

Spatially Explicit Metrics of Species Diversity, Functional Diversity, and Phylogenetic Diversity: Insights into Plant Community Assembly Processes

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Keywords

biotic neighborhood, community assembly, individual-based neighborhood
analysis, fully mapped plots, point pattern analysis, spatial diversity metrics

Abstract

Spatial processes underlie major species coexistence mechanisms. A range of
spatial analysis techniques are increasingly applied to data of fully mapped
communities to quantify spatial structures in species and phylogenetic and
functional diversity at some given spatial scale with the goal of gaining

insights into processes of community assembly and dynamics. We review these techniques, including spatial point pattern analysis, quadrat-based analyses, and individual-based neighborhood models, and provide a practical roadmap for ecologists in the analysis of local spatial structures in species and phylogenetic and functional diversity. We show how scale-dependent metrics of spatial diversity can be used in concert with ecological null models, statistical models, and dynamic community simulation models to detect spatial patterns, reveal the influence of the biotic neighborhood on plant performance, and quantify the relative contribution of species interactions, habitat heterogeneity, and stochastic processes to community assembly across scale. Future works should integrate these approaches into a dynamic spatiotemporal framework.

1. INTRODUCTION

Modern ecology is driven by an interest in processes that are inherently spatial. This has not always been the case. Until the mid-1980s most ecological research avoided the explicit consideration of space (Legendre & Fortin 1989), but during the last three decades ecology reached a point where it became necessary to adopt a spatially explicit perspective to advance the science (e.g., Levin 1992, Tilman & Kareiva 1997). Current ecological theories provide increasing evidence that spatial pattern and process play an important role in the assembly, dynamics, and functioning of ecological communities across scales (Chesson 2000, Bolker et al. 2003, Leibold et al. 2004, McIntire & Fajardo 2009). For example, plants interact mostly with their nearest neighbors (Canham & Uriarte 2006), plant performance depends on the species composition of their neighborhood (Uriarte et al. 2010a) as well as their abiotic neighborhood (i.e., habitat filtering, in which species arrive at a site but fail to persist owing to the abiotic conditions; van der Valk 1981, Kraft et al. 2015a), and dispersal limitation can generate patchy species distributions that reduce encounters with competitively dominant species and slow down competitive exclusion (Pacala & Levin 1997). These processes operate over somewhat different spatial scales (McGill 2010a): For example, in plant communities, microclimatic conditions and species interactions can vary over the scale of centimeters to meters, whereas dispersal in some species can drive patterns at tens to thousands of meters. These insights suggest that many of the key ecological processes individual plants are subjected to have the potential to generate spatial patterns but most likely at different spatial scales (McGill 2010a), thereby retaining signatures of the underlying processes.

In addition to the increasing consideration of spatial pattern and process in ecological studies, the consideration of phylogenetic and functional relationships among species has advanced our understanding of coexistence and assembly mechanisms in ecological communities (e.g., Webb et al. 2002, Cavender-Bares et al. 2004, Kraft et al. 2008, Uriarte et al. 2010a, Fortunel et al. 2016). For example, statistical neighborhood analysis has revealed that survival and growth of plants often depend on functional and evolutionary relationships with neighbors (e.g., Webb et al. 2006, Metz et al. 2010, Uriarte et al. 2010a, Lasky et al. 2014), and community assembly theory predicts that deterministic processes such as habitat filtering and competition that act on niche differences between species can generate contrasting spatial patterns such as phylogenetic clustering (i.e., local co-occurrence of more closely related species than expected by chance) or overdispersion (i.e., local co-occurrence of less closely related species) (Webb et al. 2002, Kraft & Ackerly 2014), though the specifics of these predictions can be complex (e.g., Mayfield & Levine 2010).

