



Challenges in linking trait patterns to niche differentiation

Rafael D'Andrea and Annette Ostling

R. D'Andrea (rdandrea@umich.edu) and A. Ostling, *Ecology and Evolutionary Biology, Univ. of Michigan, Ann Arbor, MI, USA. AO also at: Center for Macroecology, Evolution and Climate, Univ. of Copenhagen, Denmark.*

Among approaches to establish the importance of niche differentiation for species coexistence, the use of functional traits is attractive for its potential to suggest specific coexistence mechanisms. Recent studies have looked for trait patterns reflective of niche differentiation, building on a line of research with a deep but somewhat neglected history. We review the field from its foundation in limiting similarity theory in the 1960s to its resurgence in 2000s, and find the theory of trait patterning still in a stage of development. Elements still to be accounted for include environmental fluctuations, multidimensional niche space, transient dynamics, immigration, intraspecific variation, evolution and spatial scales. Recent empirical methods are better than early approaches, but still focus on patterning arising in simplistic models, and should rigorously link niche space with trait space, use informative null models, and adopt new metrics of pattern as theory develops. Because tests based on overly simplistic expectations of trait pattern are of little value, we argue that progress in the field requires theory development, which should entail exploring patterns across a set of conceptual and system-specific models of competition along trait axes.

Synthesis

Traits relate to ecological performance and are easy to measure. Trait patterns can thus be a practical tool for inferring community assembly processes, and have been extensively used for this purpose. Classical trait patterning theory dates back to the 1960s, and despite heavy criticism still persists in empirical studies. Here we highlight steps needed for traits to realize their potential. These include firmly linking them to niche axes, and updating pattern expectations to consider recent results from models of niche dynamics, such as the emergence of species clusters. Further theory development should reveal whether there is a common traits-based signature across different niche mechanisms.

The idea that competition relates to species similarity is central to theoretical community ecology, and has been verified in experimental studies (Johansson and Keddy 1991, Jiang et al. 2010, Burns and Strauss 2011). Its corollary, that coexistence is predicated on species differences, forms the basis of niche theory. Recent debates over the importance of niche differentiation (see Box 1 – Glossary) for coexistence and community structure (Chesson 2000, Bell 2001) have reignited empirical efforts to parse how strongly niche differentiation drives community assembly and maintains biodiversity (HilleRisLambers et al. 2012). Key approaches include direct verification of frequency-dependence (Siepielski and McPeck 2010), experimental removal of stabilization (Adler et al. 2007), searching for phylogenetic signatures of niche differentiation (Cavender-Bares et al. 2009), and examining the goodness of fit of coexistence models to observed species abundance distributions (Chave et al. 2002). As fruitful as these approaches may prove to be, they leave open questions about the specific niche mechanisms at work, and their role in shaping the presence and relative abundance of species.

In parallel, there has been a recent drive among ecologists to understand communities in terms of traits impacting individual fitness via their effects on growth, reproduction and survival, so-called “functional traits” (Violle et al. 2007). According to McGill et al. 2005, “statements about traits give generality and predictability, whereas [research based on species identities] tends towards highly contingent rules and special cases”, because traits are more easily tied to physical, chemical and biological processes. Of particular interest has been the use of trait-based patterns as evidence of niche differentiation: sorting species by their trait value, one looks for a pattern in species occurrence and/or abundance along the trait axis (Stubbs and Wilson 2004). This approach to establishing niche differentiation could point towards specific niche mechanisms and a generalizable understanding of their influence on species abundances.

Linking trait patterns to niche differentiation is not new; rather, it represents the return of a classical line of inquiry dating back to the 1960s. Early research in this area was the subject of critical reviews highlighting methodological issues and the many simplifications of models

Box 1 – Glossary

Cluster: a set of species with similar trait values and relatively high abundance, separated from other such sets by sparsely populated regions on the trait axis.

Community-wide character displacement: the idea that species coexisting within a community will differ from each other more than expected by chance, which will be reflected as trait overdispersion.

Competition function, a.k.a. competition kernel: function describing the competitive suppression of a species' per capita growth rate caused by one individual of the same or another species. In trait-based models, it is often a function of species traits. It is the extension of the community matrix in the limit of a continuum of species.

Expected scale of trait dispersion/scale of the niche mechanism: the spatial scale of sampling required to observe trait pattern. Different niche mechanisms lead to trait patterning at different spatial scales. For example, Janzen–Connell effects are expected to lead to overdispersion at spatial scales within the range of interactions between individuals, whereas niche mechanisms that rely on habitat heterogeneity are expected to lead to overdispersion at scales commensurate with the grain of the environment.

Fitness (sensu Chesson): in the context of a consumer–resource model, it is the mean per capita growth rate of the species in the absence of resource limitation, scaled by the rate at which the per capita growth rate declines as resource abundance declines. For stable coexistence, fitness differences must be compensated by the stabilization term.

Limiting similarity: has taken on multiple meanings over time. In the 1960s it was understood as a rule for coexistence that imposed a specific minimum limit to the similarity of two coexisting species, namely the distance between two consumers' resource use curves could not be smaller than one standard deviation of those curves. Later, it was redefined more generally by Abrams (1983) as the recognition that limits to the similarity of coexisting competitors always exist, but their value depends on the species/system involved. It is also sometimes equated with community-wide character displacement.

Niche axis: the axis of variation involved in a niche mechanism, if that variation can be sensibly arranged on an axis. For a successional niche tradeoff, the axis runs from gap-specialist to shade-tolerant species.

Niche differences/differentiation: species differences that lessen competition between them. As argued by Chesson (1991), these are necessary for stable coexistence. Niche differences will involve one or more niche mechanisms and may or may not fall on a one-dimensional niche axis.

Niche mechanism: a process or set of circumstances whereby variation across species can lessen competition between them. In a niche mechanism, the nature of species interactions, plus sometimes the presence of tradeoffs, lead to opportunities for species to differ in their interaction with limiting factors (Levin 1970). Examples include enemy specialization, variation in resource use, and the successional niche tradeoff, where plant species differ by age of patches exploited.

Resource use curve: specifies a consumer's preferences among a large array of substitutable resources. In the MacArthur–Levins 1967 paper, it describes the probability of use of a given resource in a unit time by an individual.

Robust coexistence: an equilibrium state that resists changes in parameters that regulate dynamics. For example, a species is robustly coexisting if it is still able to coexist upon a (small) reduction in its carrying capacity due to removal of nesting sites.

Stabilization: in Chesson's formalism, it is the contribution to the invasion growth rate from differences between species competitive influence on themselves and their competitive influence on other species. It contains the frequency-dependent part of a species' growth rate, and can enable stable coexistence by causing a negative correlation between a species' abundance and its growth rate.

Stable coexistence: an equilibrium state that resists (small) changes in species abundances. For example, if some individuals from one of the species are removed, the species will tend to bounce back towards higher abundance.

Trait: any measurable feature of an organism's physiology/morphology/behavior/phenology, such as a canine's tooth size, or a plant's specific leaf area. Often 'traits' is used implying specifically 'functional traits', meaning those that impact individual fitness via their effects on growth, reproduction and/or survival.

Trait pattern: non-random distribution of species along a one-dimensional trait axis. This distribution may be based on presence–absence or weighed by species abundances.

Trait–niche axis relationships: niche differences are not necessarily available for easy measurement, so variation in more accessible traits are often used as proxy for niche differentiation. However, a relationship needs to be established between a species' placement on the niche axis and the trait axis before overdispersion in the latter can be taken as indication of niche differentiation.

used to derive expectations of pattern (Simberloff and Boecklen 1981, Abrams 1983). In the 2000s, the subject acquired renewed momentum. A number of studies have reported patterns of trait dispersion that are interpreted as reflecting niche differentiation (Stubbs and Wilson 2004, Kraft et al. 2008, Cornwell and Ackerly 2009, Wilson and Stubbs 2012).

Despite the rich literature and existing reviews on related topics (Götzenberger et al. 2012, HilleRisLambers et al. 2012, Adler et al. 2013), there has not been a synthesis of the theoretical basis for pattern-based trait analysis specifically. Here, we revisit this science from early work to latest developments, assess how current research deals with past shortcomings, identify remaining and new issues, and map out next steps to meet those challenges. The central message of our review is that further theoretical development is critical for moving forward in this line of research, as current theory of trait patterning arising from niche differentiation is too rudimentary to inform us of the pattern we should truly expect in nature.

The section 'Early trait pattern research: rise and fall of limiting similarity' reviews the origins of modern trait-pattern work in the classical limiting similarity theory of the 1960s and 70s, and describes the methodological and theoretical criticisms raised at the time. The section 'New perspectives and prospects on limiting similarity' considers new insights on the concept of limiting similarity, but suggests that this concept is just one element of a more comprehensive theory of trait patterning arising under niche differentiation. The section 'Recent empirical approaches in the context of past criticisms' argues that new empirical approaches have met some but not all of the early criticisms. The section 'Further elements to be considered in trait research' describes new challenges that have come to light as interest in trait pattern research resurged. The section 'Toward a theory of trait patterning under niche differentiation' proposes that examining trait pattern across a set of conceptual and system-oriented niche models can help refine predictions of trait pattern under niche differentiation.

Early trait pattern research: rise and fall of limiting similarity

The general expectation about species coexisting in the teeth of competition is that there should be limits to their similarity. This is an old idea in ecology, found in one form or another in the works of Gause, Hutchinson and others. In his famous Santa Rosalia piece, Hutchinson (1959) proposed heuristically that competition leads to a pattern of regularity in the body size ratio of trophically similar species, which he backed up with empirical evidence from waterbugs. A few years later, a similar assembly rule was derived by MacArthur and Levins (1967). Using a simple Lotka–Volterra competition model with species arranged along an axis of resource preference, and assuming that the strength of competition between species is proportional to the overlap in resource preference ("niche overlap"), they obtained a quantitative limit to species similarity consistent with coexistence. In particular, they showed that when carrying capacities are equal across species, a new species can only invade and coexist between two residents if it is

separated from each by at least one standard deviation of the resource use curve (Fig. 1A). This niche overlap rule marked the beginnings of the theory of limiting similarity.

May and MacArthur (1972) refined the theory by adding considerations of robustness. They showed that limits to similarity depend on species' carrying capacities, and that arbitrarily similar species can stably coexist if those values are just right, but the carrying capacity range consistent with coexistence decreases drastically with species similarity (Fig. 1B). Limiting similarity occurs because coexistence of very similar competitors depends upon fine-tuned parameters, whereas in nature those parameters are expected to fluctuate. By that logic, one could expect limits to similarity to be contingent upon the degree of environmental variation. However, May (1973) argued that the one-standard-deviation niche overlap rule proposed by MacArthur and Levins was universal, on two grounds. First, he highlighted that when distance between resource use curves d is less than one standard deviation σ , only a small range of carrying capacity parameters allows for coexistence, but once $d > \sigma$, that range rises sharply (Fig. 1B). Second, upon adding white environmental noise to carrying capacities in the Lotka–Volterra competition model, he found that the rule holds for species-rich communities regardless of the magnitude of environmental variation, so long as it is not too large (Fig. 1C).

