions are not favorable for germination or long-term survival. These filters can impact plants at any life stage and can involve any of a number of abiotic factors singly or in combination.

Many plant species have specific abiotic requirements for successful germination, and thus the germination stage represents the first point at which habitat filtering can occur. Germination cues can include moisture, temperature, light, photoperiod, and even fire or smoke in some species adapted to fire-prone environments. Many species require specific combinations of abiotic cues, such as a period of cold temperature followed by a photoperiod indicative of long days. Reliance on these cues can help to ensure that a species will not germinate and die in unfavorable conditions. Some species are able to persist in a dormant state as a seed for long periods of time waiting for the proper cues to trigger germination, but the length of time that seeds remain viable varies widely among species. The ability of some species to persist for extended periods in the seed bank can complicate the task of quantifying community membership at a particular site, and an examination of

the seed bank (and testing for seed viability) may be required to definitively conclude that a species is absent from a site. This is most relevant in communities that exhibit substantial variation in abiotic conditions over time, as different species may use the same habitat at different times of the year or in different years, depending on year-to-year variation in weather, remaining dormant in the seed bank at other times.

Abiotic factors can also cause mortality or prevent successful reproduction at any time during the life cycle from germination through reproductive maturity. Species vary in requirements for light, nutrients, and water as well as in tolerance to drought and temperature, and any of these factors can cause mortality at any stage. An important consideration is that brief, extreme climatic events can have strong impacts on species survival. For example, the average climatic conditions at a site may be ideal for the growth and reproduction of a species, but a brief period of extreme cold or heat or a short but severe drought that occurs infrequently can cause significant mortality and effectively remove particular species from a site. For example, a severe drought associated with an El Niño event in the 1980s is thought to have had persistent and long-lasting impacts on the species composition, and associated functional traits, of a tropical forest on Barro Colorado Island, Panama (Feeley et al. 2011). Therefore, in considering the role of abiotic conditions in filtering species from a site, it may be just as important to consider the variance or the extremes of abiotic conditions as it is to consider the average values.

Practically speaking, it can be challenging to distinguish between habitat filtering and dispersal limitation when a species is completely absent from a site. Simple experiments can be helpful in testing for habitat filtering. On the most basic level, these experiments involve transplanting individuals either as adults or as seeds to the site and monitoring germination and/or survival. In situations where these experiments are impractical, seed traps or detailed examination of the seed bank can be useful in ruling out dispersal limitation as the cause of a species absence.

An important consequence of abiotic filtering is that species composition typically changes along environmental gradients. For example, there is widespread evidence that plant communities change in predictable ways along gradients of light, water availability, soil fertility, elevation and latitude, among other factors. These changes in species identity are also often reflected in changes in the functional traits of species, such that average trait values across species in the community can shift along a gradient. For example, woody plant leaf functional traits change consistently across a gradient of soil water availability in coastal California and across microtopographic gradients in the Ecuadorian Amazon (Kraft et al. 2008; Cornwell and Ackerly 2009). Another frequently documented pattern is that the breadth or variance of strategies seen at any point along the gradient is often smaller than is seen across the gradient as a whole. The significance of these observations – i.e., shifts in the mean of trait values and reduction in the range or variance in trait values at points along a gradient – is typically documented using a null model approach, comparing observed communities to hypothetical communities assembled at random from the regional species pool.



## Biotic Interactions

Just as abiotic factors can serve as filters to prevent establishment of species, interactions between plants and other organisms can have important consequences for community assembly. Competition and natural enemies (herbivores, parasites, and pathogens) can reduce growth and survival of plants at a particular site, and positive interactions can allow species to establish and persist at sites where they would otherwise be unable to survive. In many conceptual models of community assembly, biotic interactions are often considered to impact community assembly after abiotic filtering has occurred. While this may be true if the primary habitat filter occurs at the germination stage, in reality biotic and abiotic factors are likely important throughout the lifecycle of most plants. Persistence in a community requires tolerance of stresses in the germination, establishment, and adult reproductive phases, to ensure reproduction of the next generation.