The increasing interest in spatial processes has gone hand in hand with efforts to map the spatial position of organisms within ecological communities. For example, starting in 1981 with

a plot at Barro Colorado Island, the Smithsonian ForestGeo network now comprises numerous forest dynamics plots for which a complete census is taken every five years using standardized protocols (Condit 1998, Anderson-Teixeira et al. 2015). Such spatially explicit multivariate data (a.k.a. fully mapped plots) that comprise information on the location, size, and species identity of all free-standing plants within the plot—often together with spatially explicit environmental information—contain invaluable information for detecting underlying spatial processes.

With the integration of a spatial component into studies of community ecology, it has become necessary to develop tools required for characterizing and analyzing spatial patterns and their relationships with spatial processes. Earlier analyses of fully mapped plots applied essentially nonspatial methods developed in community ecology, biogeography, and conservation ecology (e.g., Connor & Simberloff 1979, Gotelli 2000, Webb 2000) to detect phylogenetic clustering or overdispersion (e.g., Kembel & Hubbell 2006). One of our objectives here is to describe two emerging perspectives that take a more nuanced approach to spatial analyses on diversity metrics: point pattern analyses (Wiegand & Moloney 2014, Velázquez et al. 2016) and regression-based statistical neighborhood models (Canham & Uriarte 2006). The recent point pattern framework of diversity metrics integrates the spatially explicit perspective with information on functional and phylogenetic relationships (Shen et al. 2013; Wiegand & Moloney 2014; Péliissier & Goreaud 2015; Wang et al. 2015, 2016) to quantify functional or phylogenetic spatial structures in the neighborhood of individual plants as a function of spatial scale. An example is the analysis of changes in functional or phylogenetic dissimilarity of local communities with spatial distance (Wang et al. 2015). Statistical neighborhood models relate the performance of individual plants (i.e., recruitment, growth, and survival) to their biotic and abiotic neighborhood with a spatial scale defined a priori or estimated (e.g., Hubbell et al. 2001; Uriarte et al. 2004a, 2010a; Stoll & Newbery 2005). We define a neighborhood as the distances over which the ecological mechanisms of interest operate. For example, dispersal limitation in trees may occur at scales up to a few hundred meters (Morlon et al. 2008, Wang et al. 2015), whereas the neighborhood relevant for competitive interactions among trees typically ranges over 1–30 m (Uriarte et al. 2004b, Wiegand et al. 2007).

The ultimate goal of most approaches to analyzing fully mapped plots is to provide insights into the mechanisms underlying the assembly and dynamics of the community by exploring the link between (spatial) pattern and process. Existence of such a link is a source of long-lasting dispute in ecology (Wiens 1989, Gotelli & Graves 1996). Early refutations of the pattern–process link argue that various processes can create the same patterns or that multiple processes acting together can effectively erase the spatial signatures of individual processes (e.g., Colwell & Winkler 1984). However, McIntire & Fajardo (2009) have cogently argued that prior studies questioning the spatial pattern–process link may, in part, suffer from limitations such as (a) imprecise quantification of patterns and focus on single patterns, (b) imprecise biological hypothesis on spatial patterns, and (c) lack of a priori alternative hypotheses. Imprecise quantification of patterns especially includes the misuse of metrics that are unable to dissect diversity patterns as a function of spatial scale. Application of spatially explicit, scale-dependent metrics may reveal that different processes create a similar pattern, but at different spatial scales (McGill 2010a), and that opposing processes may cancel each other out only if scale is ignored. Although the link between spatial pattern and process is not always straightforward, we argue that spatial patterns retain signatures of the underlying processes to be uncovered with recent methods of spatial analysis (McIntire & Fajardo 2009, Wiegand & Moloney 2014).