These papers, along with Hutchinson's original conjectures on coexistence constraints, triggered extensive empirical exploration focused on specific rules of trait separation, such as the aforementioned niche overlap rule and Hutchinson's constant body size ratios. By the mid-1970s, the literature featured numerous reports of confirmation of such rules (reviewed by May 1973). Later, however, these studies were questioned regarding the quality and consistency of the results and methodology. Abrams (1975) contended that overlap in commonly examined traits such as body size and bill dimensions may not be truly representative of niche overlap, and listed a number of studies where overlap was found to be in disagreement with the MacArthur–Levins rule. Furthermore, in a series of influential papers sparking heated debate among community ecologists, Simberloff and co-workers (Strong et al. 1979, Simberloff and Boecklen 1981) explained away much of the claimed evidence for limiting similarity as either lacking statistical rigor or not distinguishable from null expectations. Their relentless campaign for a Popperian approach to community ecology led to the widespread incorporation of null models in subsequent studies.

The criticism did not stop at the empirical evidence; the theoretical basis for the rules were questioned as well (Abrams 1983). Roughgarden (1974) showed that the minimum trait difference between resident species and a successful invader depends heavily on the shape of the resource use curve. Abrams (1975) contended that the MacArthur–Levins rule and May and MacArthur's expansion of it were problematic because they ignored extinction of resources and hinged on the particular way overlap in resource use translates to Lotka–Volterra competition coefficients in the model. He emphasized that different assumptions lead to different formulas for the competition coefficients, which in turn lead to different limiting similarity rules. Turelli (1981)

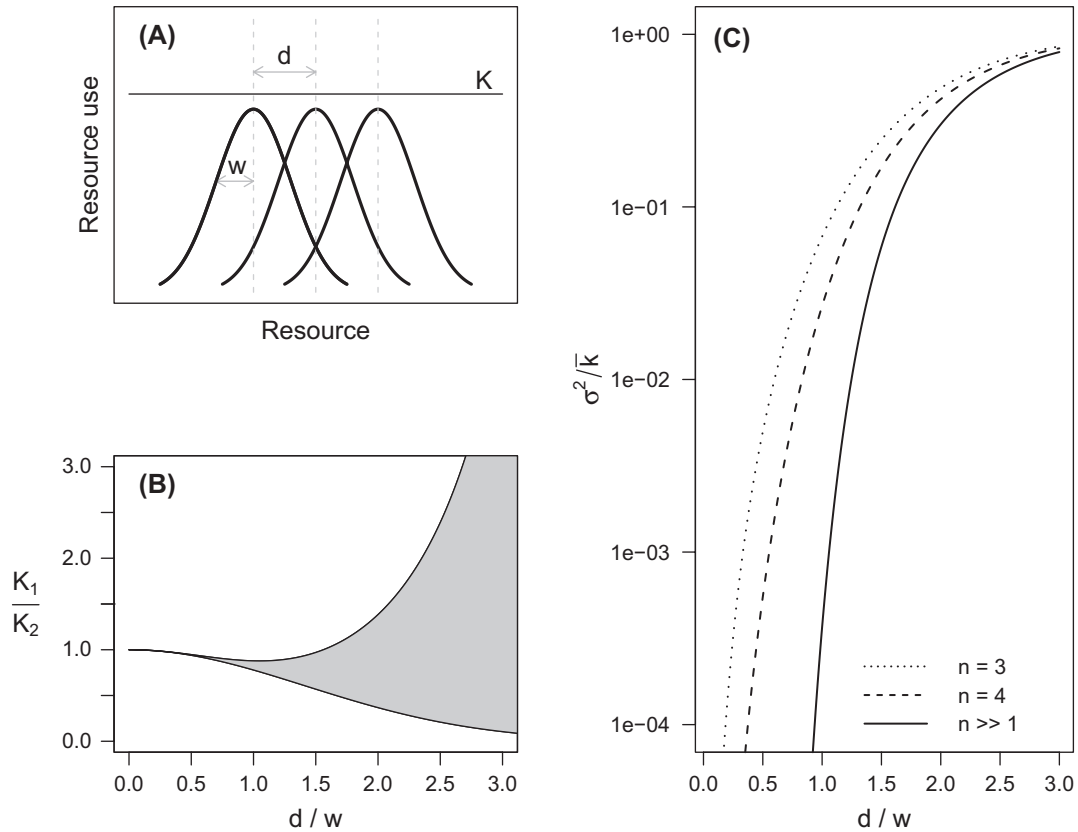


Figure 1. The niche overlap rule. (A) MacArthur and Levins (1967) concluded that if the separation d between nearest-neighbors were much smaller than the standard deviation w in resource use curves, coexistence would not be possible. (B) The range of parameters allowing three-species equilibrium ('coexistence bandwidth'), as a function of niche overlap, d/w . For simplicity, resident species 1 and 3 are chosen to have the same carrying capacity, $K_1 = K_3$. The bandwidth (shaded area) is narrow for similar species ($0 < d/w < 1$), and disappears as d/w approaches zero (adapted from May 1973). (C) 'The closest niche overlap d/w consistent with community stability in a randomly varying environment with fluctuations characterized by variance σ^2/K . Over a wide range, the variance has little influence on the species packing distance for a number of surviving species $n > 2$ ' (from May and MacArthur 1972).

criticized May's mathematical approach to environmental stochasticity, and through an alternative approach concluded that "practical limits to similarity can be obtained by simply ignoring the stochastic terms" (i.e. by using species' average carrying capacities). Abrams (1983) used this to argue that limits to similarity will depend on the system and the species. Further, he suggested that observed spacing between species may often not conform to its theoretical minimum, as any such minimal separation would be enlarged by evolutionary character displacement. Later, he pointed out that theoretical studies that consider coevolution between competitors often find that the ecological and evolutionary effects of competition differ, either increasing or decreasing similarity depending on the circumstances (Abrams 1990).

Given all these issues, one might conclude that limiting similarity is irrelevant to natural systems. That, however, is unjustified. Abrams did not dismiss limiting similarity as much as he expanded its meaning and highlighted its system-specific character. "What is needed instead is a broader definition of limiting similarity. The concept should be represented as a relationship between the difference in competitive ability and the maximum similarity that will permit coexistence. Such a relationship has the potential to be different for every different pair of species and will generally be different for a given pair of species in different

environments" (Abrams 1983). Abrams saw a need for system-specific, field-parameterized competition models, and comparison of limits to similarity predicted by those models with similarity observed in nature.

Technically, the principle that limits to similarity always exist is unfalsifiable. One can always argue that the actual limits are smaller than those probed empirically. But this is mostly of academic interest, as most ecologists ask not whether limits to similarity exist, but whether they shape community structure. This can be answered by comparing observed trait structure with null hypotheses.

The term "limiting similarity" has lost purchase over the past two decades (Google Ngram Viewer 2015). Yet, most empirical trait-based studies of community assembly still expect biotic (niche) interactions to lead to trait overdispersion, an expectation that has its basis in limiting similarity theory.

New perspectives and prospects on limiting similarity

Abrams's redefinition of the concept of limiting similarity was recast by Chesson (2000) in his increasingly influential framework for coexistence mechanisms. Chesson introduces fitness-equalizing forces, which decrease average differences in "fitness" between species, and stabilizing forces, which

allow species to invade each other from low abundance. By “fitness” Chesson means the maximal population growth rate in the absence of resource limitation, scaled by the sensitivity of the species growth rate to resource availability. Chesson’s “stabilizing” forces are those causing species’ competitive influence on themselves to differ from that on other species and hence leading to species’ population growth rates to be positive at low abundance. They require niche differentiation between species (Chesson 1991). Coexistence mechanisms involve one force or the other, or very often both. In fact, Chesson casts the population growth rate of an invading species as the sum of two terms: one quantifying the fitness differences between the invader and the residents, and the other quantifying the effect of the stabilizing forces. Chesson revisits limiting similarity by pointing out that for coexistence to be possible, “the smaller the average fitness differences, the smaller the stabilizing niche differences can be.”

Chesson’s perspective has had a strong influence on community ecology (Adler et al. 2007), as it highlights how species differences can either favor or disfavor coexistence. However one must be careful in applying it. Chesson’s ideas seem to naturally imply that 1) if there are no fitness differences between species, there are no limits to similarity; 2) conversely, if there are fitness differences, there must be limits to similarity. From a dynamic stability standpoint, both conclusions turn out to be incorrect for coexistence between more than two species. In the case of no fitness differences, the niche-axis Lotka–Volterra model proposed by MacArthur and Levins (1967) does not allow for stable coexistence between three or more arbitrarily similar species. It must be the case that Chesson’s stabilization term of the growth rate of the potential third invader is actually negative unless the two resident species are far enough apart on the trait axis. On the other hand, some competition coefficient choices in the same model lead to coexistence of an indefinitely large number of arbitrarily similar species despite fitness differences caused by differences in carrying capacities. (Hernández-García et al. 2009).

Critically, these instances of stable coexistence of arbitrarily similar competitors do not warrant the conclusion that there may be systems in nature without limits to similarity, at least not yet. Limits to similarity pervade all competition models if one considers robustness to fluctuations in model parameters set by environmental conditions. For example, it has been shown for a large spectrum of models that small changes in the carrying capacity of a single species brings extinction to a number of its closest competitors (Barabás et al. 2012, 2013a, D’Andrea et al. 2013), while changes in the carrying capacities of multiple species throughout the trait axis lead to spacing between all stably coexisting species (Barabás and Mészéna 2009).

The concept of robustness, or structural stability, has not gained as much traction as the concept of dynamic stability, even though it may be equally relevant for analysis of model predictions (Barabás et al. 2014). In a dynamically stable state, species abundances return to their previous equilibrium values after a perturbation, whereas in a structurally stable state species equilibrium abundances change little when environmental conditions setting the carrying capacity are perturbed. Because both abundances and environmental conditions can be expected to fluctuate

in nature, a predicted equilibrium state is arguably not biologically relevant unless it is both dynamically and structurally stable.

However, there is an unresolved tension between Turelli’s work on environmental fluctuations, the robustness analysis of Barabás and coworkers, and work by Chesson on environmental fluctuations (Chesson and Huntly 1997). Turelli (1981) concludes that small environmental fluctuations are of little consequence for limiting similarity theory, whereas Barabás and coworkers ascribe them primary importance. The latter approach differs from the former by considering potentially long-term changes in environmental conditions. Chesson suggests environmental fluctuations can enhance coexistence when species’ responses to them are negatively correlated, but in this case environmental fluctuations open up new niche axes along which there will be limits to similarity (The reverse idea, that biodiversity stabilizes community-level responses to environmental fluctuations, has been borne out empirically (Gross et al. 2014). This has been theorized to occur if species-level responses to the environment are asynchronous (Yachi and Loreau 1999), which presumably requires that species differ sufficiently in traits related to such responses). Resolving this tension is needed to achieve a clearer picture of whether one does expect any special systems where limiting similarity does not hold, and a more general understanding of the likely role of environmental fluctuations relative to inherent population dynamics in setting the limits to similarity in nature. Doing so requires answering the empirical question of whether negatively correlated responses to the environment are common, and whether environmental fluctuations are fast and small enough for Turelli’s analysis to apply, or longer term as assumed by the robustness analysis of Barabás et al. Yet even once the nature of environmental fluctuations is better known, limiting similarity theory will be just one ingredient in a comprehensive theory of trait patterning. Imposing dynamic and structural stability constraints on simple niche models gives conceptual insight into what competition might do to communities, but it seems unlikely that it should be able to tell us what trait pattern to actually expect to find in nature, where so many additional complexities ignored in these models come into play. The next two sections will discuss the current status of trait pattern research in the context of old and new challenges to formulating such comprehensive theory and developing better empirical methods.