As stated earlier, competition has long been considered to be a central biotic factor in community assembly, dating back to Jared Diamond's initial study of bird communities on islands (and before that back to Darwin, writing in the *Origin of Species*). Competition is hypothesized to impact community assembly by the failure of species to establish or persist at a location in the face of competitive interactions. Early community assembly theory focused on the competitive exclusion principle (Hardin 1960), which hypothesizes that "complete competitors cannot coexist," meaning that species are more likely to be able to coexist if they have niche differences. Early work in this area focused on the concept of limiting similarity, which hypothesized that there was a finite limit to how similar two coexisting species could be. While theoretical work has since suggested that there is not likely to be an absolute limit to similarity, the general idea that differences between species promote coexistence by reducing competition has persisted as a central theme in many community assembly studies. To date, many plant community assembly studies have approached competition by documenting differences in the niches or phenotypes of co-occurring species and testing whether those differences are greater than what might be expected by chance. For example, co-occurring plants in sand dune plant communities in New Zealand and forests in the Ecuadorian Amazon are often more phenotypically distinct from each other than predicted by null models (Stubbs and Wilson 2004; Kraft et al. 2008). In many ways, this approach has direct links to Jared Diamond's initial approach of documenting "forbidden combinations" of species on islands. While phenotypic patterns that are consistent with competition are regularly detected in plant communities, they are far less common than evidence for habitat filtering.

Herbivores, parasites, and pathogens, collectively referred to as natural enemies, can also have important and wide-reaching consequences for community assembly. One challenge in this area is that community assembly studies typically focus just on members of one guild or functional type (e.g., trees or herbaceous plants) and often have not considered other trophic levels. In some cases, the impact of natural enemies can be studied primarily through plant distributions. For example, if species suffer primarily from natural enemies that are species specific, seedlings growing near adult

trees of the same species should suffer more negative effects than seedlings growing far from adults, as natural enemies can become concentrated near adult trees (reviewed in Wright 2002). In this case, the study of plant distribution patterns within communities can offer some insight into the role of natural enemies. However, in other cases, we likely need improved conceptual models and approaches to effectively incorporate natural enemies into community assembly studies.

Positive interactions between species can also have profound impacts on community assembly, allowing species to establish or persist at sites where they would otherwise be unable to survive. Many of these associations are between plants and other organisms. For example, associations with mycorrhizae and nitrogen-fixing bacteria allow many plant species to gain access to essential nutrients more effectively, and many species rely on insect or animal pollinators for reproduction. The absence of these mutualist partners can effectively exclude plants from particular sites. Our understanding of these relationships in a community assembly context is hampered by the same limitations as our understanding of natural enemies – many studies typically focus just on plants, not on other groups within a community. While it is possible to study some consequences of plant-pollinator interactions primarily through the plant community (Sargent and Ackerly 2008), new approaches will be needed to fully incorporate positive interactions that extend beyond a single trophic or functional group into community assembly studies.

It is also well understood that plants can have positive effects on each other. These impacts most commonly involve an amelioration of environmental stress or a reduction in herbivore pressure via associational defenses. For example, in hot and dry environments, some species are known to function as “nurse plants” by modifying the nearby microclimate enough to allow other species to be able to establish. However, many positive interactions between plants are known to be highly context dependent. For example, in one globally replicated experimental study, plants growing at lower elevations on mountains were often found to compete with one another, while species growing at higher elevations on the same mountains (which is presumably a more stressful environment) were found to have positive effects on one another (Callaway et al. 2002). These findings highlight that most positive interactions (and perhaps many species interactions in general) typically include both a positive and a negative component and that the relative importance of these components for community assembly can shift as abiotic conditions change. This also highlights a general but understudied challenge within the topic of community assembly – disentangling the interactions among abiotic and biotic filters.

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## **Relationship Between Community Assembly and Coexistence Theory**

An important ongoing area of development in community assembly theory is in improving the models of competition to incorporate insights from coexistence theory that have occurred since the development of the community assembly

approach (HilleRisLambers et al. 2012). Community assembly analyses, as discussed above, have typically considered competition to be a process that favors coexistence between species that are phenotypically distinct, assuming that differences in functional traits or functional types between species are related to niche differences. This assumption is grounded in early theories of competition and differentiation in resource use but is incomplete with respect to continuing developments in the theory of species coexistence.