Our objectives here are to summarize techniques that allow for precise quantification of a variety of spatial diversity patterns in fully mapped communities and to highlight advances in addressing key ecological questions. We explain how spatially explicit and scale-dependent diversity metrics can be used in concert with spatially explicit null models, statistical models, and dynamic

Table 1 Summary of key biological questions that can be addressed using multivariate spatial point pattern methods, quadrat-based analysis, and statistical neighborhood analysis

Main task	Key objectives	Methods
(A) Detection of spatial patterns in diversity	Spatial scales at which functional or phylogenetic clustering occurs (A1) Spatial scales at which functional or phylogenetic overdispersion occurs (A2) How species are embedded into (or how they impact) their biotic neighborhood (A3) Local dominance of species (A4) Conspecific versus heterospecific negative density dependence in plant performance (A5)	Quadrat-based analysis (Webb 2000, Kembel & Hubbell 2006, Hardy 2008, Miller et al. 2017) or point pattern analysis (Shen et al. 2013, Parmentier et al. 2014) using dissimilarity matrix Multivariate point pattern analysis using dissimilarity matrix (Wiegand et al. 2007, Wang et al. 2016) Statistical neighborhood analysis (Comita et al. 2010, Paine et al. 2012)
(B) The contribution of different features of species patterns in explaining spatial diversity patterns	The species area relationship (B1) The distance decay of similarity (B2) Phylogenetic or functional diversity–area relationships (B3) Phylogenetic or functional beta diversity (B4)	Multivariate point pattern analysis using dissimilarity matrix (Shen et al. 2009; Wang et al. 2011, 2013, 2015; Yang et al. 2013)
(C) Indirect inference on processes (same as A and B, but with additional biological assumptions and hypotheses)	The relative importance of habitat filtering and species interactions in explaining phylogenetic or functional clustering or overdispersion (C1) The relative importance of ecological mechanism in explaining spatial diversity patterns (C2)	Quadrat-based analysis (Webb 2000, Kembel & Hubbell 2006, Hardy 2008, Miller et al. 2017) or point pattern analysis (Shen et al. 2013, Parmentier et al. 2014) using dissimilarity matrix Multivariate phylogenetic point pattern analysis using dissimilarity matrix (Shen et al. 2009; Wang et al. 2011, 2013, 2015)
(D) Direct inference on processes based on spatial diversity patterns	Influence of the biotic/abiotic neighborhood of plants and its traits on recruitment, growth, and survival (D1); for example: <ul style="list-style-type: none"> ■ Species equivalence hypotheses ■ Trait or phylogenetic similarity hypothesis ■ Trait hierarchy hypothesis Relative importance of ecological mechanism in shaping community assembly and species coexistence (D2) Test of spatial coexistence mechanism (D3)	Statistical neighborhood analysis (Canham & Uriarte 2006; Uriarte et al. 2004a, 2010a; Kunstler et al. 2012) Multivariate point pattern metrics and individual-based, spatially explicit simulation models (May et al. 2015, 2016; Brown et al. 2016)

community simulation models to provide insights into the mechanisms underlying assembly and dynamics of natural communities. In addition, we integrate this spatially explicit perspective with information on functional and phylogenetic relationships among species. Because quadrat-based approaches have been reviewed elsewhere (e.g., Miller et al. 2017 and references therein) and discard important spatial information within quadrats, we focus on multivariate spatial point pattern methods and individual-based neighborhood statistical models. In this review, we first provide a summary of key biological questions that can be addressed using spatial analysis (**Table 1**). We then summarize the analytical methods that underlie these approaches and outline how they can be used to address these key biological questions. Finally, we conclude with prospects for future research in this area.

Our focus is on fully mapped multivariate data sets (i.e., multiple units of analyses, be it species, functional traits, or clades). We exclude methods that simply analyze the topology of phylogenetic trees and focus instead on measures that use a matrix δ_{ij}^P to describe some metric of ecological

dissimilarity between species i and j . This approach allows for a unified analytical treatment of the different types of ecological dissimilarities considered here. For simplicity, we focus our descriptions below on phylogenetic dissimilarity measures, though functional similarity or any other measure of ecological dissimilarity can be substituted with no additional modifications. We also exclude variation partitioning because it does not rely on the explicit location of individuals and is covered elsewhere (e.g., Anderson et al. 2011, Dray et al. 2012). As a final note, our review targets the local neighborhood scale, and therefore we do not consider biodiversity maintenance processes that occur primarily at the regional scale, such as immigration or source–sink dynamics.