Recent empirical approaches in the context of past criticisms

A variety of recent studies look for patterns of spread and evenness in the distribution of species along a trait axis (Stubbs and Wilson 2004, Dayan and Simberloff 2005, Kraft et al. 2008, Cornwell and Ackerly 2009, Wilson and Stubbs 2012, reviewed by Götzenberger et al. 2012). The observed distribution of species traits is compared with a null distribution, typically a random draw from the regional species pool, often weighted by regional abundance and constrained by the number of individuals or species in the sample. Analysis focuses on species differences, and in particular how widely and evenly the observed species are distributed on one or more trait axes. Box 2 describes common

Trait-based metrics. A variety of trait metrics have been used to detect niche differentiation. Here we describe key metrics used in empirical studies, which can be presence–absence or abundance-weighted, one-dimensional or multivariate. Multivariate metrics tend to be direct analogues of one-dimensional metrics. In common, almost have been applied with the expectation that niche differentiation will lead to high trait dispersion and/or high evenness in the distribution of species across trait space. As discussed in the main text, this is problematic because more complex niche differentiation mechanisms (e.g. hierarchical tradeoffs) do not necessarily predict even spacing nor overdispersion and emergent clusters may occur. We also describe some metrics that have been proposed to look for patterns of clustering, and offer suggestions for further metric development.

Presence–absence metrics

Trait range. If strength of competition declines as species differ, species traits should spread over a wider range than could be expected by chance (Stubbs and Wilson 2004). However, trait range is impacted in the opposite direction by habitat filtering (Weiher et al. 1998), making it difficult to parse the influences of filtering and limiting similarity that may act on the same trait simultaneously. It is also sensitive to outliers (Laliberté and Legendre 2010), and does not incorporate abundance.

Minimum distance between nearest neighbors. This offers a direct measure of the potential limits to similarity, which would be reflected as larger-than-random minimum separation between species (Stubbs and Wilson 2004).

Mean distance between nearest neighbors. A larger value than expected by chance could be indicative of competition dependent on trait differences (Stubbs and Wilson 2004). Mean distance is not independent of trait range and hence subject to the same confounding influence of habitat filtering.

Trait evenness. Measures variation in trait differences between adjacent species on the trait axis. Like the mean, the standard deviation of nearest neighbor distances scales with trait range and hence is subject to the confounding effects of habitat filtering (Lake and Ostling 2009). Normalized measures such as the coefficient of variation and the ratio between the standard deviation and the range are used to account for that effect (Kraft and Ackerly 2010). Limiting similarity is expected to be expressed as excess evenness and thus low coefficient of variation. For related metrics, Stubbs and Wilson 2004.

Abundance-weighted metrics

Functional regularity index (FRO). An abundance-weighted measure of trait evenness, based on trait differences between adjacent species on the trait axis scaled by the total abundance of the pair (Mouillot et al. 2005).

Functional divergence (FDvar). Measures the abundance-weighted mean of the deviation of species traits from the mean species trait. A high functional divergence signals high niche differentiation (Mason et al. 2005).

Community-wide abundance-weighted distance. \sum all pairs $d_{ij} n_i n_j$, where i and j represent two species, n is their abundance, and d is the trait difference (Vergnon et al. 2009). This index should be higher in communities driven by niche differentiation than in communities where trait value are unrelated to abundance. A similar metric, *Rao's quadratic diversity*, is defined as \sum all pairs $d_{ij} p_i p_j$ where p represents the relative species abundance, $p_i = n_i / \sum n_k$. It is the expected dissimilarity between two individuals randomly sampled from the community (Laliberté and Legendre 2010).

Multidimensional metrics

Functional richness (FRic), or convex hull volume. The hypervolume spanned by the trait means of observed species in multidimensional trait space (Cornwell et al. 2006, Villéger et al. 2008). It is the multidimensional equivalent of the trait range, and hence suffers from the same problems as a metric for niche differentiation.

Minimum spanning tree. A measure of the functional diversity spanned by the species in a community. Essentially collapses multidimensional trait space into a one-dimensional space. It is constructed by joining all species together in a tree, with branches weighed by Euclidean distances in multidimensional trait space. Large trees and even spacing within trees are indicative of niche differentiation (Franzén 2004).

Functional evenness (FEve). Measures the regularity with which species abundances are distributed across the minimum spanning tree (Villéger et al. 2008). It is a multivariate extension of the functional regularity index.

Multivariate functional divergence (FDiv). Multivariate analogue of FDvar. Calculates the abundance-weighted deviations between species traits and the trait center of gravity in multidimensional trait space (Villéger et al. 2008).

(Continued)

Functional dispersion (FD_{is}). The abundance-weighted mean distance between species and their abundance-weighted centroid (Laliberté and Legendre 2010). It is related to Rao's quadratic diversity, which expresses the mean Euclidean distance between two randomly selected individuals (Laliberté and Legendre 2010).

Metrics proposed to detect clustering on the trait axis

Trait clustering. Variation in trait differences between adjacent species on the trait axis can reflect clustering if it is higher than expectations from a null (Yan et al. 2012). It should be noted that many of the metrics listed above would work equally well to detect clustering, as that would be reflected as the opposite direction from overdispersion in the metric.

Distribution of species richness along the trait axis. Based on the idea that similarity in fitness between similar species, coupled with partitioning of the trait axis into niches, may lead to an uneven distribution of species along the axis (Vergnon et al. 2009).

Distribution of distance to nearest abundant species. Proposed in Jeraldo et al. 2012 for genetic sequences of gastrointestinal organisms as an alternative to rank-abundance plots. A proportion of the sequences ('species') is arbitrarily selected as modal (highly abundant), and the distribution of distances of all other sequences to their nearest modal sequence (the most similar modal sequence) is obtained and compared with the expected distribution from a neutral community. But see D'Andrea and Ostling 2015 for a discussion that appropriate null models must be used so that clustering from mutation alone can be discarded.

Potential sources for further metric development

Time series analysis. Species abundances on a trait axis can be taken as a time series, with the trait axis being time and the abundances being the signal. Fourier and wavelet analysis can be run to look for periodic waves of high and low abundance on the axis, corresponding to the emergent groups (niches) found by Scheffer and van Nes (2006).

Spatial descriptive statistics. Spatial descriptive statistics that are normally used in geographic information systems (GIS), such as Ripley's K, could be used to measure the degree of clustering in the distribution of species trait values in trait space. Clustering in trait space, as determined by such metrics, would indicate filtering, while overdispersion would indicate niche differentiation. This would be especially useful in multivariate analyses.

Trends in abundance as a function of distance to niche centers. Based on the idea that niche differentiation will lead to clustering, metrics focusing on patterns of species abundances as a function of the position of a species in relation to others within a cluster could prove useful. To our knowledge, this has not been investigated yet, and remains a promising line of research.

metrics and test statistics used. If niche differences associated with that particular trait are an important driver of community assembly, or if evolution has driven niche differences in sympatric species, then species are expected to be more widely or evenly distributed than in the null models. Filtering of traits best suited for local abiotic conditions can also influence trait patterns in a local community and is expected to lead to the opposite patterns. Authors typically look for both processes, and in some cases factor filtering into the null model for niche differentiation by restricting the species pool (Cornwell and Ackerly 2009, de Bello et al. 2012), or employ metrics that should have little impact from filtering (Box 2).

Such current approaches are an improvement over the first wave of empirical efforts of the 1960–1970s. Increased trait range and even spacing may arise regardless of the particular size of the niche spacing between species needed for robust and stable coexistence. Further, use of null models conferred the statistical rigor lacking in the purely observational studies that were previously the norm. Still, given the intense past debates in the literature and mixed results in detecting limiting similarity, careful assessment of recent

approaches in the context of past methodological critiques is warranted.

Some recent empirical trait patterning studies take novel approaches, such as experiments to see how successful invading species impact community trait pattern (Breitschwerdt et al. 2015), and looking at trait patterning along ontogenetic, successional, productivity, and environmental gradients (Carboni et al. 2014, Letten et al. 2014, Silva and Brandão 2014, Lasky et al. 2015) to gain additional evidence for community assembly processes (e.g. differences in trait pattern between saplings and adults may reveal processes influencing organism survival). We do not specifically address these approaches here, but our assessment of theoretical and methodological issues applies equally well to them.

Is evenness to be expected?

Despite improvements in the pattern expectations of empirical studies, a closer look on whether limiting similarity theory truly supports those revised expectations quickly turns up potential issues. In particular there are issues with the expectation of even trait spacing, which has been the

focus of a number of studies due to the potential for this type of pattern to be indicative of niche differentiation. To our knowledge, Abrams (1990) was the first to explicitly question even spacing as a general feature of competition, and he had previously argued that limits to similarity may vary between different species pairs in a single system (Abrams 1983).

The idea that niche assembly leads to even trait spacing follows intuitively if interspecific competition depends solely on species similarity. Indeed, evenness features strongly in the MacArthur–Levins model (Fig. 1A). However, that model assumes a great deal of simplifying symmetry, including uniformity of carrying capacities and resource utilization function shapes and widths across species. It also assumes competition coefficients that depend exclusively on trait differences and not the trait value itself, a simplification that does not hold for traits such as plant size (Schwinning and Weiner 1998). It is also not seen in other models, for instance models with competitive hierarchies such as the competition-colonization (Tilman 1994) and tolerance-fecundity tradeoff (Muller-Landau 2010).

Simulations of the MacArthur–Levins model in a few example cases with heterogeneous carrying capacity exhibit even spacing (Barabás and Meszéna 2009, Barabás et al. 2013a), suggesting the effects of fitness differences on evenness may be small. In contrast, the dependence of competition on trait values can have large effects, as models with this dependence yield spacing rules that can involve irregular intervals between species (Kinzig et al. 1999, Haegeman et al. 2014). For example, examination of patterns in the Tilman–May–Nowak hierarchical competition model reveal no obvious signs of evenness in species placement along the trait axis (cf. figures in Buttel et al. 2002). Even in models that predict even spacing, evenness may only be expected when the niche space is full, i.e. when there are as many species present as can stably and robustly coexist. Lower diversity could allow for more variation in species spacing, unless fast-acting evolutionary forces drove species to more even spacing. We know of no multispecies evolutionary studies that investigate impact on even spacing (or more generally on the distribution of stably coexisting species, but see Fussmann et al. 2007), although those would be critical to establish whether evenness is to be expected at evolutionary time scales.