In particular, Chesson (2000) has advocated for a consideration of two distinct phenomena in competitive interactions. First, coexistence between a pair of species is made more likely by the presence of stabilizing niche differences, defined as differences in resource use that give both species an advantage when rare. These advantages allow each species to recover from low abundance, buffering each species against competitive exclusion. Thus, coexistence is enhanced by niche differences, exactly as modeled in much of community assembly theory. However, Chesson goes on to consider another component of the interaction, termed average fitness differences. Average fitness differences reflect differences in the average competitive ability of species, and these differences can lead to the exclusion of the less fit species even if there are niche differences between the two species. Therefore, a pair of species is most likely to be able to coexist when they have large niche differences and minimal fitness differences.

This viewpoint leads to multiple potential phenotypic outcomes of competitive exclusion. If the functional traits of organisms under consideration primarily reflect niche differences, then competition should result in phenotypic disparity between co-occurring organisms. However, if the traits under study correlate instead with average fitness differences, then phenotypically similar species may be more likely to coexist. If traits correlate with both niche and fitness differences, then the outcome may be a combination of patterns or something that appears essentially random. One of the major limitations in making progress in this area is a lack of understanding of the extent to which commonly measured plant functional traits correlate with niche differences, average fitness differences, or some combination of the two. Detailed manipulations that measure functional traits in communities as well as quantifying niche and fitness differences among species will be needed to make progress in this area.

One major difference between community assembly theory and many coexistence approaches is that coexistence theory primarily focuses on species that are able to survive and persist at a site, whereas community assembly considers a broader suite of species and the process of abiotic habitat filtering. This gap highlights the progress that could be made from a better unification of these two areas. Some of the issues and challenges in unifying these approaches are discussed in the last section of this chapter.

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## Phylogenetic Patterns

In a famous quote from the *Origin of Species* (1859), Darwin noted that “As the species of the same genus usually have...much similarity in habits and constitution, . . . the struggle will generally be more severe between them, if

they come into competition with each other, than between the species of distinct genera.” His observation reflected the general knowledge of any experienced systematist or field naturalist that related species tend to be ecologically similar; e.g., one would expect two grass-eating rabbit species to compete directly for the same food sources, whereas a grain-eating mouse and a carnivorous fox are utilizing quite different resources. In the first half of the twentieth century, experimental studies of competition by Gause and the development of Lotka-Volterra competition theory led to the development of the competitive exclusion principle (Hardin 1960), discussed earlier, which posits that species competing for the same resources could not coexist in a community. Putting these ideas together, ecologists in the mid-twentieth century suggested that species of the same genus would not live together in local communities, at least not as often as one might expect if communities were assembled randomly from the available species in a regional species pool. This prediction was supported in studies of animal communities on islands, compared to the fauna of adjacent mainland regions. These studies provide some of the earliest examples of null models in ecology, discussed above.

Starting in the 1960s, the study of phylogenetics was revolutionized by conceptual, computational, and empirical advances, most notably the breakthroughs in molecular biology leading to the modern era of DNA sequencing. With high-resolution, well-supported phylogenies available, new methods have been developed to reexamine classical questions in ecology and evolutionary biology. The study of plant communities presented particular challenges, as the deeper structure of the angiosperm phylogeny had never been well understood and molecular data brought a number of surprises. The first breakthroughs came in the 1990s, quickly leading to a broad community effort under the Angiosperm Phylogeny Group and a rapidly growing consensus about major patterns in flowering plant phylogeny. Plant ecologists moved quickly to utilize the newly available phylogenies to tackle large-scale problems in adaptive evolution, diversity, and community assembly (Webb 2000). Molecular data also provide branch lengths that quantify the degree of relatedness among species, and fossil calibrations can be applied to estimate branch lengths in millions of years since species diverged from their most recent common ancestor. The phylogenetic distance between two species is defined as the distance from one species down the phylogeny to the common ancestor and back up to the other species (in other words, two times the age of their most recent common ancestor).

The phylogenetic structure of a community can be described in a number of ways, using quantitative metrics based on the phylogenetic relationships for the community, “pruned” from the larger phylogeny of all plants. As in the examples discussed above, statistical analyses of phylogenetic community structure consider a local community relative to a null model of communities assembled from a regional species pool. Two simple measures of phylogenetic community structure are the mean phylogenetic distance, defined as the average of the phylogenetic distances between all pairs of taxa in a community, and the mean nearest neighbor distance, defined as the average distance from each species to its closest relative. Using these measures, the net relatedness index (NRI) and nearest taxon index (NTI)

can be calculated comparing observed communities to hypothetical communities constructed under a null model. These metrics allow us to describe communities along a continuum, from those in which co-occurring species are more closely related ( $NRI > 0$ ) or more distantly related ( $NRI < 0$ ) than expected by chance under the null model. Similarly, NTI measures whether each species' closest relative is more closely ( $NTI > 0$ ) or more distantly ( $NTI < 0$ ) related than expected by chance. NTI is loosely analogous to the study of species/genus ratios, asking whether species tend to co-occur with very close relatives (Webb 2000).

