Rethinking Community Assembly through the Lens of Coexistence Theory

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biotic filters, clustering, environmental filters, relative fitness differences, stabilizing niche differences, overdispersion

Abstract

Although research on the role of competitive interactions during community assembly began decades ago, a recent revival of interest has led to new discoveries and research opportunities. Using contemporary coexistence theory that emphasizes stabilizing niche differences and relative fitness differences, we evaluate three empirical approaches for studying community assembly. We show that experimental manipulations of the abiotic or biotic environment, assessments of trait-phylogeny-environment relationships, and investigations of frequency-dependent population growth all suggest strong influences of stabilizing niche differences and fitness differences on the outcome of plant community assembly. Nonetheless, due to the limitations of these approaches applied in isolation, we still have a poor understanding of which niche axes and which traits determine the outcome of competition and community structure. Combining current approaches represents our best chance of achieving this goal, which is fundamental to conceptual ecology and to the management of plant communities under global change.

1. INTRODUCTION

What drives the assembly of communities? By community assembly, we mean the process by which species from a regional pool colonize and interact to form local communities. Though there is still extensive debate about the details of community assembly, processes operating at a diverse range of spatiotemporal scales are thought to be important (**Figure 1**). For example, environmental drivers generate large-scale biogeographic patterns in diversity (Wiens & Donoghue 2004), whereas competitive interactions occurring in a small neighborhood contribute to local coexistence (Chesson 2000). The composition of local communities is constrained by the evolutionary history of the regional species pool (Ricklefs 2004), but also influenced on short timescales by demographic stochasticity (Tilman 2004). In short, the study of community assembly unites disciplines as diverse as evolutionary biology, biogeography, and community ecology.

Community assembly has not always been so broadly defined. From the 1970s through the 1980s, studies on community assembly primarily asked whether competitive interactions between species generated predictable patterns of species co-occurrence in communities (i.e., assembly

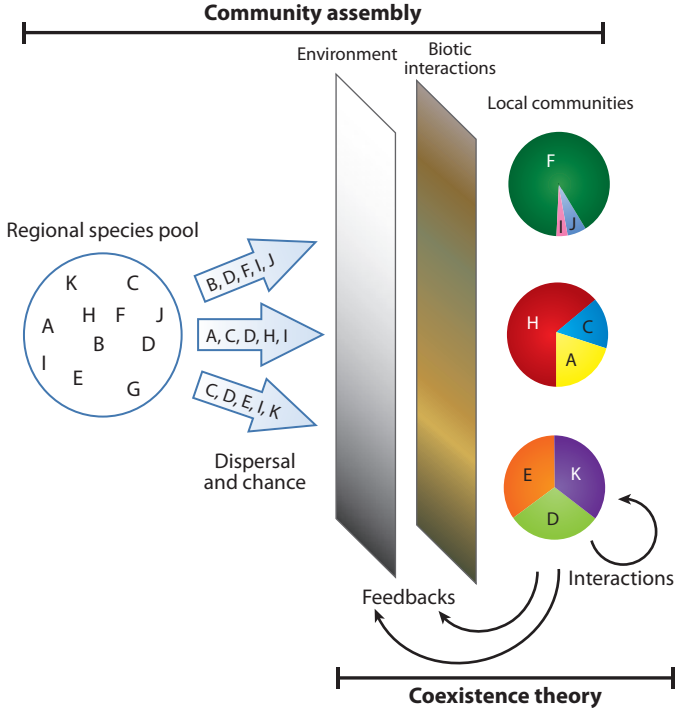

Figure 1

Community assembly is influenced by processes operating at a wide range of spatiotemporal scales. Species belong to a regional species pool that is constrained by historical processes (including evolution). A subset of the regional species pool (influenced by chance and dispersal limitation) is available for colonization of a particular site. The most common modern metaphor of community assembly then describes this subpool of species passing through an environmental (abiotic) filter and a biotic filter (e.g., Belyea & Lancaster 1999, Chase 2003, Götzenberger et al. 2012). Local communities are thus assumed to reflect the cumulative effects of these processes. In this review, we argue that contemporary coexistence theory, by highlighting the role of relative fitness differences and stabilizing niche differences, provides a more nuanced perspective on the role interactions between species and their environment (both abiotic and biotic) play during community assembly.

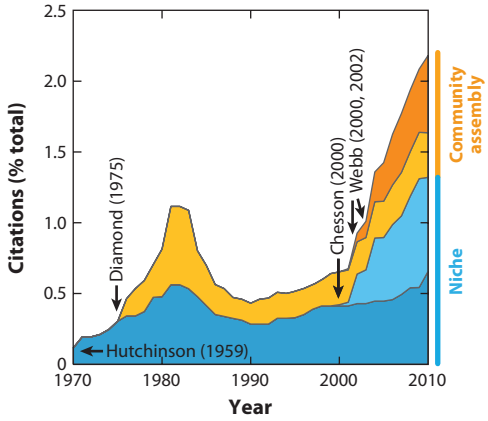

Figure 2

Relative interest in community assembly and the niche over the past 50 years, as reflected by the citation histories of influential articles about the niche (Hutchinson 1959, Chesson 2000) and community assembly (Diamond 1975, Webb 2000, Webb et al. 2002); their publication dates are indicated by the black arrows. Citation effort was standardized by the total number of articles published by journals in which these citations were published. We do not plot the overlaps because there are few (<5% of articles published since 1975 that cite Hutchinson and/or Chesson also cite Diamond and/or Webb).

rules; Diamond 1975, Weiher et al. 2011). The resurgence of interest in community assembly in the past decade, and arrival of a broader perspective, was fostered by two important developments (**Figure 2**). First, ecologists began integrating newly available phylogenetic data with community data, introducing an evolutionary perspective to community assembly (Webb 2000, Webb et al. 2002, Cavender-Bares et al. 2004a). Second, Hubbell's unified neutral theory, which explains high diversity with slow stochastic drift when species are equivalent in their competitive ability (i.e., are neutral), reinvigorated debate that the processes influencing diversity include both local and short-term mechanisms as well as regional processes occurring over longer timescales (Sale 1977, Hubbell 2001).