Some ecologists believe that models based on an indefinite number of consumer species feeding on a continuum of substitutable resources, such as the ones discussed in the previous paragraph, have little relevance for expected pattern in nature because most natural systems have a small number of resources and relatively limited species diversity. Of course any real system has a finite number of consumers and resources, so the real question is how large the number of species/resources needs to be for models based on continuums to be useful ('All models are wrong, but some are useful'). For the purposes of predicting features of trait pattern among local species sorting from a regional pool of species, continuum models seem appropriate when the number of species in the pool and number of potential local resources for them greatly exceeds the number of stably coexisting species allowed by the model. There are often

more potential resources or "limiting factors" (Levin 1970, Chesson 2000) than a first look might reveal. For example, terrestrial plants may be limited by the availability of patches of different ages since disturbance, as in successional niche models (Kohyama 1993, Pacala and Rees 1998).

Further exploration is in order before conclusions can be drawn, but if evenness is not a universal feature of niche differentiation, then empirical studies should shift focus to other aspects of pattern more robustly suggestive of niche differentiation.

Identifying niche axes and multidimensionality

Two important criticisms leveled at early trait studies continue to be overlooked or not fully addressed in much of the empirical literature.

First, to rigorously connect trait patterning and niche differentiation, one must establish an explicit link between candidate niche axes in a given system – i.e. the aspects of organism performance in which differentiation confers stable coexistence – and the actual traits measured in field studies. Early trait studies were criticized because it was unclear that axes of variation being examined actually corresponded to niche differentiation.

Attempts at making such linkages have certainly been made, but there are stumbling blocks. Consider plant traits such as maximum height, seed size and specific leaf area. These are known to influence species' distributions along abiotic gradients (Wright et al. 2004), but they are also thought to be proxies for species' positioning on life history axes (Moles and Westoby 2004) and to enable coexistence through a successional niche tradeoff (Pacala and Rees 1998, Kohyama 2006). Many studies have connected these traits to demographic performance (e.g. seed output, or growth or mortality at various life stages); however, due to limitations in the prevalence of different light conditions in forests, what is typically considered is performance in full sun or in the understory, and not the demographic response to shading that is critical to successional niche differentiation (Poorter et al. 2008, Wright et al. 2010, but see Sterck et al. 2011). Beyond tree traits, theory is still developing regarding which types of trait variation and tradeoffs are related to stabilization and which are simply related to fitness differences and/or fitness equalization (Herben and Goldberg 2014).

Another problem is that it is much easier to associate traits with individual performance than with population growth rates, but it is their effect on the latter that matters for niche differentiation. Very few studies have tried to verify that connection empirically (but see Adler et al. 2014). Considering competition models formulated in terms of individual performance, Kohyama's (1993) model of size-structured competition in forests, or even more detailed models like individual-based forest simulators (Pacala et al. 1993), may aid this process.

These hurdles have recently been circumvented in annual plant systems, where manipulative experiments can get at population dynamics and be used to parameterize competition models, to provide what seems at least compelling evidence of which trait differences contribute to stabilization (Kraft et al. 2014, Lasky et al. 2014a). But such manipulation is not always possible.

Adler et al. (2013) provide a useful road map to the broad types of niche axes – spatial and temporal heterogeneity, natural enemies, and resource partitioning – that could be considered in forming linkages between traits and performance more informative of potential niche mechanisms. The next step is to develop mechanistic competition models geared to specific example systems (Kohyama 1993) in order to get a detailed sense of the candidate niche axes there, and then link traits to these niche axes through both empirical correlations and physiological theory (Sterck et al. 2011). Adler et al. (2013) suggest that ecologists abandon pattern-based analysis altogether in favor of establishing trait–niche axis relationships. However, showing that trait variation drives variation along a viable niche axis does not in itself indicate that it is substantial enough, or of the right nature, to enable stable coexistence. Pattern-based trait analysis, when coupled with the establishment of trait–niche axis relationships, provides a means to gain suggestive evidence that the trait variation is actually enabling coexistence.

The second issue is that the niche space in most cases likely involves many dimensions. There is a dearth of models providing predictions for trait patterning caused by niche interactions mediated by multiple traits. Multidimensionality means more niche space, and hence more potential for empty niche space in low-diversity systems, and for trait patterns to be more complex or random-looking as a result. In addition, the number of dimensions of niche space can have effects on limits to similarity. For example, the minimum multidimensional spacing required for coexistence can be lower than the one-dimensional limit (Yoshiyama and Roughgarden 1977). Multidimensionality can also lead to greater sensitivity to environmental noise (May 1973, p. 164). Finally, perfectly even niche segregation occurring in multiple dimensions can elude detection on individual trait axes. For example, if the niche space is two-dimensional and niche axes are not parallel to measured trait axes, species that are evenly distributed in the full niche space might seem unevenly distributed when examined on a single trait axis. (Fig. 2).

Empirical trait studies typically deal with this by calculating distances in multidimensional trait space (Mason et al. 2005, Mouillot et al. 2005, Villéger et al. 2008, Laliberté and Legendre 2010, Paine et al. 2011) or performing a principal-component analysis to determine the axes where trait segregation is strongest (Swenson and Enquist 2009). Those are not without issues, though. Most of these multivariate metrics are direct extensions of their single-trait cousins (Box 2), and therefore inherit the same limitations: namely, they are based on the idea that niche differentiation will lead to high trait dispersion and/or evenness, which may not always be justified. Furthermore, there are multiple ways to calculate distance in multidimensional space (Deza and Deza 2006), and without some guiding theory one is left with finding whatever leads to the strongest signal. Similarly, with PCA one heuristically finds which axes give the strongest pattern, and must interpret the result after the fact. The problem then is analogous to the Texas sharpshooter fallacy: by looking everywhere, one is bound to find pattern somewhere, but its meaning may be lost. Such heuristic measures may thus fail to identify combinations of traits from which the niche mechanisms involved can be surmised. An alternative

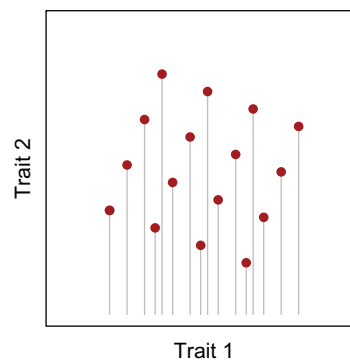


Figure 2. Multidimensionality may mask species differences. When separation between species is defined in multidimensional space, limiting similarity may be hidden from the viewpoint of a single axis. Here, even though species are evenly distributed when the full two-dimensional trait space is considered, such structure is lost when we take a projection onto a single axis. For example, the coefficient of variation (CV) of the adjacent-neighbor distances between the projections on the axis shown above is 0.9. In contrast, the CV in 2-D is 0. When compared with 10 000 null distributions with the same number of species and same first and last positions but random positions in between, almost half of the null CVs are found to be lower than 0.9. Thus the assemblage above, as seen from that axis, would be indistinguishable from random. Note that different angles between the orientation of the lattice and the axis will lead to different CVs and p-values.

approach is to develop and ground-truth system-specific mechanistic models to identify candidate niche axes, and then identify the multiple traits that may be driving them using physiological theory and phenomenology.

The null model

Trait studies may have universally accepted the importance of comparisons with a null model, but not enough attention has been given to what exactly the null model is supposed to represent. In recent trait studies, null assemblages normally consist of abundance-weighted random draws of a fixed number of species or individuals from the regional pool, or some related form of randomization of the observed data. Some authors use more sophisticated randomized statistical null models that, for instance, account for habitat filtering by selecting only species that have been observed to survive in the local environment (Cornwell and Ackerly 2009, de Bello et al. 2012). But are randomized null models our best option?

Many ecologists say yes. Gotelli and McGill (2006), citing Gotelli and Graves (1996), argue that null expectations intrinsically involve randomizations of observed patterns. To them, null models should function as “a standard statistical null hypotheses, in contrast to a scientific hypothesis, which is a mechanism to explain the pattern”.

Others disagree. Some authors (Roughgarden 1983, Manly 1991, Wilson 1999) argue that null models should, as far as possible, represent explicit ecological processes by which the community would have been assembled in the absence of the process of interest. In other words, process-based null models are preferable to statistical null models. For example, Pigot and Etienne (2015) incorporate historical processes of speciation and extinction ignored by

statistical null models, and show that the latter may lead to false detection of limits to phylogenetic relatedness.

Roughgarden (1983) pointed out that “fabricating random communities [...] does not bear the relationship to ecology that the neutrality hypothesis does to population genetics.” However, little resulted from this insight because at the time there was no framework in community ecology comparable to neutral theory in population genetics. Yet the past fifteen years have seen the development of a neutral theory for community ecology (Hubbell 2001, Rosindell et al. 2011), and we believe trait patterning studies should move towards using it. Indeed one study suggests the use of a neutral model instead of a purely random null can lead to different results regarding patterns of species co-occurrence (Ulrich 2004).

The idea of neutral theory as a null model in community ecology is not new, and has its opponents. Interestingly, while Gotelli and McGill (2006) reject it because neutral models are mechanistic rather than purely statistic, Clark (2012) rejects it because to him they are not mechanistic enough. Our perspective is that neutral theory presents some difficulties. First, it may require quite a bit of information about a system, and the formulation of complex neutral models accounting for that information. For example, details regarding the nature of dispersal limitation (Ostling 2012), demographic complexity (e.g. size or age dependence of reproduction and death, Waples et al. 2011), and the spatial distribution of species in the regional pool, may all have important consequences for expected distributions in the absence of niche differentiation. However, less sensitivity to at least some of these details might be achieved by shifting focus from traditional species abundance distributions to distributions of species abundance in trait space, where more specific types of departures from neutral expectations might be expected. Power analyses and theoretical exploration of example tests could indicate what information is most vital, and in what situations the use of a neutral model rather than a pure random model is particularly important. Another issue is scale. It is very hard to get good information on the nature of neutral processes operating at the regional scale, such as speciation, and this makes it difficult to build a good neutral model at that scale. However, if data on current regional abundances are available and can be used to make adequate predictions of expected local abundances based on dispersal alone, one can test for non-neutral dynamics at the local scale without needing to make assumptions about neutrality at the regional scale.

It should be noted that alternative methods that do not use null models are also possible. For example, approximate Bayesian computation algorithms (Beaumont 2010) have been used to estimate the relative importance of different community assembly processes in shaping trait patterns by comparing trait-based summary statistics produced under different model assumptions about process with summary statistics from the data (van der Plas et al. 2015).

Further elements to be considered in trait research

In addition to the classical methodological and conceptual issues discussed in the previous section, new challenges have come to light as interest in trait pattern research has

resurged. As will be seen below, emergent clusters arising from classical niche models offer fresh perspectives on expectations of trait dispersion. Intraspecific variation presents challenges in the degree of sampling needed to discern pattern, and could impact coexistence and hence trait patterning predictions. The spatial scale of both the mechanisms of niche differentiation and the sampling design impact the likelihood of detecting pattern and the nature of the pattern to be expected.

Emergent clusters

The MacArthur–Levins 1967 study and much subsequent work focus on system equilibria, as nonlinear models typically cannot be solved but their equilibria can often be found analytically. However, there is no guarantee that time to reach these equilibria is short enough that real-world communities can be expected to be at equilibrium. Advances in computer power have opened the door to simulations of model dynamics that were unavailable in the 1960s, and such simulations reveal that transient regimes may be in striking contrast to expectations from equilibria.