Advances in phylogenetics, together with the assembly of large trait databases, have also allowed broad tests of the extent to which closely related species tend to be ecologically similar. This pattern is referred to as phylogenetic signal, where a high degree of signal indicates that close relatives exhibit similar trait values. A null model can be used to evaluate the significance of these patterns, by randomizing trait values across the tips of the phylogeny to determine the extent of phylogenetic signal that would occur by chance. In broad-scale studies, especially those spanning large global databases, most ecological traits exhibit moderate to strong patterns of phylogenetic signal. However, this pattern may not be observed in smaller, local communities where the set of co-occurring taxa represents a very few representatives across numerous major clades; in these situations, each species closest relative in a community may not be close at all, on a global scale, so the signal of trait evolution is diluted.

As described above, the concept of habitat filtering suggests that species living together in a community will be more ecologically similar than expected, relative to a broader regional species pool. If traits exhibit significant phylogenetic signal, then ecologically similar species will also tend to be closely related. In this situation, local communities may be composed of closely related species (relative to the null model), with  $NRI > 0$ . Thus, studies that detect positive  $NRI$  values may be used to infer that habitat filtering processes are significant in the assembly of a local community. On the other hand, there are two scenarios that could lead to  $NRI < 0$ , with communities composed of distantly related species. First, habitat filtering may occur, but the traits that influence species habitat distributions may exhibit low signal, possibly due to rapid divergence among close relatives. Thus, ecologically similar species that co-occur would be distant relatives. Alternatively, co-occurring species may be ecologically distinct from each other, reflecting the outcome of biotic interactions or one of the coexistence mechanisms discussed above. If the associated traits exhibit high phylogenetic signal, then again the species co-occurring in communities will be widely dispersed across the phylogeny and more distantly related than expected by chance.

A study of the community assembly of oaks (*Quercus*) in northern Florida illustrates these latter patterns. The communities are strongly structured along soil moisture gradients, from seasonally flooded bottomlands to dry, sandy uplands. As expected, species that live together share traits related to drought tolerance, a case of habitat filtering with respect to these traits. However, these traits exhibit very low phylogenetic signal, with convergent evolution of low, medium, and high soil moisture tolerance across several sub-clades within *Quercus*. As a result, local

communities are composed of distantly related species, and other differences between the sub-clades suggest that they may exhibit trait differences that enhance coexistence within these communities (Fig. 2).

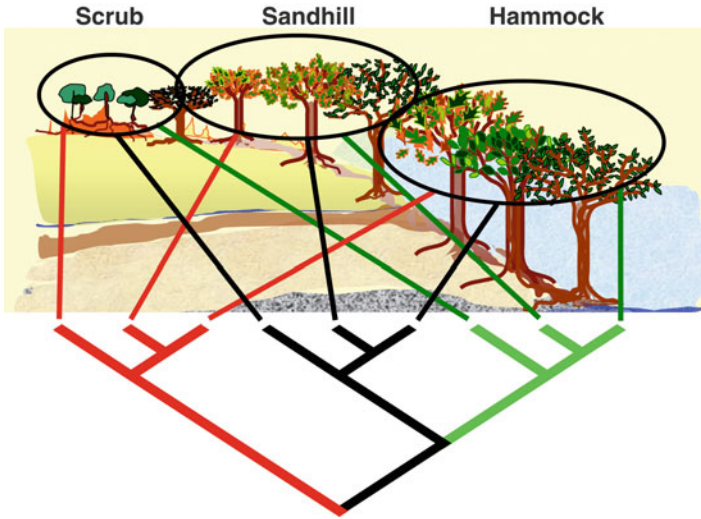
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## **Biogeography and the Build Up of Species Pools**

As we have discussed above, local communities are assembled from a regional pool of available species. Thus, an understanding of the processes that shape the diversity and the functional and phylogenetic composition of regional biota is valuable for a deeper understanding of local communities. How big is the regional species pool? This is a difficult, perhaps impossible, question to answer precisely as the appropriate temporal and spatial scale defining the regional pool will depend on the size of the communities and the dispersal biology and longevity of the organisms under consideration. In many cases, the delineation of the regional pool for the purposes of empirical studies is constrained practically by availability of data, though the growth and refinement of regional and global biodiversity databases (e.g., GBIF, the Global Biodiversity Information Facility) may eventually overcome this obstacle.