Recent theoretical advances in coexistence theory suggest, however, that there is still much to learn about how competitive interactions at a local scale influence community assembly (Chesson 2000) (**Figure 1**). In this review, we therefore do not focus on forces operating over longer temporal or larger spatial scales, like speciation or historical constraints to regional species pools, which are covered by other studies and reviews (e.g., Emerson & Gillespie 2008, Pavoine & Bonsall 2011), nor do we address how demographic drift or dispersal influences local communities. We do not mean to imply that these processes do not influence community assembly, but simply that they operate in addition to, not instead of, the environmental factors and biotic interactions that influence the composition and structure of communities at local scales. Contemporary coexistence theory can help link evidence from different empirical approaches, and in some cases refines our understanding of their central assumptions (Mayfield & Levine 2010). Our goal with this review is therefore to explore empirical studies relevant to community assembly through the lens of contemporary coexistence theory, and by doing so, identify important ways forward. We do so in three steps:

1. We redefine community assembly from the perspective of contemporary coexistence theory, distinguishing between stabilizing niche differences and relative fitness differences (Chesson 2000). (For expanded definitions of these terms, see sidebar, Coexistence Theory Terms Relevant to Community Assembly.)

2. Using this framework, we review studies that come from three empirical approaches: (*a*) experimental manipulations of niche differences and/or fitness differences; (*b*) quantification of relationships between community composition, traits and/or phylogenetic relatedness, and the environment; and (*c*) quantification or manipulation of frequency-dependent population growth (the signature of niche differences; see sidebar, Coexistence Theory Terms Relevant to Community Assembly).
3. Finally, we describe future directions that take advantage of developments in coexistence theory as well as the complementary strengths of the three approaches described to better understand the forces driving community assembly at local scales.

2. CONTEMPORARY COEXISTENCE THEORY AND COMMUNITY ASSEMBLY

Although the often-used metaphor of independent environmental and biotic filters is intuitively appealing (**Figure 1**), the role of the niche in determining community membership is more

COEXISTENCE THEORY TERMS RELEVANT TO COMMUNITY ASSEMBLY

- *Frequency-dependent population growth rates* occur when the per capita population growth of a species is determined by its frequency (relative abundance) within the community. Negative frequency-dependent population growth rates are the hallmark of stabilizing niche differences and arise when a focal species suppresses itself more than it does the resident species with which it competes, which can serve to "stabilize" coexistence (see definition of stable coexistence below). Negative frequency-dependent population growth can thus be used to assess whether community composition during community assembly is stabilized by niche differences. Frequency-dependent population growth rates can be measured directly by following population sizes of co-occurring species over time (Clark & McLachlan 2003) or from population dynamic models parameterized with field-based vital rates (e.g., germination, seed production) in communities where focal species differ in their frequency (Adler et al. 2006, Levine & HilleRisLambers 2009).
- *Stabilizing niche differences* are those differences that cause species to more strongly limit themselves than others through, for example, resource partitioning, host-specific natural enemies, or storage effects. When these stabilizing niche differences are greater than relative fitness differences, they foster diversity during community assembly by preventing competitive exclusion of inferior competitors by superior competitors. Stabilizing niche differences are challenging to quantify because they depend on all the interactions unique to the environment and the species composition of the community. However, they can be derived from phenomenological population dynamic models parameterized with field-based vital rates and interaction coefficients (Adler et al. 2010).
- *Relative fitness differences* are those differences between species that predict the outcome of competition in the absence of stabilizing niche differences. They have also been called fitness inequalities (Chesson 2000, Adler et al. 2007). Note that fitness is used in an ecological, not evolutionary, context—species are the unit of comparison for fitness differences in coexistence theory, not individuals (as in evolutionary studies). As with stabilizing niche differences, these fitness differences can arise through many mechanisms, including environmentally mediated differences in fecundity or differences in the ability to take up limiting resources and/or tolerate herbivores. Relative fitness differences influence the relative abundance of species (i.e., species composition) during community assembly. Similar to stabilizing niche differences, relative fitness differences depend on the specific environmental conditions and species composition unique to the community. They can be quantified by parameterizing population dynamic models with field-based estimates of vital rates (see Adler et al. 2007, 2010; Levine & HilleRisLambers 2009). Practically, relative fitness differences are difficult to disentangle from stabilizing niche differences.

- *Competitive exclusion* occurs when the presence of one competitor causes population growth rates of another to go from positive to negative, thus driving the extinction of the competitively inferior species. This occurs when stabilizing niche differences are smaller than is needed to overcome relative fitness differences. Competitive exclusion is often represented by the "biotic filter" (or the Hutchinsonian realized niche) in community assembly studies. Competitive exclusion may be observed following an experimental manipulation (by measuring population sizes of co-occurring species; e.g. Suding et al. 2005, Suttle et al. 2007) or can be inferred as having occurred by comparing trait distributions and phylogenetic relatedness in communities (e.g., Slingsby & Verboom 2006, Cornwell & Ackerly 2009).
- *Stable coexistence* refers to a community of species that stably co-occur within communities over long periods of time, with members of the community buffered from extinction. This occurs when stabilizing niche differences of species are greater than their relative fitness differences. Because stabilizing niche differences and relative fitness differences depend on both the environmental conditions and biotic interactions unique to that community, stable coexistence is sensitive to any perturbation of the environment and species composition of communities.

complicated and dynamic. For one, the niche of a species includes both its response to and impact on the abiotic and biotic environment (as emphasized by Hutchinson and Elton, respectively; Hutchinson 1957, Chase & Leibold 2003). Thus, while an environmental filter may reasonably describe how abiotic factors like climate prevent species without certain physiological traits from occurring in local communities (e.g., species without frost tolerance may not occur in alpine communities), it does not adequately describe the dynamic response to or impact of plant species on limiting resources and consumers (Tilman 1982). Second, species interactions with co-occurring competitors, consumers, mutualists, and natural enemies (the biotic environment) will not only depend on the environment, but can feed back to influence the environment (Tilman 1982). Our understanding of how these feedbacks influence the outcome of species interactions has greatly benefited from recent advances in coexistence theory (Chesson 2000).

Contemporary theory emphasizes that coexistence depends on both niche differences and fitness differences (see sidebar, Coexistence Theory Terms Relevant to Community Assembly). That niche differences are essential for long-term coexistence has long been recognized. After all, the competitive exclusion principle (see sidebar, Coexistence Theory Terms Relevant to Community Assembly), which states that no two species with the same niche can stably coexist, was first formulated by Gause in the 1930s (Gause 1934). In contemporary coexistence theory, the niche differences that underlie stable coexistence are termed stabilizing niche differences because they cause species to have higher population growth rates when the species is rare than when common, buffering them from extinction (see sidebar, Coexistence Theory Terms Relevant to Community Assembly) (Chesson 2000, Adler et al. 2007). The niche differences (and species' traits) driving this frequency-dependent population growth can arise from differences among species in their effect on and response to limiting factors like shared resources, consumers, and mutualists. These stabilizing niche differences can be extracted from mechanistic coexistence models, including those involving resource partitioning, storage effects, and density-dependent natural enemies (**Figure 3**) (Chesson 2000, Chase & Leibold 2003).