Key among newly discovered phenomena is the spontaneous emergence of groups of similar species under competition. In simulations of the MacArthur–Levins model, starting with a large number of species randomly placed on a trait axis, Scheffer and van Nes (2006) found a transient regime composed of clusters of similar species with high abundance, separated by sparsely populated regions on the axis (Fig. 3A).

The appearance of transient clusters in the competitive context can be informally understood as follows. Because competition increases with similarity, minimal interspecific competition is achieved by partitioning the trait axis into evenly spaced spots (determined by any small initial heterogeneity in species abundances). Species located at those spots will face the lowest competition and thus thrive, while all others are eventually excluded. This arrangement is the final equilibrium to which the system eventually converges. On the other hand, species close together on the trait axis are similar to one another in the competition they experience from other species. Transient clustering arises because it takes time for the species at the favored spots to exclude their slightly inferior neighbors. One can interpret the region surrounding each spot as a niche, and describe the dynamics as a two-stage process, the first characterized by species being sorted into niches, and the second characterized by within-niche competition leading to the exclusion of all but one species per niche.

We note that fitness differences (*sensu* Chesson 2000) play no necessary role in the formation of these clusters. In Scheffer and van Nes’s (2006) model, all species have equal intrinsic growth rates and carrying capacities, and can be distinguished only by their position on the niche axis; yet, clusters arise spontaneously. Transient clusters could also arise from fitness differences (Mayfield and Levine 2010) and/or habitat filtering, but those would differ in trait space from Scheffer and van Nes’s clusters: unless there were some substructure of resource availability driving a multimodal fitness curve, fitness differences would cause a single cluster around the fittest species. In contrast, the emergent clusters in discussion here consist of multiple regions on the trait axis

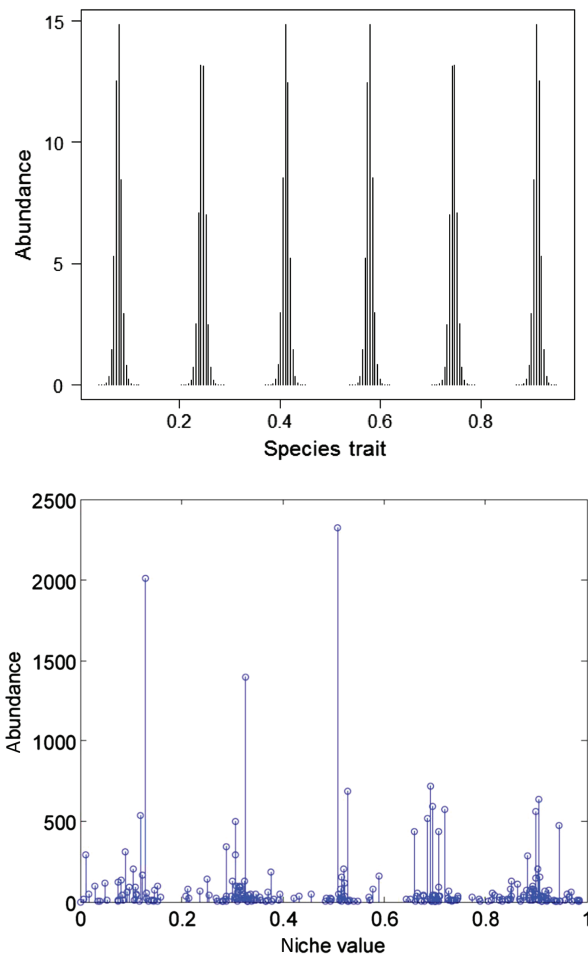


Figure 3. Emergent clusters. (A) Transient regime in the MacArthur–Levins model. The community is initially packed with species lined along the trait axis. Before the final state of species at their limits to similarity is reached, clusters are formed around the favored sites on the axis. (B) Outcome when immigration is added to the MacArthur–Levins model. The clusters differ from (A) in that they are maintained by immigration, and are thus a permanent feature of the community. This patterning was highlighted recently in Barabás et al. 2013a.

– as many as the number of species that would stably coexist at equilibrium.

Scheffer and van Nes showed clustering patterns for a limited parameter range in one simple model, but clusters have since been seen in many studies. Fort et al. (2010) verified the robustness of the clustering pattern in Lotka–Volterra niche overlap models with finite niche axes by showing that it arises as a transient under a variety of niche dimensions, competition functions, niche boundary conditions, species initial abundances, species intrinsic growth rates and carrying capacities. Furthermore, Scheffer et al. showed that the addition of a stabilizing term to the population dynamical equations of the MacArthur–Levins model leads to permanent rather than just transient clusters (Scheffer and van Nes 2006, Vergnon et al. 2012, but see Barabás et al. 2013b). Further, clusters are permanent in niche models that include the effects of frequent environmental variation (Ernebjerg and Kishony 2011), mutation (Bonsall et al. 2004), and immigration (Barabás

et al. 2013b) – see Fig. 3B. Lastly, Scheffer and van Nes found that implementing evolution by allowing species to move along the trait axis makes clusters more robust to variations in species carrying capacities (Scheffer and van Nes 2006). Indeed, clusters are no strangers to the evolution literature: it has been shown that phenotypic clustering can appear due to selection (Doebeli et al. 2007, Leimar et al. 2008, Jeraldo et al. 2012), or simply due to mutation in mutation-drift processes (Lawson and Jensen 2007, D’Andrea and Ostling 2015).

In nature, clustering in the positioning of species on trait axes has been seen in European aquatic beetles, Dutch freshwater algae, American prairie birds (Scheffer and van Nes 2006), marine and saline lagoon phytoplankton (Vergnon et al. 2009, Segura et al. 2011), and alpine woody plants (Yan et al. 2012). Some of the evidence is simply in the form of visually apparent modes in histograms of species counts along discrete portions of body size axes (Scheffer and van Nes 2006), but other studies used quantitative metrics such as looking for peaks in the curve of species density on the trait axis (Vergnon et al. 2009), or looking for a larger coefficient of variation in nearest neighbor distances than expected by chance (Yan et al. 2012). In addition to local peaks in richness on the trait axis, Vergnon et al. (2009) and Segura et al. (2011) also found evidence of local peaks in abundance, like those predicted in Lotka–Volterra models, using an abundance-weighted trait distance metric and a test looking for peaks in Shannon–Weaver diversity respectively.

In sum, clusters appear in nature and feature in Lotka–Volterra competition models, as well as evolutionary models. It seems reasonable to expect clusters to arise in a wide range of models of ecoevolutionary dynamics. More thorough examination using system-specific ground-truthed models is needed, in particular regarding whether clusters will arise for realistic levels of environmental variation, mutation and immigration. If clusters prove to be a general feature of niche models, this will have profound implications for trait-patterning studies, as a clustered community is the exact opposite of the type of trait dispersion generally associated with niche differentiation. Future metric development should take this into account (Box 2).

Spatial scales

Spatial scales have been brought to bear extensively on examinations of community assembly patterns and ecosystem processes (Weiher and Keddy 1999), with focus on scale-dependence of species diversity, composition and spatial distribution (Cody 1999), phylogenetic relatedness (Cavender-Bares et al. 2006, Swenson et al. 2007), and ecosystem function (Bond and Chase 2002). Here, we highlight the relevance of scales to patterns of trait dispersion in the context of how niche mechanisms relate to scales of species dispersal and environmental heterogeneity.

Consider terrestrial plants. It may appear at first that competition occurs primarily among neighboring individuals, so niche patterns should occur at the neighborhood scale (Kraft and Ackerly 2010, Uriarte et al. 2010). But in reality, all individuals sending propagules to a location potentially compete with one another. Therefore, expectations of niche differentiation must encompass more than

just local resource competition (Kneitel and Chase 2004, Kraft and Ackerly 2010). In addition, niche mechanisms often require spatial variation in the environment to enable coexistence. For example, species may simply differ in habitat preference, so that variation in the conditions of local habitat are required for coexistence. At a small spatial scale encompassing a limited range of habitats, one would tend to find trait filtering, reflecting selection for tolerance to those habitats. At a larger scale, one would expect niche differentiation (Fig. 4; Tilman 2004, Gravel et al. 2006). The Supplementary material Appendix 1 describes how patterning across spatial scales might similarly emerge for niche mechanisms based on life history tradeoffs, and discusses some examples of traits and the respective scales at which niche patterning is expected.

Once one considers a variety of types of niche mechanisms, it becomes clear that the spatial scale at which trait-based niche patterns will be found depends on the particular niche

mechanism. If trait variation stabilizes coexistence through spatial heterogeneity in the environment, then the grain of environmental heterogeneity will affect the expected scale of trait dispersion. This scenario presents a logistical hurdle for trait-based analyses that may be difficult to overcome: data may be needed from large swaths of land, and power issues may ensue (Kraft and Ackerly 2010).

Spatially explicit population dynamic models should be applied to more rigorously derive and refine predictions of pattern. But, save for a few cases (Pacala and Tilman 1994, Hubbell 2006), this path remains essentially unexplored. Such studies must account for the potential interactions of organismal dispersal limitation and the scale of the niche mechanism. For instance, Adler and Muller-Landau (2005) showed that the degree to which Janzen–Connell effects maintain diversity in trees depends on the relative scales of dispersal limitation and enemy-mediated density dependence.