2. KEY QUESTIONS TO BE ADDRESSED WITH SPATIAL ANALYSIS

We divide the objectives that can be addressed with spatial analyses of fully mapped plots into four general tasks (**Table 1**): (A) detection of scale-dependent diversity patterns, (B) determining the relative importance of different features of species distribution patterns in explaining spatial diversity patterns, and (C) indirect and (D) direct inference on processes. Tasks A and B can be mostly addressed by combining scale-dependent diversity metrics with null model approaches. Indirect inference is based on pattern detection but requires additional assumptions and appropriate hypothesis (McIntire & Fajardo 2009), whereas direct inference uses methods of statistical inference teamed with statistical (Uriarte et al. 2004a) or stochastic simulation models (Grimm et al. 2005, May et al. 2015).

A number of spatial, scale-dependent diversity patterns are involved in—or emerge from—spatial mechanisms of community assembly. Because fully mapped data are complex, have many dimensions, and can be viewed over a range of spatial scales and phylogenetic depths, detecting patterns in such data is a highly nontrivial task (objectives A1–A5 for task A, **Table 1**). A common example is detection of patterns of phylogenetic or functional clustering in ecological communities. A wealth of methods aim to infer the action of community assembly processes on the basis of patterns (e.g., Webb et al. 2002, Cornwell et al. 2006, Helmus et al. 2007, Kembel et al. 2010). In the context of this review, we focus on the detection of local-scale correlations in the ecological dissimilarity of neighboring individuals (i.e., neighborhood phylogenetic clustering and overdispersion) and the determination of the spatial scales and/or phylogenetic depths over which these patterns occur (objectives A1 and A2) (Shen et al. 2013, Parmentier et al. 2014). For example, Parmentier et al. (2014) studied phylogenetic turnover in a fully mapped African rain forest up to scales of several hundreds of meters to find evidence for habitat filtering.

The neighborhood perspective focuses on analyzing how plants of a given focal species are spatially embedded into their biotic or abiotic neighborhood or how they impact their neighbors (objective A3). Typical analyses focus either on the role that focal species play in increasing or decreasing local diversity (e.g., Wiegand et al. 2007, Punchi-Manage et al. 2015, Chacón-Labela et al. 2016, Perry et al. 2017) or on the functional and phylogenetic diversity of the biotic neighborhood of a focal species (Wang et al. 2016). The neighborhood scales investigated in this type of analysis depend on the size of the plants and range up to 50 m for forests (Wiegand et al. 2007, Punchi-Manage et al. 2015, Wang et al. 2016), up to 6 m in the shrubland (Perry et al. 2017), and up to 50 cm in the Mediterranean dwarf shrubland (Chacón-Labela et al. 2016). Insights into the mechanism of coexistence can be provided by detecting patterns of local dominance of species (Wang et al. 2016) (objective A4) that increase the frequency of intraspecific interactions (relative to interspecific) and delay competitive exclusion (Stoll & Prati 2001). Finally, the search for evidence for stabilizing mechanisms (sensu Chesson 2000) in species-rich communities has focused on detection of patterns consistent with negative density dependence (Comita et al. 2010, Uriarte et al. 2010a, Paine et al. 2012) (objective A5).

Fully mapped community data contain numerous features (e.g., species aggregation, pairwise co-occurrences, or spatial phylogenetic clustering), and null model randomization-based approaches that keep certain features of the data constant can be used to detect the main features that explain spatial diversity patterns such as species area relationships or distance decay of similarity (Morlon et al. 2008, Shen et al. 2009) (objectives B1–B4 for task B). Given appropriate assumptions, this approach allows for the indirect inference of the relative importance of processes such as dispersal limitation, habitat filtering, species interactions, and stochastic variation in explaining biodiversity patterns (e.g., Shen et al. 2009; Wang et al. 2011, 2015) (objectives C1 and C2).