Coexistence theory illustrates, however, that not all differences between species are stabilizing niche differences. Rather, some differences drive competitive dominance and are termed relative fitness differences, as in Chesson's framework (see sidebar, Coexistence Theory Terms Relevant to Community Assembly) (Chesson 2000). For example, consider two plant species, both with growth limited by the same resources, but one has lower minimum requirements for those resources

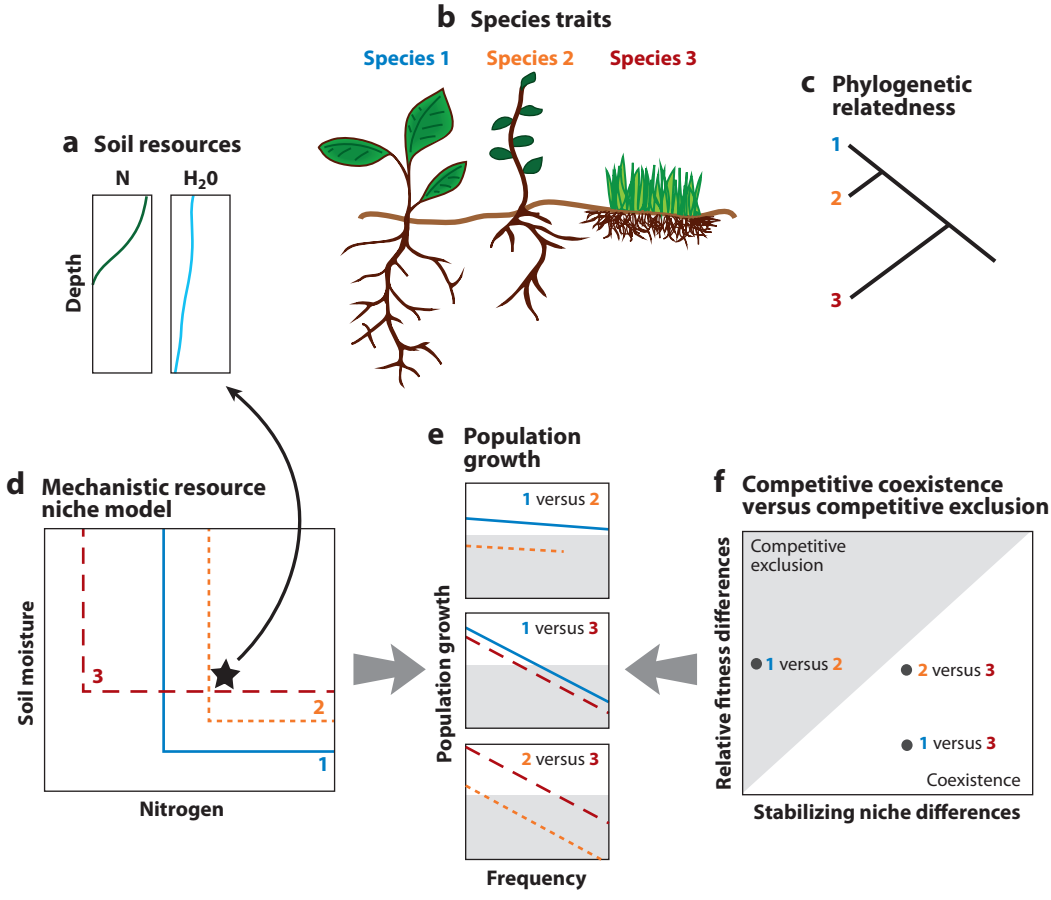

Figure 3

Relationship between the environment (*a*), species traits (*b*), phylogenetic relatedness (*c*), resource uptake (*d*), population growth rates (*e*), and coexistence (*f*). Species 1 is the superior competitor for water because its deeper roots (*b*) can access pools of soil water not available to species 2 and 3 (*a*). Species 3 is the superior competitor for nitrogen because it has greater root density at shallow soils (*b*), where nitrogen concentrations are high (*a*). Species 1 is closely related to species 2 (*c*), and therefore also more similar in rooting traits (*b*). In a mechanistic resource niche model, species 1 and 2 are similar in their resource uptake for the two resources, and differ from species 3 [in *d*, *lines* indicate the lowest levels at which each species can survive; see Tilman (1982), Chase & Leibold (2003)]. Species 1 and 3 or 2 and 3 can coexist at resource supply rates indicated by the star, but species 1 competitively excludes 2 because their resource uptake patterns are too similar (*d*). This is reflected in frequency-dependent population growth rates of each species pair (in *e*, *gray* represents population growth rates below zero), and the balance between stabilizing niche differences and the magnitude of fitness differences (in *f*, *gray* indicates competitive exclusion of one member of the species pair; *white* indicates coexistence; see Adler et al. (2007)].

(**Figure 3**). In theoretical terms, these species differ in their R^* for those resources (Tilman 1982, Chase & Leibold 2003), and one species will competitively exclude the other. Such relative fitness differences are what stabilizing niche differences must overcome to generate coexistence (Chesson 2000), and they can arise from some of the same traits and limiting factors that drive stabilizing niche differences (**Figure 3**).

The main message of Chesson's framework is that stabilizing niche differences facilitate coexistence, whereas relative fitness differences drive competitive exclusion (**Figure 3**) (see sidebar, Coexistence Theory Terms Relevant to Community Assembly). But how is this relevant

to community assembly? First, competitive exclusion can either preferentially eliminate taxa that are too functionally similar when trait differences function as stabilizing niche differences or preferentially eliminate all taxa that do not possess the near optimal trait when such trait differences translate into fitness differences. Second, both stabilizing niche differences and relative fitness differences are influenced by abiotic and biotic factors. For both reasons, patterns of trait dissimilarity or similarity cannot easily be used to infer the relative importance of environmental versus biotic (competitive) filters, which is an important goal of community assembly studies (**Figure 1**). Third, frequency-dependent population growth rates are the signature of all stabilizing niche differences (Adler et al. 2007) and can thus be used to infer niche differences, but frequency-dependence alone cannot identify the mechanisms allowing for stable coexistence, which is another central goal of community assembly studies. Armed with these insights from contemporary coexistence theory, we next review three empirical approaches to understanding the role of competitive interactions and niches during community assembly.