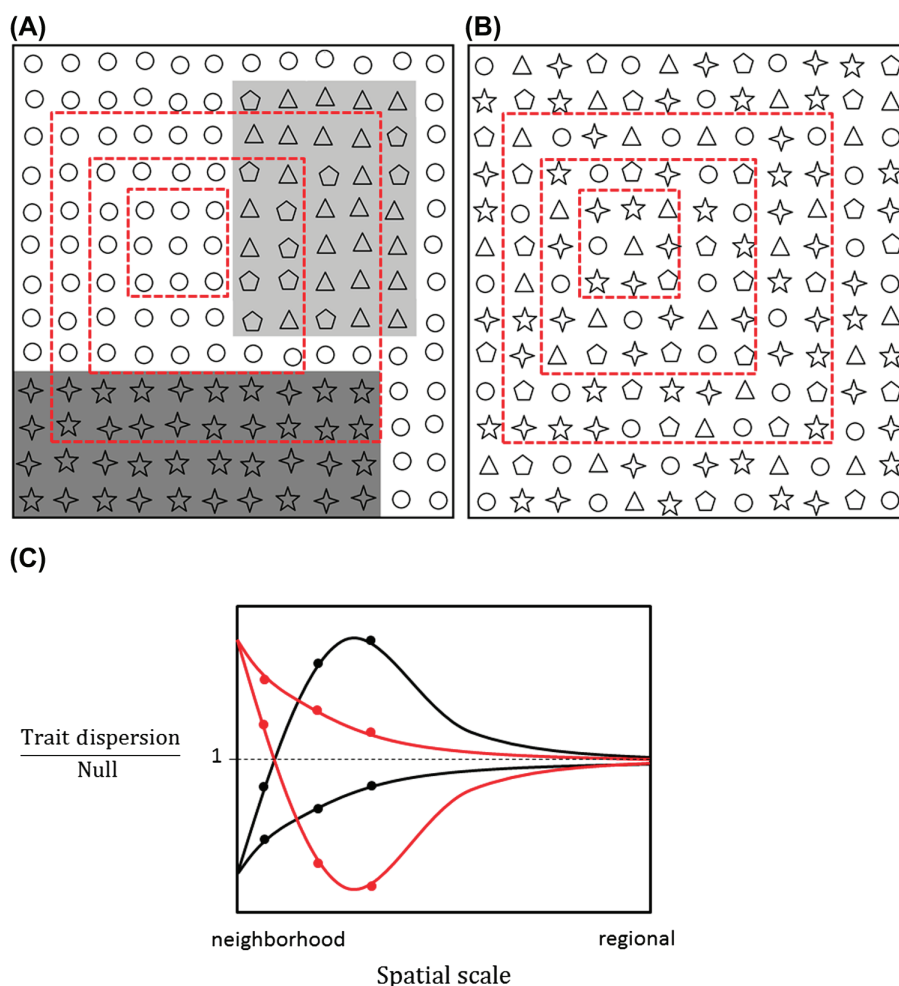


Figure 4. Niche mechanisms and spatial scales. Top panels: representation of niche assembly operating at different spatial scales. Different symbols represent individuals from different species distributed spatially. (A) Case where coexistence relies on a heterogeneous environment. Species traits associate with environmental condition (represented by shading color). In this scenario, evidence of niche assembly is stronger at intermediate or large scales rather than the neighborhood scale. (B) Case where the coexistence mechanism acts at the smallest scale, such as Janzen–Connell effects. In that case, evidence for trait dispersion is strongest at the neighborhood scale. Three sampling scales are shown in each scenario (dashed squares). (C) Compared to a null assemblage, dispersion in local samples can be expected to decrease from small to intermediate or large scales if assembly mechanisms operate at the immediate vicinity of individuals (grey curves), but increase if assembly mechanisms rely on environmental heterogeneity (black curves).

Intraspecific variation

Substantial trait diversity within populations is common in nature, and the subject has received extensive coverage in the past few years. Recent reviews have discussed potential implications for functional diversity, population productivity and stability, coexistence, and ecosystem processes (Albert et al. 2011, 2012, Araújo et al. 2011, Bolnick et al. 2011). However, less is known about the potential implications for trait patterning.

Intraspecific variation raises obvious issues. For example, the common practice of using trait means to represent a species has been criticized for inaccurately representing resource use and strength of competition (Violle et al. 2012, Fig. 5). Indeed, empirical studies have found that considering intraspecific variation may reveal otherwise obscure pattern (Siefert 2012, Lasky et al. 2014b, Carlucci et al. 2015). For example, Siefert (2012) found that detection of habitat filtering and niche differentiation is stronger when considering variation in trait expression within populations at the plot level and especially at the individual level, compared to using species means at the regional level.

Sampling effort is also a concern. Plant studies looking for niche differentiation rarely sample more than ten individuals per species, premised on the idea that trait variation is substantially larger across than within species. However, given observed levels of variation within populations, more recent studies suggest that sample sizes of 10 to 20 individuals are needed to reliably distinguish between species (Hulshof and Swenson 2010). Potential consequences of undersampling include false indication of the degree of trait spacing between species (Lake and Ostling 2009) and missing spatial structure in trait expression that is critical for niche differentiation. A sampling theory to guide empirical work on the appropriate sample size for estimating species means could be helpful, but one may ultimately need to move from using species means to indices of functional diversity designed with intraspecific variation in mind (Schleuter et al. 2010, Albert et al. 2012, Siefert 2012, Violle et al. 2012), or to grouping individuals by trait values rather than by species.

In addition to issues with sampling, likely impacts of intraspecific variation on trait patterning depend on how it affects coexistence (we discuss recent research on this question in the Supplementary material Appendix 2). For example, if intraspecific variation facilitates coexistence by slowing down competitive exclusion, then transient patterns such as emergent clusters can be expected to be persistent and easily maintained by immigration. Alternatively, if intraspecific variation enables coexistence by allowing species to occupy more than one viable niche, then coexistence between species with any trait means is possible. Any trait mean in a particular range can be achieved by having some individuals at a viable niche on one end of that range and some at the other. Thus one would expect weak to no patterning in species mean traits. In contrast, abundance patterns of individuals grouped by trait values rather than species would be preserved.

Very few theoretical studies have tried to verify how intraspecific variation affects trait distribution between coexisting species (but see Barabás and D'Andrea 2016). In simulations of the competition–colonization model,

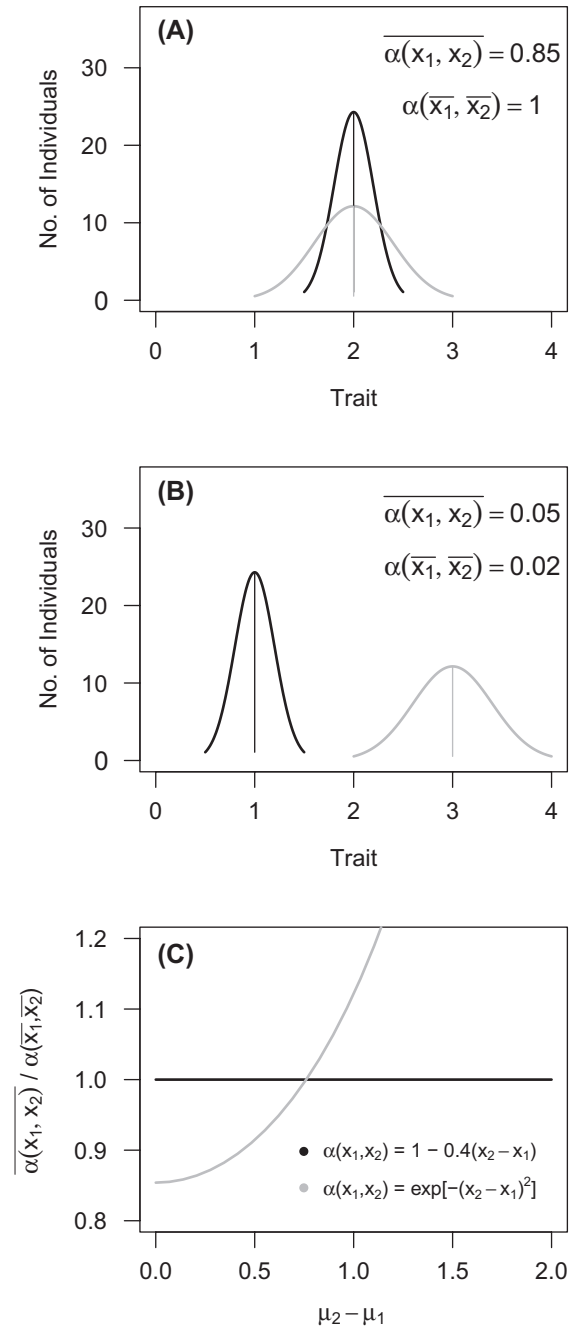


Figure 5. Effect of intraspecific variation on competition. We consider competition between individuals with traits x_1 and x_2 following $\alpha(x_1, x_2) = \exp(-(x_1 - x_2)^2)$, as in MacArthur and Levins 1967, and compare the strength of competition estimated from species mean trait values, $\alpha(\bar{x}_1, \bar{x}_2)$ to the average strength of competition between pairs of non-conspecific individuals, $\overline{\alpha(x_1, x_2)}$. (A) and (B): consider two species whose trait distribution and means are shown in the black and grey curves and lines, respectively. If intraspecific variation is neglected, competition is overestimated when the two species have the same means (A), but underestimated when the distance between the species means is large compared to the trait spread (B). C: The ratio $\overline{\alpha(x_1, x_2)} / \alpha(\bar{x}_1, \bar{x}_2)$ increases from lower to higher than 1 with distance between species means. For comparison, if competition depends linearly on species positions (black curve), intraspecific variation brings no difference, on average, to the competition between homogeneous species.

Courbaud et al. (2010) found that the addition of intraspecific variation changes the region of trait space that allows for coexistence between two species. In particular, a species with intermediate fecundity and mean growth rate can coexist with another very similar species only if intraspecific variation is present. The authors conclude that intraspecific variation in that model leads to the disappearance of limits to similarity. (Importantly, robustness to parameter changes was not examined. Indeed, it seems that a slight variation in mean growth of a coexisting competitor could result in exclusion.) Moving forward, theoretical studies of the impact of intraspecific variation on coexistence and trait patterning should model intraspecific variation not just as a fixed parameter, as is often done, but as a dynamical quantity shaped by a combination of selection and the genetic details of trait inheritance.

Toward a theory of trait patterning under niche differentiation

The primary challenge in linking trait patterns with niche differentiation is gaps in the theoretical foundation from which empirical expectations are derived. Theoretical progress can be made by exploring a spectrum of niche-axis coexistence models for insight on the types of patterns to be found under different biological conditions. We suggest a two-pronged approach with analyses of both conceptual and ground-truthed system-specific models.

Simple conceptual models allow exploration of the impact of the most salient features of competitive interactions commonly found in nature. In the MacArthur–Levins model, competition strength depends strictly on trait differences. This is a common feature of nature (Johansson and Keddy 1991, Jiang et al. 2010, Burns and Strauss 2011) and the defining property of a niche mechanism. The pattern arising from the model can be taken to represent the effect of niche differentiation on trait distribution when acting alone. The competition–colonization (Tilman 1994) and tolerance–fecundity tradeoff (Muller-Landau 2010) are simple representations of competitive hierarchies that may be prevalent in nature (Kunstler et al. 2012) but do not fit into the MacArthur–Levins framework due to the dependence of competition on traits as well as trait differences. We suggest that the MacArthur–Levins model and simple hierarchical tradeoff models are a good starting point for developing trait pattern theory. This review discussed natural phenomena likely to contribute to pattern which are absent in these models, such as environmental fluctuations, multidimensional niche space, immigration, intraspecific variation, evolution and spatial scale-dependent interactions. A systematic approach starting with these conceptual models and adding in simple representations of each of these additional factors in turn could provide insight into the separate and combined effects of different processes on trait dispersion.

Examining this spectrum of models will no doubt be revealing. Yet it does not exhaust the complexity of competitive interactions in nature. For example, competition between neighboring trees in forests is size-structured, and it is unclear how this local scale complexity translates into population-level competition. Hence to complement study of

conceptual models, we suggest that a suite of system-specific models also be developed and studied for trait pattern predictions. Such models would be built on empirical measurements of how traits determine an individual's response to resources and other individuals in the system of interest. Here we envision models with a level of detail similar to the forest architecture hypothesis model (Kohyama 1993). Additional phenomena like those mentioned above (environmental fluctuations, immigration, etc) can be incorporated to the degree to which measurements suggest they are prevalent in the system of interest.

These model-based studies will give insight into the range of trait patterns reflecting niche differentiation in species assemblages, and culminate in more sophisticated predictions for trait pattern and new metrics designed to better handle potentially complex pattern than the ones currently available (Box 2). That said, it is entirely possible that no distinguishable pattern will be observed under some circumstances, such as high immigration and severe competitive asymmetries that depart from the distance-based MacArthur–Levins competition. In that case, trait-pattern analysis will probably be of little avail, and more data-heavy methods such as experiments to directly verify stable dynamics would be required. When trait pattern is distinctive, analysis of pattern across spatial scales and environmental gradients could lead to hypotheses about the predominant community assembly processes, to be then further tested with experiments or observational studies.