Direct inference of processes of community assembly and dynamics can be accomplished in two different ways. First, spatially explicit statistical neighborhood approaches (Canham & Uriarte 2006) relate key demographic processes of individual plants to features of its biotic and abiotic neighborhoods (objective D1) by using inference based on likelihood methods, information theory, or hierarchical Bayesian approaches (Lasky et al. 2014, Fortunel et al. 2016, Uriarte et al. 2016). Second, individual-based simulation models (Grimm et al. 2005; May et al. 2015, 2016) include dynamic representations of alternative hypotheses on processes, and use of recent techniques of statistical inference for stochastic simulation models (Hartig et al. 2011) allows for model selection and inference on the hypothesis that is most compatible with the data (objectives D2 and D3).

3. POINT PATTERN DIVERSITY METRICS

3.1. General Framework for Point Pattern Diversity Metrics

We generalize the two basic diversity indices, species richness S and the Simpson index D , toward spatially explicit metrics of species diversity, functional diversity, and phylogenetic diversity. Point pattern extensions of S and D consider properties of pairs of individuals within an observation window W that are a given distance r apart (for metrics of beta diversity) or that are a smaller distance than r apart (for metrics of alpha diversity) (**Figure 1a**) (Shimatani 2001, Wiegand & Moloney 2014, Péliissier & Goreaud 2015). Thus, the point pattern metrics quantify spatial structures in the neighborhood of individual plants as a function of spatial scale.

Our general framework results in eight metric families that arise by crossing the level of analysis (community versus species level) with the diversity metric (S versus D) with alpha versus beta diversity (see **Supplemental Appendix 1** and **Supplemental Table 1** therein for details). The metrics of the framework are implemented in the software *Programita* (Wiegand & Moloney 2014).

3.2. Beta Diversity at the Community Level

The Simpson index $D = \sum_{i=1}^S \sum_{j=1}^S \delta_{ij} f_i f_j$ is the probability that two randomly selected individuals in the observation window W are heterospecific (Simpson 1949), where f_i is the relative abundances of species i in W , S is the total number of species in W , and $\delta_{ij} = 1$ for heterospecifics and $\delta_{ij} = 0$ for conspecifics. **Supplemental Figure 5 (Supplemental Appendix 1)** shows a summary scheme of the Simpson index family. The Simpson index can be generalized to take a continuous measure of ecological dissimilarity δ_{ij}^p between species i and j into account (Clarke & Warwick 1998). The resulting metric $D^p = \sum_{i,j=1}^S \delta_{ij}^p f_i f_j$ is the mean pairwise dissimilarity between individuals in W (Rao 1982). To remove some of the overt dependence of D^p on species