3. A REVIEW OF EMPIRICAL APPROACHES

The literature exploring how species differences relate to the outcome of competitive interactions is enormous; for this reason, we do not review all empirical approaches used to test the niche concept or its various definitions. Instead, we focus on three approaches that provide relevant and contemporary (but not always complete) insights into our understanding of the interplay between stabilizing niche and relative fitness differences during community assembly. First, we review experimental manipulations of stabilizing niche differences and relative fitness differences, studies designed to directly test specific coexistence mechanisms (e.g., Turnbull et al. 1999). Second, we review studies relating trait and phylogenetic distributions within communities to the environment; these are the studies that are driving the recent resurgence of interest in community assembly (**Figure 2**) (Webb et al. 2002, Ackerly & Cornwell 2007). Finally we review studies that derive stabilizing niche differences and relative fitness differences from demographic data, studies that were directly inspired by recent breakthroughs in coexistence theory (Chesson 2000, Adler et al. 2007). Although community assembly processes are clearly relevant to all organisms, we primarily review literature associated with plant communities because this reflects our expertise and the predominant focus of recent studies. However, we emphasize that the conceptual topics reviewed here are relevant to all communities of interacting and competing organisms (e.g., Helmus et al. 2007, Horner-Devine et al. 2007, Chase 2010, Fukami et al. 2010).

3.1. Experimental Manipulations

To understand how community assembly is regulated by stabilizing niche differences and relative fitness differences, one can experimentally manipulate the environmental and biotic factors that control these forces (e.g., through nitrogen addition, herbivore removal, or competitor removal). On the plus side, such experimental manipulations can provide strong evidence that specific environmental factors or biotic interactions are critical for community assembly. However, a major challenge is the sheer amount of information needed to rigorously relate the results of such treatments to coexistence theory. For example, relating the impacts of nitrogen addition to predictions from a mechanistic resource niche model requires information on the differential abilities of species to compete for nitrogen and an understanding of what drives stabilizing niche differences (in a simple two-resource model, for example, the identity of the other limiting resource and the tradeoffs involved). Perhaps this explains why, despite the large number of experiments manipulating niche axes or competitive interactions within plant communities, surprisingly few explicitly test coexistence theory (Siepielski & McPeek 2010).

Virtually every experiment in the history of community ecology manipulates relative fitness and stabilizing niche differences whether the investigators intend to or not. We thus narrow our review to those studies intentionally aiming to manipulate these determinants of coexistence. We highlight the following three types of studies: those that manipulate factors thought to control relative fitness differences (see Section 3.1.1), those that reduce stabilizing niche differences (see Section 3.1.2), and those that manipulate aspects of community assembly (see Section 3.1.3). We identify the circumstances under which each type of experiment can be linked to specific coexistence mechanisms and, thus, highlight the relative importance of fitness differences and stabilizing niche differences for community assembly.

3.1.1. Experimental manipulations of relative fitness differences. Direct manipulation of limiting factors can reveal their role in generating relative fitness differences among co-occurring species. For example, resource competition models predict that the composition of plant communities limited by two resources depends on the relationship between resource uptake and the supply rate of those resources (**Figure 3**). If so, an increase in the supply rate of one of those resources should predictably lead to an increase in the abundance of the species that is most limited by that resource (Wedin & Tilman 1993). Similarly, community responses to experimental manipulations of rainfall (Suttle et al. 2007), consumers (HilleRisLambers et al. 2010), and pathogens (Allan et al. 2010) can provide information on the factors driving relative fitness differences and the species traits that underlie them.

For example, nitrogen (N) is the resource most often manipulated in terrestrial resource addition experiments because it often limits productivity, and the impacts of N deposition on ecosystem and community dynamics are of major concern in many ecosystems (Suding et al. 2005 and references therein; Clark et al. 2007 and references therein). N addition experiments generally lead to changes in species composition that are broadly consistent with predictions from resource competition theory. For example, N-fixing forbs and C4 grasses (considered good N competitors) generally decreased in abundance with N addition, whereas C3 grasses (less competitive for N) increased in abundance (Suding et al. 2005). A recent study provides even stronger mechanistic links: It demonstrates that changes in abundance following N addition are predictable from species-specific indices of competitive ability for N (R^* for N), with good competitors for N losing ground to species that are worse competitors for this limiting resource (Harpole & Tilman 2006).

However, these experiments also illustrate the complexity of experiments aiming to manipulate relative fitness differences. N addition is often accompanied by diversity loss, suggesting that the magnitude of stabilizing niche differences is also influenced by the addition of N (Clark et al. 2007). The mechanism for this is uncertain; one hypothesis holds that nutrient addition shifts the limiting resource to light, a resource for which relative fitness differences are more asymmetric (Hautier et al. 2009). Consistent with this hypothesis, Hautier et al. (2009) found that the addition of light reversed the decline in species diversity seen with fertilization alone. However, N addition can also reduce resource heterogeneity (Harpole & Tilman 2007), potentially affecting stabilizing niche differences and, thus, influencing diversity. In all, these results suggest that the traits that influence relative fitness differences can also influence stabilizing niche differences (e.g., resource uptake), complicating inference.

3.1.2. Experimental reductions in stabilizing niche differences. A number of experimental studies aim to manipulate stabilizing niche differences by removing the environmental or biotic variables that provide species with their competitive advantages when rare. These manipulations can therefore take a wide range of forms, depending on the factors underlying stabilizing niche differences. For example, Turnbull et al. (1999) tested whether a competition-colonization

trade-off maintained plant diversity in limestone grassland in England by experimentally eliminating colonization limitation. They found that even when seeds of large-seeded species were added in high numbers, high diversity remained, suggesting that the competition-colonization trade-off was not necessary for coexistence (Turnbull et al. 1999). By contrast, Dornbush & Wilsey (2010) reduced soil depth in an effort to eliminate resource partitioning and did find a decrease in species richness, suggesting impacts on stabilizing niche differences. Similarly, Carson & Root (2000) and Allan et al. (2010) excluded insects and foliar fungi from plant communities to remove the frequency-dependent advantage host-specific natural enemies might provide, and they also found reductions in plant diversity.

Just as with experimental studies aiming to manipulate relative fitness differences (see Section 3.1.1 above), a complicating factor is that it is almost impossible to manipulate a stabilizing niche difference without also affecting relative fitness differences. For example, the loss of diversity following the addition of multiple limiting resources to grasslands can result from the increased fitness differences that accompany competition for light (Dybzinski & Tilman 2007, Hautier et al. 2009), the reduction in the number of limiting resources (i.e., niche dimension; Harpole & Tilman 2007), or the removal of spatial heterogeneity in the limiting resources (a source of stabilizing niche differences; Tilman 1982). Similarly, forcing plants into a shallow rooting zone may eliminate niche differences, but will also alter the competitive balance between species by favoring shallow-rooted species (Dornbush & Wilsey 2010). Finally, eliminating natural enemies (Carson & Root 2000, Allan et al. 2010) may reduce the stabilizing effects of host-specific natural enemies, but will also alter frequency-independent performance of co-occurring species. It can therefore be difficult to distinguish which effect dominates using experimental manipulations of limiting factors alone.