Conclusions

Empirical efforts should be informed by theory, and recent modeling results regarding the distribution of species along trait axes depart from classical expectations of overdispersion and even spacing in trait space. Recent field studies look for a less restrictive signature of niche differentiation than earlier ones, but continue to focus on patterns arising in overly simplistic models. Most still fall short of establishing firm links between trait axes and niche axes, and use null models that may not accurately represent expected background processes. The next generation of field studies should be founded on expectations that contemplate patterns coming out of more realistic implementations of niche models.

The theory of trait patterning is itself still a work in progress. Particularly needed are exploring more complex niche mechanisms than the distance-dependent interactions in the MacArthur–Levins model, elucidating the influence of environmental fluctuations on pattern, incorporating intraspecific variation and explicit spatial structure in models, and extending our purview to out-of-equilibrium phenomena such as transients and factors that interact with such dynamics, such as immigration and evolution. Further work on conceptual models may shed light on how different assembly processes shape communities, while system-specific models may clarify the range of patterns to be expected in nature.

Ultimately, trait pattern analysis is but one tool in the toolbox of inference methods. There are of course many complementary empirical approaches to infer niche differentiation from a wide array of observational or experimental

data, including phylogenetic dispersion (Mayfield and Levine 2010), variations in species composition through time (McGill et al. 2005), direct measurement of frequency-dependent competition (Wills et al. 1997), etc. As trait patterning research matures, it can be used in tandem with other methods to paint a more complete picture of community assembly than currently available.

Acknowledgements – We would like to thank Chris Klausmeier, Gary Mittlebach and Cyrille Violle for comments that helped improve the manuscript, and Gyuri Barabás for helpful discussions. *Funding* – This work is supported by the National Science Foundation under grant 1038678, “Niche versus neutral structure in populations and communities” funded by the Advancing Theory in Biology program. We acknowledge the Danish National Research Foundation for support of the Center of Macroecology, Evolution and Climate (grant DNRF96).

References

- Abrams, P. 1975. Limiting similarity and the form of the competition coefficient. – *Theor. Popul. Biol.* 8: 356–375.
- Abrams, P. 1983. The theory of limiting similarity. – *Annu. Rev. Ecol. Syst.* 14: 359–376.
- Abrams, P. 1990. Ecological vs evolutionary consequences of competition. – *Oikos* 57: 147–151.
- Adler, F. R. and Muller-Landau, H. C. 2005. When do localized natural enemies increase species richness? – *Ecol. Lett.* 8: 438–447.
- Adler, P. B. et al. 2007. A niche for neutrality. – *Ecol. Lett.* 10: 95–104.
- Adler, P. B. et al. 2013. Trait-based tests of coexistence mechanisms. – *Ecol. Lett.* 16: 1294–1306.
- Adler, P. B. et al. 2014. Functional traits explain variation in plant life history strategies. – *Proc. Natl Acad. Sci. USA* 111: 740–745.
- Albert, C. H. et al. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? – *Persp. Plant Ecol. Evol. Syst.* 13: 217–225.
- Albert, C. H. et al. 2012. On the importance of intraspecific variability for the quantification of functional diversity. – *Oikos* 121: 116–126.
- Araújo, M. S. et al. 2011. The ecological causes of individual specialisation. – *Ecol. Lett.* 14: 948–958.
- Barabás, G. and Meszéna, G. 2009. When the exception becomes the rule: the disappearance of limiting similarity in the Lotka–Volterra model. – *J. Theor. Biol.* 258: 89–94.
- Barabás, G. and D’Andrea, R. 2016. The effect of intraspecific variation and heritability on community pattern and robustness. – *Ecol. Lett.* 19: 977–986.
- Barabás, G. et al. 2012. Continuous coexistence or discrete species? A new review of an old question. – *Evol. Ecol. Res.* 14: 523–554.
- Barabás, G. et al. 2013a. Species packing in nonsmooth competition models. – *Theor. Ecol.* 6: 1–19.
- Barabás, G. et al. 2013b. Emergent neutrality or hidden niches? – *Oikos* 122: 1565–1572.
- Barabás, G. et al. 2014. Sensitivity analysis of coexistence in ecological communities: theory and application. – *Ecol. Lett.* 17: 1479–1494.
- Beaumont, M. 2010. Approximate Bayesian computation in evolution and ecology. – *Annu. Rev. Ecol. Evol. Syst.* 41: 379–406.
- Bell, G. 2001. Neutral macroecology. – *Science* 293: 2413–2418.
- Bolnick, D. I. et al. 2011. Why intraspecific trait variation matters in community ecology. – *Trends Ecol. Evol.* 26: 183–192.
- Bond, E. M. and Chase, J. M. 2002. Biodiversity and ecosystem functioning at local and regional spatial scales. – *Ecol. Lett.* 5: 467–470.
- Bonsall, M. B. et al. 2004. Life history tradeoffs assemble ecological guilds. – *Science* 306: 111–114.
- Breitschwerdt, E. et al. 2015. Do newcomers stick to the rules of the residents? Designing trait-based community assembly tests. – *J. Veg. Sci.* 26: 219–232.
- Burns, J. and Strauss, S. 2011. More closely related species are more ecologically similar in an experimental test. – *Proc. Natl Acad. Sci. USA* 108: 5302–5307.
- Buttel, L. et al. 2002. Competition and species packing in patchy environments. – *Theor. Popul. Biol.* 61: 265–276.
- Carboni, M. et al. 2014. Changes in trait divergence and convergence along a productivity gradient in wet meadows. – *Agric. Ecosyst. Environ.* 182: 96–105.
- Carlucci, M. B. et al. 2015. Between- and within-species trait variability and the assembly of sapling communities in forest patches. – *J. Veg. Sci.* 26: 21–31.
- Cavender-Bares, J. et al. 2006. Phylogenetic structure of Floridian plant communities depends on taxonomic and spatial scale. – *Ecology* 87: S109–S122.
- Cavender-Bares, J. et al. 2009. The merging of community ecology and phylogenetic biology. – *Ecol. Lett.* 12: 693–715.
- Chave, J. et al. 2002. Comparing classical community models: theoretical consequences for patterns of diversity. – *Am. Nat.* 159: 1–23.
- Chesson, P. 1991. A need for niches? – *Trends Ecol. Evol.* 6: 26–28.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. – *Annu. Rev. Ecol. Syst.* 31: 343–366.
- Chesson, P. and Huntly, N. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. – *Am. Nat.* 150: 519–553.
- Clark, J. S. 2012. The coherence problem with the unified neutral theory of biodiversity. – *Trends Ecol. Evol.* 27: 199–203.
- Cody, M. L. 1999. Assembly rules at different scales in plant and bird communities. – In: Weiher, E. and Keddy, P. (eds), *Ecological assembly rules: perspectives, advances, retreats*. Cambridge Univ. Press, pp. 165–204.
- Cornwell, W. K. and Ackerly, D. D. 2009. Community assembly and shifts in plant trait distributions across an environmental gradient in coastal California. – *Ecol. Monogr.* 79: 109–126.
- Cornwell, W. K. et al. 2006. A trait-based test for habitat filtering: convex hull volume. – *Ecology* 87: 1465–1471.
- Courbaud, B. et al. 2010. Intra-specific variability and the competition–colonisation tradeoff: coexistence, abundance and stability patterns. – *Theor. Ecol.* 5: 61–71.
- D’Andrea, R. and Ostling, A. 2015. Can clustering in genotype space reveal “niches”? – *Am. Nat.* 187: 130–135.
- D’Andrea, R. et al. 2013. Revising the tolerance–fecundity tradeoff; or, on the consequences of discontinuous resource use for limiting similarity, species diversity and trait dispersion. – *Am. Nat.* 181: E91–E101.
- Dayan, T. and Simberloff, D. 2005. Ecological and community-wide character displacement: the next generation. – *Ecol. Lett.* 8: 875–894.
- de Bello, F. et al. 2012. Functional species pool framework to test for biotic effects on community assembly. – *Ecology* 93: 2263–2273.
- Deza, M. M. and Deza, E. 2006. *Dictionary of distances*. – Elsevier.
- Doebeli, M. et al. 2007. Multimodal pattern formation in phenotype distributions of sexual populations. – *Proc. R. Soc. B* 274: 347–357.