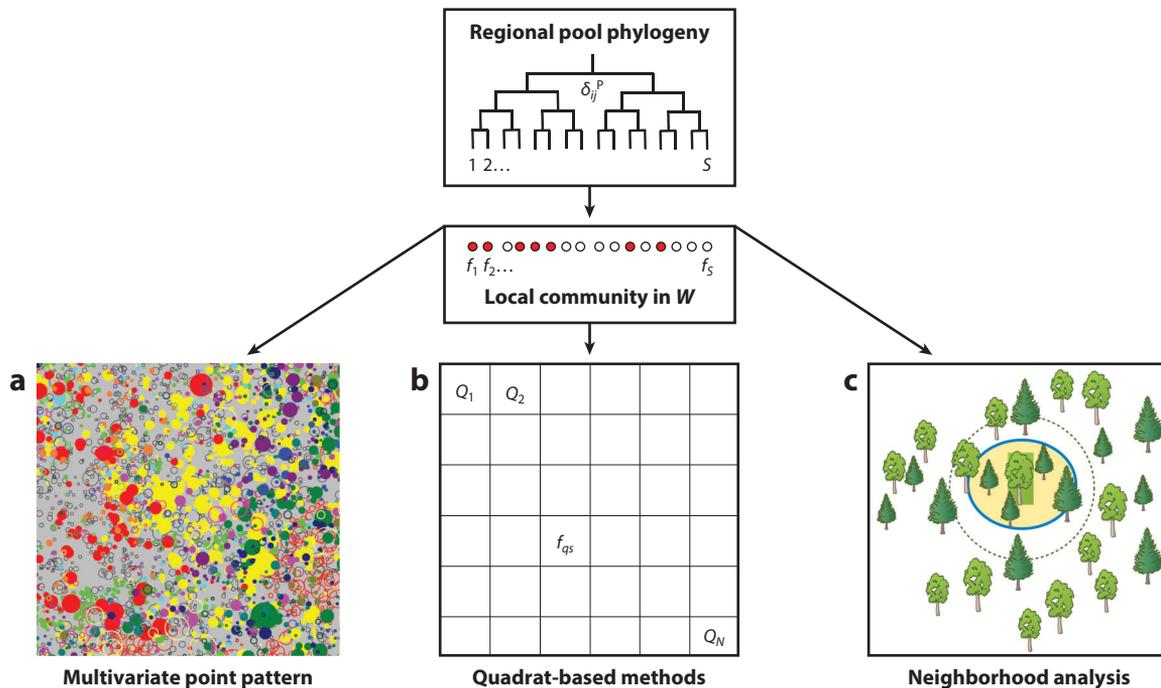


Figure 1

Scheme to allocate different methods to analyze multivariate data sets of fully mapped individuals within an observation window W (i.e., a local community). Pairwise species dissimilarities δ_{ij}^P can be based on measures of phylogenetic, functional, or any other ecological distance between species. Nonspatial phylogenetic analysis tests if community members in W show an even or clustered distribution on the regional pool phylogeny (phylogenetic community structure) or if abundant species are randomly distributed across the phylogeny (abundance phylogenetic structure). Filled circles indicate the positions of local community members on the phylogeny, f_i is the relative abundance of species i in W , and S is the species richness of the regional pool. (a) Point pattern analysis tests for scale-dependent correlations in the ecological dissimilarity of neighboring individuals in W . (b) Quadrat-based methods divide W into quadrats Q_q and reduce the full spatially explicit information to the abundance (or presence/absence) f_{qs} of species s in quadrat q . (c) Statistical neighborhood analysis relates the performance of individual plants to features of their biotic and abiotic neighborhood.

abundances, Clarke & Warwick (1998) normalized with D

$$c_d = \frac{D^P}{D} = \frac{\sum_{i,j} \delta_{ij}^P f_i f_j}{\sum_{i,j} \delta_{ij} f_i f_j} = \frac{\text{Rao}}{\text{Simpson}} = \text{MPD} \quad 1.$$

and obtained the mean pairwise dissimilarity c_d between all heterospecific individuals in W , which is identical to the abundance weighted mean pairwise dissimilarity (*MPD*) used in quadrat-based phylogenetic analyses (de Bello et al. 2016) to address objectives A1 and A2 (**Table 1**).

To make the Simpson index spatially explicit and scale dependent to represent beta diversity, Shimatani (2001) looked at pairs of individuals in W that are distance r apart. This condition allows for precise detection of spatial patterns in taxonomic turnover and its strength over different spatial scales (Wiegand & Moloney 2014). This condition is implemented by using the mark connection function $p_{ij}(r) = f_i f_j g_{ij}(r)/g(r)$, which gives the conditional probability that of two randomly selected individuals distance r apart, the first belongs to species i and the second to species j (Illian et al. 2008). The $g_{ij}(r)$ is the partial pair correlation function of the species pair i - j , and $g(r)$ is that

of all individuals within W . The spatially explicit Simpson index (Shimatani 2001),

$$\beta_S(r) = \sum_{i=1}^S \sum_{j=1}^S \delta_{ij} p_{ij}(r) = \sum_{i=1}^S \sum_{j=1}^S \delta_{ij} f_i f_j \frac{g_{ij}(r)}{g(r)}, \quad 2.$$

is therefore the probability that two randomly selected individuals in W that are distance r apart are heterospecifics. This is a metric of spatial species turnover between locations distance r apart and directly related to the distance decay of species similarity (Condit et al. 2002).