3.1.3. Invasion/assembly experiments. A complementary approach to perturbing stabilizing niche differences or relative fitness differences is to experimentally manipulate the community assembly process itself. For example, several studies have documented a negative relationship between the relative abundance of a functional group in established communities and the probability that a new member of that functional group can invade (Fargione et al. 2003, Mwangi et al. 2007, Roscher et al. 2009, Hooper & Dukes 2010, Petermann et al. 2010). Specifically, Fargione et al. (2003) and Hooper & Dukes (2010) showed that invasion success was greatest when phenological differences between the invader and resident species were maximized. These results suggest that competitive interactions are more intense with other members of the same functional group, which is consistent with functional group differences translating into stabilizing niche differences (e.g., Burns & Strauss 2011). Other studies have documented a negative relationship between the functional diversity of resident species and invasibility (Levine 2000, Kennedy et al. 2002, Fargione et al. 2003). These experiments support the idea that more diverse systems should leave less vacant niche space for colonization, which also supports a role for stabilizing niche differences. Finally, the convergence in functional composition of experimentally assembled communities, despite dissimilar initial compositional starting points, suggests that strong relative fitness differences, rather than stochasticity, drive community composition toward species with similar functional traits (Seabloom et al. 2003, Fukami et al. 2005, but see Koerner et al. 2008). In all, invasion and experimental assembly experiments can provide strong but indirect evidence of stabilizing niche differences and relative fitness differences.

3.2. Trait-Phylogeny-Environment Relationships

A second approach to studying community assembly is to relate observed patterns of species presence/absence or abundance in communities to null expectations. Most of these approaches

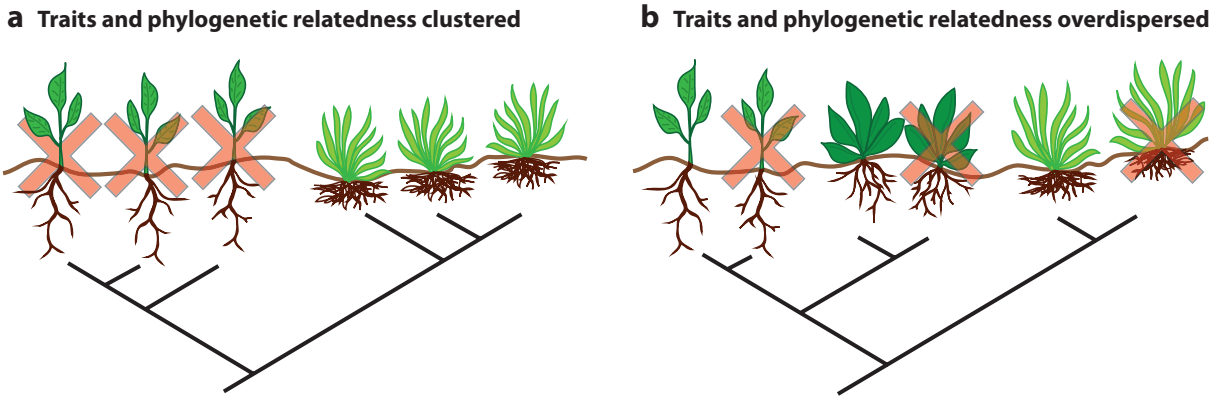

Figure 4

An example of (*a*) trait (and phylogenetic) clustering and (*b*) overdispersion, where species excluded from local sites (but present in the regional species pool) are marked by a red X. In panel *a*, closely related species with high root densities co-occur in communities, leading to trait and phylogenetic clustering, whereas in panel *b*, species competitively exclude closely related species with similar traits, leading to trait and phylogenetic overdispersion (see Mayfield & Levine, 2010).

are descendants of Diamond's assembly rules and earlier studies that used genus-to-species ratios in communities to test the competition relatedness hypothesis (**Figure 2**) (Diamond 1975, Webb 2000, Cavender-Bares et al. 2004b, Ackerly & Cornwell 2007). In the past decade, these approaches have been expanded in two important ways. First, the development of statistical methods to compare trait distributions within and between communities has increased our understanding of how traits are distributed among interacting species at various spatial scales (Ackerly & Cornwell 2007); and second, the insight that phylogenetic relatedness can be used as a proxy for trait similarity has expanded our ability to understand these interactions, even in the absence of trait data (Webb 2000, Webb et al. 2002, Cavender-Bares et al. 2004a). Contemporary studies using these approaches now relate trait distributions (see Section 3.2.1), sometimes with phylogenetic information (see Section 3.2.2) to null expectations to determine the overall importance of environmental factors and biotic filters for community assembly (**Figure 1**). Studies that incorporate trait, phylogenetic, and environmental data can further identify links between function and process (Mayfield et al. 2009, Pavoine et al. 2011).

There are clear advantages to trait- and/or phylogeny-based studies. First, community composition reflects the cumulative effects of stabilizing niche differences and relative fitness differences (as well as long-term evolutionary processes not considered here), as mediated by the environment and species interactions, during community assembly (**Figure 1**). Second, temporal replication or logistically difficult treatments are not required, and community composition data, trait data, and phylogenetic data are already available for many plant communities (e.g., Rees et al. 2001, Kattge et al. 2011). However, there are also disadvantages to these approaches. Contemporary coexistence theory demonstrates that large fitness differences and competitive exclusion can lead to trait clustering (**Figure 4**) (Mayfield & Levine 2010), calling into question the assumption that trait (or phylogenetic) clustering is solely the outcome of environmental filters. The interpretation of phylogenetic overdispersion as reflecting limiting similarity is also complicated because this pattern may reflect a lack of stabilizing niche differences between closely related species (if traits are conserved) or environmental filtering of species with similar traits (if traits are convergent; Cavender-Bares et al. 2004b, 2009). Finally, phylogenetic or trait distribution patterns that do not deviate from null expectations are difficult to interpret as these could reflect a combination or

cancelling out of environmental filters, relative fitness differences, or stabilizing niche differences (Mayfield et al. 2005). Despite these disadvantages, advanced statistical techniques are continually improving our ability to infer processes from patterns (Pillar & Duarte 2010, Chase & Myers 2011, Ives & Helmus 2011, Pavoine et al. 2011).