The diversity of a regional flora and fauna reflects the interaction of three fundamental processes: arrival of new lineages by dispersal from other regions, speciation within the region, and local extinction of lineages. Dispersal can occur across substantial distances. As described earlier, the colonization of oceanic islands by seeds dispersed by wind or water currents or by animal agents provides direct evidence of the potential for long-distance dispersal. Similar types of long-distance dispersal events occur across and among continents as well, though they are harder to detect. As climates shift and the combination of continental drift and fluctuating sea levels have altered the connections between landmasses, dispersal can also occur as a stepping-stone process with populations migrating along corridors that provide favorable environments for at least short-term establishment and subsequent reproduction. For example, in the Northern Hemisphere, there has been extensive migration between North America and Europe across a North Atlantic land bridge, during the Eocene and possibly into the Oligocene, while more recently Asia and North America have been connected by the Bering land bridge during periods of low sea level.

On evolutionary timescales, speciation is a key process increasing diversity within biogeographic regions. During the speciation process, evolutionary shifts in habitat affiliation and the climatic tolerances of a lineage tend to change slowly. As a result, individual clades will tend to diversify and spread across major climatic zones, and these biotic similarities then come to define distinctive biogeographic regions around the world. Based on phylogenetic and fossil evidence, it is believed that flowering plants originated in tropical regions and diversified extensively during the Cretaceous. Around 55 million years ago during the Eocene, the world was much warmer overall, and tropical forests extended to midlatitudes, far beyond their current distribution. Cooling and drying trends since then have led to the



**Fig. 2** Phylogenetic community structure of oak-dominated communities in Florida, demonstrating phylogenetic overdispersion within each of the three habitat types. Oaks within each of the three major phylogenetic lineages occur in each community, and null model analysis reveals that this pattern is not expected by chance (Redrawn with permission from Cavender-Bares et al. (2004b))

emergence of temperate climates, and many of these ancestral, tropical lineages gave rise to temperate plant groups that spread and diversified as the cooler climate spread at mid- and high latitudes. Many well-known clades in the temperate flora, such as maples and oaks, first appear in the fossil record during this time and then spread around the Northern Hemisphere in the temperate regions of Asia, Europe, and North America. Drying trends that began in the Oligocene led to the emergence of the semiarid and arid floras, including the world's modern deserts and Mediterranean-type climate zones. Diversification and adaptation to arid climates in these areas tends to be very recent, resulting in many distinctive and locally endemic groups. For example, close to half of the native flora of California is endemic to the Mediterranean-climate region west of the Sierra Nevada.

The Miocene and Pliocene also witnessed a profound ecological transition that continues to shape our modern ecosystems and regional floras around the world. During this time, woodland ecosystems gradually transitioned to open grasslands, likely due to drying and then to an increase in the frequency of wildfire. The hot, open conditions, combined with relatively low atmospheric  $\text{CO}_2$ , promoted the evolution and diversification of  $\text{C}_4$  grasses (grasses that utilize a specialized photosynthetic pathway to concentrate  $\text{CO}_2$  at the biochemical site of carbon fixation). Subsequently,  $\text{C}_4$  grasses spread and became the dominant species in subtropical and warm temperate grasslands, though the particular characteristics of species that become ecosystem dominants are not well understood (Edwards et al. 2010). As illustrated by this example, past environmental conditions have a direct

influence on the evolutionary history and adaptive evolution of regional floras around the world. The functional diversity available in the regional species pool reflects the cumulative results of diversification and adaptive evolution, and the footprint of the past is evidence (though sometimes only on close inspection) in the structure and function of modern ecosystems.