- Ernebjerg, M. and Kishony, R. 2011. Dynamic phenotypic clustering in noisy ecosystems. – *PLoS Comput. Biol.* 7: e1002017.
- Fort, H. et al. 2010. The clumping transition in niche competition: a robust critical phenomenon. – *J. Stat. Mech. Theor. Exp.* 2010: P05005.
- Franzén, D. 2004. Plant species coexistence and dispersion of seed traits in a grassland. – *Ecography* 27: 218–224.
- Fussmann, G. F. et al. 2007. Eco-evolutionary dynamics of communities and ecosystems. – *Funct. Ecol.* 21: 465–477.
- Google Ngram Viewer. 2015. Limiting similarity. – Google books Ngram Viewer.
- Gotelli, N. J. and Graves, G. R. 1996. Null models in ecology. – Smithsonian Institution.
- Gotelli, N. J. and McGill, B. J. 2006. Null versus neutral models: what's the difference? – *Ecography* 29: 793–800.
- Götzenberger, L. et al. 2012. Ecological assembly rules in plant communities—approaches, patterns and prospects. – *Biol. Rev.* 87: 111–127.
- Gravel, D. et al. 2006. Reconciling niche and neutrality: the continuum hypothesis. – *Ecol. Lett.* 9: 399–409.
- Gross, K. et al. 2014. Species richness and the temporal stability of biomass production: a new analysis of recent biodiversity experiments. – *Am. Nat.* 183: 1–12.
- Haegeman, B. et al. 2014. Predicting coexistence of plants subject to a tolerance–competition tradeoff. – *J. Math. Biol.* 68: 1815–1847.
- Herben, T. and Goldberg, D. E. 2014. Community assembly by limiting similarity vs competitive hierarchies: testing the consequences of dispersion of individual traits. – *J. Ecol.* 102: 156–166.
- Hernández-García, E. et al. 2009. Species competition: coexistence, exclusion and clustering. – *Philos. Trans. R. Soc. A* 367: 3183–3195.
- HilleRisLambers, J. et al. 2012. Rethinking community assembly through the lens of coexistence theory. – *Annu. Rev. Ecol. Evol. Syst.* 43: 227–248.
- Hubbell, S. P. 2001. The unified theory of biodiversity and biogeography. Monogr. Popul. Biol. – Princeton Univ. Press.
- Hubbell, S. P. 2006. Neutral theory and the evolution of ecological equivalence. – *Ecology* 87: 1387–1398.
- Hulshof, C. M. and Swenson, N. G. 2010. Variation in leaf functional trait values within and across individuals and species: an example from a Costa Rican dry forest. – *Funct. Ecol.* 24: 217–223.
- Hutchinson, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? – *Am. Nat.* 93: 145–159.
- Jeraldo, P. et al. 2012. Quantification of the relative roles of niche and neutral processes in structuring gastrointestinal microbiomes. – *Proc. Natl Acad. Sci. USA* 109: 9692–9698.
- Jiang, L. et al. 2010. An experimental test of Darwin's naturalization hypothesis. – *Am. Nat.* 175: 415–423.
- Johansson, M. E. and Keddy, P. 1991. Intensity and asymmetry of competition between plant pairs of different degrees of similarity – an experimental-study on 2 guilds of wetland plants. – *Oikos* 60: 27–34.
- Kinzig, P. et al. 1999. Limiting similarity, species packing and system stability for hierarchical competition–colonization models. – *Am. Nat.* 153: 371–383.
- Kneitel, J. M. and Chase, J. M. 2004. Tradeoffs in community ecology: linking spatial scales and species coexistence. – *Ecol. Lett.* 7: 69–80.
- Kohyama, T. 1993. Size-structured tree populations in gap-dynamic forest – the forest architecture hypothesis for the stable coexistence of species. – *J. Ecol.* 81: 131–143.
- Kohyama, T. 2006. The effect of patch demography on the community structure of forest trees. – *Ecol. Res.* 21: 346–355.
- Kraft, N. J. B. and Ackerly, D. D. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. – *Ecol. Monogr.* 80: 401–422.
- Kraft, N. J. B. et al. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. – *Science* 322: 580–582.
- Kraft, N. J. B. et al. 2014. Plant functional traits and the multidimensional nature of species coexistence. – *Proc. Natl Acad. Sci. USA* 112: 797–802.
- Kunstler, G. et al. 2012. Competitive interactions between forest trees are driven by species' trait hierarchy, not phylogenetic or functional similarity: implications for forest community assembly. – *Ecol. Lett.* 15: 831–840.
- Lake, J. K. and Ostling, A. 2009. Comment on “Functional traits and niche-based tree community assembly in an Amazonian forest”. – *Science* 324: 1015; author reply 1015.
- Laliberté, E. and Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. – *Ecology* 91: 299–305.
- Lasky, J. R. et al. 2014a. Trait-mediated assembly processes predict successional changes in community diversity of tropical forests. – *Proc. Natl Acad. Sci. USA* 111: 5616–5621.
- Lasky, J. R. et al. 2014b. The role of functional traits and individual variation in the co-occurrence of *Ficus* species. – *Ecology* 95: 978–990.
- Lasky, J. R. et al. 2015. Ontogenetic shifts in trait-mediated mechanisms of plant community assembly. – *Ecology* 96: 2157–2169.
- Lawson, D. J. and Jensen, H. J. 2007. Neutral evolution in a biological population as diffusion in phenotype space: reproduction with local mutation but without selection. – *Phys. Rev. Lett.* 98: 2–5.
- Leimar, O. et al. 2008. Evolution of phenotypic clusters through competition and local adaptation along an environmental gradient. – *Evolution* 62: 807–822.
- Letten, A. D. et al. 2014. Phylogenetic and functional dissimilarity does not increase during temporal heathland succession. – *Proc. R. Soc. B* 2014 281 20142102.
- Levin, S. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. – *Am. Nat.* 104: 413–423.
- MacArthur, R. and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. – *Am. Nat.* 101: 377–385.
- Manly, B. F. J. 1991. Randomization and Monte-Carlo methods in biology. – Chapman and Hall.
- Mason, N. W. H. et al. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. – *Oikos* 111: 112–118.
- May, R. M. 1973. Stability and complexity in model ecosystems. – Princeton Univ. Press.
- May, R. M. and MacArthur, R. H. 1972. Niche overlap as a function of environmental variability. – *Proc. Natl Acad. Sci. USA* 69: 1109–1113.
- Mayfield, M. M. and Levine, J. M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. – *Ecol. Lett.* 13: 1085–1093.
- McGill, B. J. et al. 2005. Community inertia of Quaternary small mammal assemblages in North America. – *Proc. Natl Acad. Sci. USA* 102: 16701–16706.
- Moles, A. T. and Westoby, M. 2004. Seedling survival and seed size: a synthesis of the literature. – *J. Ecol.* 92: 372–383.
- Mouillot, D. et al. 2005. Functional regularity: a neglected aspect of functional diversity. – *Oecologia* 142: 353–359.
- Muller-Landau, H. C. 2010. The tolerance-fecundity tradeoff and the maintenance of diversity in seed size. – *Proc. Natl Acad. Sci. USA* 107: 4242–4247.

- Ostling, A. M. 2012. Large-scale spatial synchrony and the stability of forest biodiversity revisited. – *J. Plant Ecol.* 5: 52–63.
- Pacala, S. W. and Tilman, D. 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. – *Am. Nat.* 143: 222–257.
- Pacala, S. W. and Rees, M. 1998. Models suggesting field experiments to test two hypotheses explaining successional diversity. – *Am. Nat.* 152: 729–737.
- Pacala, S. W. et al. 1993. Forest models defined by field measurements. I. The design of a northeastern forest simulator. – *Can. J. For. Res.* 23: 1980–1988.
- Paine, C. E. T. et al. 2011. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. – *Oikos* 120: 720–727.
- Pigot, A. L. and Etienne, R. S. 2015. A new dynamic null model for phylogenetic community structure. – *Ecol. Lett.* 18: 153–163.
- Poorter, A. L. et al. 2008. Are functional traits good predictors of demographic rates? Evidence from five Neotropical forests. – *Ecology* 89: 1908–1920.
- Rosindell, J. et al. 2011. The unified neutral theory of biodiversity and biogeography at age ten. – *Trends Ecol. Evol.* 26: 340–348.
- Roughgarden, J. 1974. Species packing and the competition function with illustrations from coral reef fish. – *Theor. Popul. Biol.* 5: 163–186.
- Roughgarden, J. 1983. Competition and theory in community ecology. – *Am. Nat.* 122: 583–601.
- Scheffer, M. and van Nes, E. H. 2006. Self-organized similarity, the evolutionary emergence of groups of similar species. – *Proc. Natl Acad. Sci. USA* 103: 6230–6235.
- Schleuter, D. et al. 2010. A user's guide to functional diversity indices. – *Ecol. Monogr.* 80: 469–484.
- Schwinning, S. and Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. – *Oecologia* 113: 447–455.
- Segura, A. M. et al. 2011. Emergent neutrality drives phytoplankton species coexistence. – *Proc. R. Soc. B* 278: 2355–2361.
- Siefert, A. 2012. Incorporating intraspecific variation in tests of trait-based community assembly. – *Oecologia* 170: 767–775.
- Siepielski, A. M. and McPeck, M. A. 2010. On the evidence for species coexistence: a critique of the coexistence program. – *Ecology* 91: 3153–3164.
- Silva, R. R. and Brandão, C. R. F. 2014. Ecosystem-wide morphological structure of leaf-litter ant communities along a tropical latitudinal gradient. – *PLoS ONE* 9 (3): e93049.
- Simberloff, D. and Boecklen, W. 1981. Santa Rosalia reconsidered: size ratios and competition. – *Evolution* 35: 1206–1228.
- Sterck, F. et al. 2011. Functional traits determine tradeoffs and niches in a tropical forest community. – *Proc. Natl Acad. Sci. USA* 108: 20627–20632.
- Strong Jr, D. R. et al. 1979. Test of community-wide character displacement against null hypotheses. – *Evolution* 33: 897–913.
- Stubbs, W. J. and Wilson, J. B. 2004. Evidence for limiting similarity in a sand dune community. – *J. Ecol.* 92: 557–567.
- Swenson, N. G. and Enquist, B. J. 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. – *Ecology* 90: 2161–2170.
- Swenson, N. G. et al. 2007. The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. – *Ecology* 88: 1770–1780.
- Tilman, D. 1994. Competition and biodiversity in spatially structured habitats. – *Ecology* 75: 2–16.
- Tilman, D. 2004. Niche tradeoffs, neutrality and community structure: a stochastic theory of resource competition, invasion and community assembly. – *Proc. Natl Acad. Sci. USA* 101: 10854–10861.
- Turelli, M. 1981. Niche overlap and invasion of competitors in random environments. I. Models without demographic stochasticity. – *Theor. Popul. Biol.* 56: 1–56.
- Ulrich, W. 2004. Species co-occurrences and neutral models: reassessing J. M. Diamond's assembly rules. – *Oikos* 107: 603–609.
- Uriarte, M. et al. 2010. Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. – *Ecol. Lett.* 13: 1503–1514.
- van der Plas, F. et al. 2015. A new modeling approach estimates the relative importance of different community assembly processes. – *Ecology* 96: 1502–1515.
- Vergnon, R. et al. 2009. Niches versus neutrality: uncovering the drivers of diversity in a species-rich community. – *Ecol. Lett.* 12: 1079–1090.
- Vergnon, R. et al. 2012. Emergent neutrality leads to multimodal species abundance distributions. – *Nat. Comm.* 3: 663.
- Villéger, S. et al. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. – *Ecology* 89: 2290–2301.
- Violle, C. et al. 2007. Let the concept of trait be functional! – *Oikos* 116: 882–892.
- Violle, C. et al. 2012. The return of the variance: intraspecific variability in community ecology. – *Trends Ecol. Evol.* 27: 244–252.
- Waples, R. S. et al. 2011. Calculating N_e and N_e/N in age-structured populations: a hybrid Felsenstein–Hill approach. – *Ecology* 92: 1513–1522.
- Weiher, E. and Keddy, P. (eds) 1999. *Ecological assembly rules: perspectives, advances, retreats.* – Cambridge Univ. Press.
- Weiher, E. et al. 1998. Community assembly rules, morphological dispersion and the coexistence of plant species. – *Oikos* 81: 309–322.
- Wills, C. et al. 1997. Strong density- and diversity-related effects help to maintain tree species diversity in a neotropical forest. – *Proc. Natl Acad. Sci. USA* 94: 1252–1257.
- Wilson, J. B. 1999. Assembly rules in plant communities. – In: Weiher, E. and Keddy, P. (eds), *Ecological assembly rules: perspectives, advances, retreats.* Cambridge Univ. Press, pp. 130–160.
- Wilson, J. B. and Stubbs, W. J. 2012. Evidence for assembly rules: limiting similarity within a saltmarsh. – *J. Ecol.* 100: 210–221.
- Wright, I. J. et al. 2004. The worldwide leaf economics spectrum. – *Nature* 428: 821–827.
- Wright, S. J. et al. 2010. Functional traits and the growth–mortality tradeoff in tropical trees. – *Ecology* 91: 3664–3674.
- Yachi, S. and Loreau, M. 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. – *Proc. Natl Acad. Sci. USA* 96: 1463–1468.
- Yan, B. et al. 2012. Trait assembly of woody plants in communities across sub-alpine gradients: identifying the role of limiting similarity. – *J. Veg. Sci.* 23: 698–708.
- Yoshiyama, R. M. and Roughgarden, J. 1977. Species packing in two dimensions. – *Am. Nat.* 111: 107–121.

Supplementary material (available online as Appendix oik-02979 at <www.oikosjournal.org/appendix/oik-02979>). Appendix 1–2.