3.2.1. Distributions of traits among and within communities. Many studies incorporating environmental data into their analyses find evidence of trait clustering (underdispersion), suggesting that local environments can exclude species without the necessary physiological trait values (**Table 1**) (Cavender-Bares et al. 2004a, Kraft et al. 2008, Cornwell & Ackerly 2009, Swenson & Enquist 2009, Kluge & Kessler 2011). For example, oak species with fire-resistant traits (thick bark, resprouting) occurred in fire-prone scrub and sandhill communities, whereas species with lower specific leaf area (SLA) and smaller leaves (correlated with drought tolerance) occurred on dry ridgetops in Amazonian forests (Cavender-Bares et al. 2004b, Kraft et al. 2008). In cases like these, where there is a clear relationship between an environmental gradient and traits, concluding that an environmental filter is important for assembly is reasonable. However, in the absence of such clear and measured environment/trait relationships, distinguishing environmental filters from competitive differences (i.e., large relative fitness differences) can be difficult (**Figure 4**). For example, are species with high requirements for N absent from infertile soils—assuming no dispersal limitation—because they cannot tolerate such low resource conditions or because they have been competitively excluded? Either scenario could lead to communities with species that have narrower trait distributions than expected (e.g., in rooting depth).

Trait-based studies have found evidence of overdispersion or limiting similarity that can be linked to stabilizing niche differences (**Table 1**). For example, several studies have found that seed size is overdispersed within local communities (Kraft et al. 2008, Cornwell & Ackerly 2009, Swenson & Enquist 2009), a finding consistent with the operation of competition-colonization trade-offs (Tilman 1994). Kursar et al. (2009) found that *Inga* species co-occurring within local communities differed more than expected in their defensive chemistry, suggesting that specialized herbivores may contribute to stabilizing niche differences between *Inga* species (Kursar et al. 2009). In other cases, trait overdispersion is more difficult to interpret. In part, this is because specific coexistence mechanisms are difficult to infer from trait differences assumed to reflect stabilizing niche differences. For example, SLA values in central Californian plant communities were more evenly spaced than expected (Cornwell & Ackerly 2009), potentially reflecting competitive interactions between species with similar SLA values. However, because SLA can reflect differences among species in water use efficiency, competitive abilities for N (Suding et al. 2005, Angert et al. 2009), or phenotypic plasticity, the exact mechanism responsible is difficult to determine.

3.2.2. Phylogenetic approaches. Traditionally, phylogenetic clustering and overdispersion are interpreted as manifestations of environmental and biotic filters, respectively, with phylogenetic relatedness assumed to be a proxy for trait and niche similarity (**Figure 4**) (Webb 2000). With contemporary coexistence theory, we can reinterpret these patterns as reflecting relative fitness differences or environmental filters in the case of phylogenetic clustering (underdispersion), and stabilizing niche differences in the case of phylogenetic overdispersion (Mayfield & Levine 2010). Critically, interpretations of these phylogenetic patterns rest on the assumption that niches are conserved (Cavender-Bares et al. 2009).

Just as in purely trait-based studies, phylogenetic studies provide evidence of both clustering (Webb 2000, Cavender-Bares et al. 2004a, Kembel & Hubbell 2006, Kraft & Ackerly 2010, Anderson et al. 2011, Fine & Kembel 2011) and overdispersion (Kembel & Hubbell 2006, Slingsby & Verboom 2006, Swenson et al. 2007, Letcher 2010, Anderson et al. 2011). Studies that combine

Table 1 Examples of studies documenting trait and/or phylogenetic "overdispersion" and "underdispersion" (clustering) in plant communities

Type of study	Habitat	Dispersion (o, over; u, under)	Source
Traits	California grasslands[a]	o, u	Ackerly & Cornwell 2007, Cornwell & Ackerly 2009
	Spanish pastures[a]	o, u	de Bello et al. 2009
	Amazonian palms	u	Anderson et al. 2011
	North American trees	u	Swenson & Weiser 2010
	Australian subtropical forests	u	Kooyman et al. 2010
	Amazonian tropical forests[a]	o, u	Kraft et al. 2008
	Tropical successional communities (Mexico)	u	Lebrija-Trejos et al. 2010
	Tropical cloud forests (China)	u	Long et al. 2011
	Tropical rain forest (French Guyana)	o, u	Paine et al. 2011
	Neotropical dry forest[a]	o, u	Swenson & Enquist 2009
	Costa Rican nontree communities	u	Mayfield et al. 2005
Phylogeny	Disturbed old fields (Canada)	u	Dinnage 2009
	California plant communities[a]	o, u	Cadotte et al. 2010
	Brazilian cerrado	u	Silva & Batalha 2009
	Bornean rainforest	u	Webb 2000
	Amazonian forests[a] (Peru)	o, u	Fine & Kembel 2011
	Neotropical forests[a] (Panama)	o, u	Kembel & Hubbell 2006
	Subtropical forests[a] (China)	o, u	Pei et al. 2011
	Tropical forests (Panama, Puerto Rico, Costa Rica)	o, u	Swenson et al. 2007
	Costa Rican secondary forests	o	Letcher 2010
Traits and phylogeny	Serengeti grasslands[a]	o, u	Anderson et al. 2011
	Algerian Xeric communities	u	Pavoine et al. 2011
	Cape Floristic region	o	Slingsby & Verboom 2006
	Dutch plant communities[a]	o, u	Prinzing et al. 2008
	Mediterranean communities[a] (Spain)	o, u	Verdu & Pausas 2007, Ojeda et al. 2010
	Minnesotan oak savannahs	u	Willis et al. 2010
	Floridian oaks[a]	o, u	Cavender-Bares et al. 2004a,b
	Floridian forests	u	Cavender-Bares et al. 2006
	Tropical lnga trees	o, u	Kursar et al. 2009
	Tropical fern communities[a] (Costa Rica)	o, u	Kluge & Kessler 2011
	Amazonian forests[a] (Ecuador)	o, u	Kraft & Ackerly 2010
	Costa Rican nontree communities	u	Mayfield et al. 2009

[a]Opposite patterns at different spatial scales, in different habitats, for different groups of species, or for different traits.

phylogenetic and trait analyses provide for a more nuanced view of assembly processes because they can test for niche conservatism versus convergence and because information on traits can help generate hypotheses as to the fitness differences and niche differences that lead to clustering or overdispersion (Cavender-Bares et al. 2004a, Mayfield et al. 2009, Kraft & Ackerly 2010). For example, phylogenetic clustering in Spanish Mediterranean communities has been linked to fire-resistance traits and, presumably, reflects differences in fire regimes across habitats (Ojeda et al. 2010), whereas phylogenetic and trait clustering in Amazonian forests was found to be related to growth traits (e.g., wood density), which likely reflects differences in the resource acquisition strategies best suited for ridgetop versus valley bottoms (Kraft et al. 2008). Similarly, phylogenetic overdispersion in co-occurring Floridian oaks likely reflects environmental filtering because these species share moisture preferences (i.e., convergent evolution), whereas phylogenetic overdispersion in co-occurring South African Sedges paired with niche conservatism in functional traits (e.g., leaf height, leaf area) is more consistent with competitive exclusion (Cavender-Bares et al. 2004b, Slingsby & Verboom 2006).