The third important process in the development of regional species pools is extinction. Extinction is also the most difficult to document, as evidence must be sought primarily in the fossil record or by indirect inference from biogeographic distributions and phylogenetic relationships. The balance of speciation and extinction can generate very different levels of diversity, even in climatically similar regions. The Northern Hemisphere flora provides important examples, as the forests of East Asia have much higher diversity of tree species than North America, and North America is in turn more diverse than Europe. This pattern is thought to be due in part to higher rates of extinction in Europe and North America during the Ice Ages (the last 500,000 years), as glaciers extended further south in these areas and plants were pushed up against oceanic barriers (e.g., the Mediterranean).

In recent decades, there has been extensive debate over the role of regional versus local processes as influences on diversity and ecology of local communities. The influence of the regional biota is evident when diversity of local communities is correlated with regional diversity, even under similar climatic and environmental conditions. This is observed in north temperate forests, as local diversity (in small areas, e.g., one hectare) is highest in East Asia, intermediate in eastern North America, and lowest in Europe. While the abiotic and biotic filtering processes discussed above may be operating in all of these forests, the resulting diversity of local communities is still higher when there are more species in the regional pool contributing to the assembly process. This suggests that communities may be structured by factors such as niche differentiation, but may not be ecologically saturated in the sense of reaching a maximum limit on diversity that is set by local ecological factors.

Patterns of ecological and functional diversity in local communities also bear the footprint of evolutionary history. The adaptation of lineages to climatic conditions experienced during their evolutionary history is an important example of “niche conservatism”, a general term for the observation that related species often maintain ecological similarities over very long periods of time. Many examples are now known where diversity and distributions at local and landscape scales reflect niche conservatism of the constituent lineages. For example, in California plants derived from northern lineages are most diverse in cooler and moister parts of the state and are also more common on cool, north-facing slopes or riparian zones of a local landscape. Plants derived from semiarid and subtropical lineages, in contrast, have primarily diversified in the drier, Mediterranean-climate zones of California and are the primary contributors to the drought-adapted chaparral (i.e., evergreen shrubland) vegetation. However, like many patterns in ecology and evolution, there is no one rule that covers all situations. The oak example discussed above illustrates how several clades within a genus can exhibit convergent evolution in habitat



tolerances, so close relatives spread out across the landscape and occupy different habitats. Improved knowledge of phylogenetic history, the fossil record, and the climatic history of different regions of the world will continue to shed light on these fundamental questions in the evolution of regional floras and their influence on the assembly of local communities.

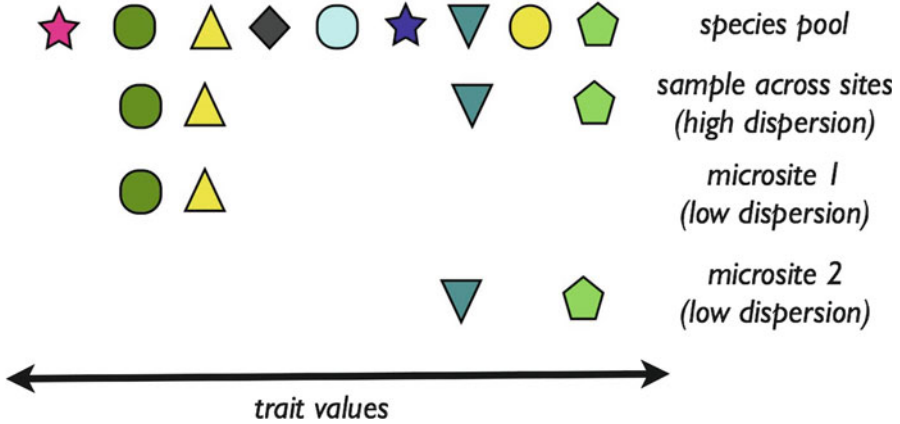
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## Scale Dependence

Community assembly studies typically focus on comparing the members of a focal community to a regional pool of potential colonists. While this step might seem clear in theory, in practice the definition of an appropriate boundary for a community and a species pool is fraught with uncertainty. It is often best to simply acknowledge that there will be several possible ways in which to delineate the community and the species pool and that each combination may reflect the action of different assembly processes. For example, a species pool could be defined as any species in the vicinity of the focal community that might be able, based on known dispersal distances, to disperse a seed into the community within 1 year or one generation of the focal species. A broader-scale analysis might consider the species pool to be any species in the region, even if it would likely take longer than one generation for some species in the pool to disperse into the local community. It is essential to include an understanding then of how the pool and community were defined when drawing conclusions based on community assembly analyses – an analysis based on a narrowly defined species pool might only be appropriate for making inferences about short-term ecological processes, whereas an analysis based on more broadly defined pool could reflect the action of processes acting over multiple generations.