3.3. Demographic Analyses

A third research approach looks for signatures of niche differences not in the composition of communities, but rather in the demographic rates of component species. This approach relies on the premise that all stabilizing niche differences influence coexistence by causing species to have greater per capita growth rates when they are rare versus common (Chesson 2000, Adler et al. 2007). A major advantage of demographic approaches is that they do not require an a priori understanding of the environmental variables, biotic interactions, and species traits that collectively determine how stabilizing niche differences and relative fitness differences combine to determine community structure. Of course, the phenomenological nature of this approach is also its disadvantage because it prevents determination of the particular mechanisms operating that influence coexistence. Moreover, extensive demographic information is needed to quantify frequency-dependent population growth rates (rather than individual fitness components), information that is not always available (see sidebar, Coexistence Theory Terms Relevant to Community Assembly). We therefore first review studies that document negative frequency-dependent performance in plant communities, some of which are able to provide indirect evidence for the underlying mechanisms responsible (see Section 3.3.1). Because the importance of such stabilizing niche differences for coexistence also depends on the magnitude of relative fitness differences, we also review studies that quantify (or manipulate) the importance of both of these factors (see Section 3.3.2).

3.3.1. Frequency-dependent performance (the signature of stabilizing niche differences). Numerous studies have documented frequency- or density-dependent performance in diverse communities, including Mediterranean grasslands, temperate woodlands, and tropical forests (**Table 2**) (Wills et al. 1997, Webb & Peart 1999, Harms et al. 2000, HilleRisLambers et al. 2002, Webb et al. 2006, Harpole & Suding 2007, Yamazaki et al. 2009, Clark 2010, Comita et al. 2010, Metz et al. 2010). For example, seedling germination and survival for many tree species are lower in high conspecific-density neighborhoods than in locations where species are rare (e.g., Webb & Peart 1999, HilleRisLambers et al. 2002, Comita et al. 2010). These studies assume that strong (negative) density-dependent effects mediated by conspecific densities translate to population growth advantages when species are rare. Inspired by the Janzen-Connell hypothesis, many of these studies also assume that host-specific natural enemies are responsible for these patterns (Janzen 1970, Connell 1971). Modern coexistence theory, however, illustrates that other stabilizing niche differences (e.g., resource partitioning) also result in frequency-dependent plant

Table 2 Examples of demographic studies documenting or quantifying frequency-dependent performance, the signature of stabilizing niche differences

Type of study	Habitat	Source(s)
Frequency-dependent performance	Tropical rainforests	Wills et al. 1997, Webb & Peart 1999, Harms et al. 2000, Hubbell et al. 2001, Peters 2003, Webb et al. 2006, Comita et al. 2010, Metz et al. 2010, Kobe & Vriesendorp 2011
	Temperate deciduous forests	HilleRisLambers et al. 2002, Clark 2010
	California annual grasslands	Harpole & Suding 2007
Frequency-dependent performance; mechanism	Prairie/climate variability	Adler et al. 2006
	Temperate forests/natural enemies	Yamazaki et al. 2009
	Temperate grasslands/soil microbiota	Klironomos 2002, Petermann et al. 2008
	Tropical forests/natural enemies	Webb et al. 2006, Mangan et al. 2010, Metz et al. 2010, Swamy & Terborgh 2010
	Tropical forests/allelochemicals	McCarthy-Neumann & Kobe 2010
Frequency-dependent performance + fitness difference	Serpentine grasslands	Levine & HilleRisLambers 2009
	Sagebrush steppe	Adler et al. 2010

performance. Regardless of mechanism, these studies are collectively consistent with the idea that niche differences stabilize community structure in many plant communities.

Which mechanisms are responsible for these stabilizing niche differences? A limited number of studies have provided insights into the processes responsible (**Table 2**). Much of the work has focused on host-specific pathogens or natural enemies. Greenhouse and field studies, for example, find evidence of microbially mediated plant-soil feedbacks that generate advantages when rare (Bever 1994, Klironomos 2002, Petermann et al. 2008, Mangan et al. 2010). Careful documentation of the agents of mortality in one study also pointed to the importance of fungal pathogens (Yamazaki et al. 2009). By contrast, McCarthy-Neumann & Kobe (2010) found that density dependence was mediated by soil chemistry; and Adler et al. (2006, 2009) combined demographic analyses with simulation modeling to demonstrate that a "storage effect" (likely mediated through climate) operated to foster diversity in a prairie community but not in a sagebrush steppe (Adler et al. 2006, 2009; McCarthy-Neumann & Kobe 2010).

3.3.2. Comparing stabilizing niche differences with fitness differences. Although the studies highlighted in the previous paragraphs demonstrate the pervasive effects of stabilizing niche differences as manifested through negative frequency-dependent population growth rates, a full understanding of the importance of niche differences also hinges on quantifying relative fitness differences (Chesson 2000, Adler et al. 2007). For example, several studies find large frequency-independent increases in seedling performance when natural enemies, which in some cases are larger than frequency-dependent effects, are excluded (McCarthy-Neumann & Kobe 2010, Swamy & Terborgh 2010, Kobe & Vriesendorp 2011). This result suggests that other agents of mortality (e.g., light, allelochemicals, generalist natural enemies) influence relative fitness differences, even while specialized natural enemies may influence stabilizing niche differences. Do the stabilizing effects of host-specific natural enemies, if present, outweigh relative fitness differences (from

impacts of generalist natural enemies as well as other factors) and result in stable coexistence? Demographic analyses incorporating frequency-dependent and -independent performance at all life-history stages and of all individuals (e.g., Clark 2010) may be able to answer this question.

Unfortunately, few studies (to our knowledge) have attempted to quantify both the stabilizing effects of niche differences and relative fitness differences because of the wealth of data needed. However, an experiment with serpentine annuals suggests that the stabilizing effects of niche differences are required to overcome large fitness differences (Levine & HilleRisLambers 2009), whereas a study of sagebrush coexisting with three perennial bunchgrasses documented stabilizing effects of niche differences that were much greater than required to overcome fitness differences (Adler et al. 2010). Both studies demonstrate that removing the demographic influence of stabilizing niche differences causes reductions in diversity (Levine & HilleRisLambers 2009, Adler et al. 2010). Analyses with other long-term demographic sets (e.g., Clark 2010, Kraft & Ackerly 2010) may allow ecologists to determine whether these findings are generally applicable across ecosystems and communities.

4. PARTING THOUGHTS

We have argued that recent theoretical developments in coexistence theory allow for a greater understanding of the importance of competitive interactions in driving community assembly. With that in mind, we have provided numerous empirical examples of how stabilizing niche differences and relative fitness differences influence community assembly by influencing, for example, the identity of species that are excluded from communities through competition, the relative abundance of species within those communities, whether coexistence in those communities is stabilized, and their invasibility. However, the overall importance of stabilizing niche differences and relative fitness differences, as well as the mechanisms underlying these differences during plant community assembly, is still poorly understood. Fortunately, our review of empirical approaches suggests a way forward.

4.1. Future Directions

We believe that combining experimental manipulations or trait-based approaches with demographic models will allow ecologists to distinguish between the traits that tend to stabilize coexistence versus those that tend to drive competitive exclusion. This approach will allow empirical approaches to catch up to theoretical predictions, which have been significantly clarified over the past decade or so (Section 2). To their credit, current manipulative experiments and empirical trait-based approaches (Sections 3.1 and 3.2) both aim to identify the specific traits and mechanisms determining the outcome of competition (coexistence versus exclusion). However, both are limited by the investigators' ability to manipulate or measure all relevant niche axes and by the difficulty of distinguishing fitness differences from stabilizing niche differences. Meanwhile, demographic approaches (Section 3.3) can quantify the net effect of stabilizing niche and fitness differences among interacting species (e.g., Levine & HilleRisLambers 2009, Adler et al. 2010), but they have generally not been used to identify the traits or mechanisms that drive the outcomes of competition (but see Angert et al. 2009). By combining these empirical approaches (**Figure 3**), we believe that ecologists will be better able to link functional traits, phylogenetic relationships, and competitive interactions to community dynamics, long a goal of community assembly studies.

For example, rather than correlating the trait differences between competitors with their presence or absence in a community, we might instead correlate these differences with stabilizing niche and relative fitness differences from phenomenological demographic models, which better

capture the actual drivers of competitive outcomes. This approach would require a diverse system, with species whose growth and interactions could be reasonably described by population dynamic models parameterized from data (e.g., Adler et al. 2006, 2010; Clark 2010). From such a model, pairwise stabilizing niche differences and relative fitness differences could be quantified (Chesson 2000, Adler et al. 2007) and correlated with their functional trait differences, including all traits thought to influence competitive outcomes.

One might find, for example, that disparities in rooting depth are excellent predictors of the stabilizing niche differences between competitors, whereas disparities in relative growth rates predict fitness differences. Given the interrelated nature of many plant traits, multivariate approaches will likely be necessary to properly disentangle the contributions of various traits to both stabilizing niche differences and relative fitness differences (many will influence both). Results such as these can not only help identify the mechanisms of coexistence but also predict the influence of competition on community assembly, i.e., overdispersion along the rooting depth axis and clustering along a relative growth rate axis. The potential power of combining demographic and trait-based approaches is exemplified by the work of Angert et al. (2009). They found that species position along a trade-off between water use efficiency and relative growth rates was predictive of how species fecundity fluctuated through time, a key ingredient of coexistence via the storage effect (Angert et al. 2009).

Finally, experiments can provide powerful empirical tests of the coexistence mechanisms inferred by such demographic and trait-based compositional analyses. In an idealized example, imagine that plant stoichiometry suggests that different species are limited by different nutrients, and that differences in species' stoichiometry correlate with the strength of stabilizing niche differences. Fertilizing with one of the limiting resources should not only erode species diversity but predictably result in the loss of species that are superior competitors for those resources, providing an experimental test of the hypothesized mechanism. It is possible that some of the many existing manipulative studies of community composition (e.g., Rees et al. 2001, Suding et al. 2005, Suttle et al. 2007, HilleRisLambers et al. 2010) can be reanalyzed using contemporary coexistence theory, leading to important insights into community assembly (e.g., Fukami et al. 2005, Cadotte & Strauss 2011). For example, using the results of a recent study manipulating the seasonality and timing of precipitation (Suttle et al. 2007) to parameterize population dynamic models (e.g., Adler et al. 2012) could provide insight into whether declining diversity with spring precipitation results from a reduction in stabilizing niche differences or an increase in relative fitness differences.

4.2. Conclusions

An understanding of how stabilizing niche differences and relative fitness differences contribute to plant community assembly is not simply an academic question. Clarifying the processes that influence the composition, diversity, and relative abundance of co-occurring species in local communities has long been a goal of community ecologists, but it holds particular urgency with the increasing impacts of humans on the environment. Climate change, habitat fragmentation, eutrophication, and invasive species have large impacts on local plant communities by altering both the environment and biotic milieu that operate during community assembly (Hobbs et al. 2009). Understanding how plant communities disassemble following these perturbations, or how we can drive reassembly to a desired outcome with restoration, can be achieved with studies that link coexistence theory (determining how species are influenced by the environment and each other) to the outcome of community assembly (see sidebar, Coexistence Theory and Global Change).

COEXISTENCE THEORY AND GLOBAL CHANGE

Global change alters the composition and relative abundance of species within communities (i.e., community disassembly), but negative impacts can be reversed through restoration (i.e., community reassembly). Contemporary coexistence theory suggests that a valuable way to predict impacts and optimize restoration is to determine how global change alters stabilizing niche differences and relative fitness differences. For example:

- Climate change impacts on plant communities range from losses of weak competitors as relative fitness differences increase (e.g., as population growth rates of warm-adapted species increase) to increased persistence of rare species as stabilizing niche differences increase (through a storage effect mediated by climate variability; Adler & Drake 2008).
- In restoration, a functionally diverse seed mix can minimize invasibility through limiting similarity (Holmes 2001, Fargione et al. 2003), and the abiotic environment can be altered to favor desirable species by increasing relative fitness differences (e.g., by decreasing N or P levels; Harpole 2006, Jeppesen et al. 2007), or these processes can be combined for the best outcomes (Funk et al. 2008).

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