With this scale dependence in mind, there are a number of cases where a single ecological process is predicted to produce contrasting patterns depending on the scale of analysis. For example, a narrowly defined community sample at a small spatial scale that only contains a single habitat type might readily demonstrate phenotypic clustering or other patterns consistent with habitat filtering when compared to a broader species pool that contains multiple habitat types. But if the community sample is broadened to include two or more habitat types in the same sample, it is conceivable that new, larger-scale analysis will reveal overdispersion, reflecting the aggregation of two or more distinct phenotypic clusters of species that are different from each other (Fig. 3). In this case, a single ecological phenomenon – environmental filtering – will produce different phenotypic dispersion patterns depending on the scale of analysis.

In summary, it is essential for researchers to be cognizant of the criteria that are used to delineate a community and a species pool in a community assembly analysis and also to recognize that any inferences from the analysis will be conditioned on those criteria, as patterns will likely shift as the scope of the pool and community is altered. When possible, explicitly varying the scope of the pool and the sample can be used to detect the action of processes operating at different spatial scales.



**Fig. 3** A single community assembly process (habitat filtering into specific microsites) can produce contrasting phenotypic patterns depending on the scale of analysis. If a microsite is compared to the species pool, either microsite will show low dispersion (phenotypic clustering). However, if a large spatial scale is used to define the community that includes both microsites, this new larger community sample across sites may reveal higher phenotypic dispersion than expected when compared to the species pool

## Future Directions

The study of community assembly theory has seen considerable development since it was pioneered in the middle of the twentieth century. However, considerable challenges remain, and here we highlight three essential areas where additional work is needed, including better methods to distinguish between multiple processes in producing community patterns, a more complete incorporation of coexistence theory into community assembly studies, and better consideration of multitrophic interactions.

## Pattern-to-Process Mapping

Early work in community assembly focused on phenotypic convergence driven by abiotic filters and phenotypic disparity driven by competitive exclusion. However, it has become increasingly apparent that many community assembly processes can produce similar patterns. For example, high phenotypic similarity of species within a community can be produced by habitat filtering, in situ speciation, or pollinator facilitation (Emerson and Gillespie 2008; Sargent and Ackerly 2008), among other processes (Cavender-Bares et al. 2009). In some cases, additional information such as the timescale of the analyses (which is implicit in the spatial and temporal criteria used to define the species pool and the community) or the pollination syndromes of the species in the community can be used to distinguish between potential mechanisms, but in other cases, definitive links between process and pattern can be

challenging. In some cases, approaches that go beyond simple comparisons of a community list to the species pool will be needed. Analyses that focus on variation in performance of individuals over time appear to be particularly promising in this area (Uriarte et al. 2010).

## Coexistence Theory and Community Assembly

Despite a long history of considering the role competition in community assembly, many of the predictions commonly tested in community assembly fail to fully reflect recent developments in coexistence theory. In particular, the recognition that phenotypic similarity can both increase the chances of competitive exclusion (if traits reflect niche differences) and decrease the chances of competitive exclusion (if traits reflect average fitness differences) has only recently been recognized in the context of community assembly (Mayfield and Levine 2010; HilleRisLambers et al. 2012). Progress in this area will depend first and foremost on a better understanding of the extent to which niche and relative fitness differences are correlated with components of the plant phenotype, as the assumption has long been that functional traits primarily capture niche differences. The data needed to properly quantify niche and fitness differences typically require more detailed measurements than most community assembly studies to date (Levine and HilleRisLambers 2009; Adler et al. 2010), and therefore new approaches will be needed to bring a consideration of these phenomena into community assembly analyses.

## Methods for Multitrophic Interactions

Most community assembly analyses focus within a trophic level, and most plant-focused studies do not explicitly consider other trophic levels except as those interactions play out implicitly among plants (e.g., Sargent and Ackerly 2008). However, given the ubiquity of trophic interactions in shaping community patterns, community assembly will not be able fully consider the multitude of ecological interactions shaping local communities until it is able to explicitly incorporate trophic interactions into analyses. Given the rapid pace of development of network theory in recent years, it may be that a robust solution to this issue will emerge from an integration of these two approaches.

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