When using a continuous measure δ_{ij}^P of pairwise species dissimilarity, we obtain the phylogenetic spatially explicit Simpson index (Shen et al. 2013, Wang et al. 2015):

$$\beta_{\text{phy}}(r) = \sum_{i=1}^S \sum_{j=1}^S \delta_{ij}^P p_{ij}(r) = \sum_{i=1}^S \sum_{j=1}^S \delta_{ij}^P f_i f_j \frac{g_{ij}(r)}{g(r)}, \quad 3.$$

the expected dissimilarity between two randomly selected individuals in W that are distance r apart. Equation 3 shows how species abundances (f_{ij}), co-occurrence [$g_{ij}(r)/g(r)$], and species dissimilarity (δ_{ij}^P) jointly produce patterns of phylogenetic beta diversity. The metrics $\beta_S(r)$ and $\beta_{\text{phy}}(r)$ are therefore especially useful to address objectives B2, B4, and C2.

To describe spatial phylogenetic turnover relative to spatial species turnover, Shen et al. (2013) divided $\beta_{\text{phy}}(r)$ by $\beta_S(r)$ and normalized with the nonspatial expectation c_d (Equation 1). The resulting phylogenetic mark correlation function is given by:

$$k_d(r) = \frac{1}{MPD} \frac{\beta_{\text{phy}}(r)}{\beta_S(r)} = \frac{1}{MPD} c_d(r), \quad 4.$$

where $c_d(r) = \beta_{\text{phy}}(r)/\beta_S(r)$ is the expected dissimilarity between two randomly selected heterospecifics in W that are distance r apart. The value of $k_d(r) = 1$ serves as a dividing line between spatial phylogenetic clustering [$k_d(r) < 1$] and spatial phylogenetic overdispersion [$k_d(r) > 1$] (Shen et al. 2013; objective C1). We find $k_d(r) = 1$ if the local community is not spatially structured [i.e., $g_{ij}(r)/g(r) = 1$] and if all heterospecific dissimilarities are the same (i.e., $\delta_{ij}^P \propto \delta_{ij}$).

To assess which spatial scales and phylogenetic depths produce phylogenetic patterns, Parmentier et al. (2014) analyzed the spatial co-occurrence of species with dissimilarities within interval $I^P = (\delta_{\min}^P, \delta_{\max}^P]$. We translate this idea into point pattern terminology by defining the phylogenetic co-occurrence function $c_{\text{phy}}(r, I^P)$ as the probability that two heterospecifics distance r apart have dissimilarities within interval I^P :

$$c_{\text{phy}}(r, I^P) = \frac{\sum_{i=1}^S \sum_{j=1}^S \mathbf{1}[\delta_{ij}^P \in I^P] p_{ij}(r)}{\sum_{i=1}^S \sum_{j=1}^S \delta_{ij} p_{ij}(r)}, \quad 5.$$

where the indicator function $\mathbf{1}[\cdot]$ has value of one if $\delta_{ij}^P \in I^P$ and a value of zero otherwise. Note that $c_{\text{phy}}(r, I^P) = 1$ if interval I^P covers all dissimilarities in δ_{ij}^P . The phylogenetic co-occurrence function precisely reveals the phylogenetic (δ_{ij}^P) distances that contribute to phylogenetic clustering or overdispersion at spatial distances r .

3.3. How Are Species Embedded Into Their Biotic Neighborhood?

To make species richness S spatially explicit we determine the number of further species that surround an individual of the target (or focal) species t on average. Using point pattern statistics, this metric, the individual species area relationship (*ISAR*), can be expressed by using the probability $D_n(r)$ that the nearest species i neighbor of an individual of the target species t is located within

distance r (Wiegand et al. 2007):

$$ISAR_t(r) = \sum_{i=1}^S \delta_{ii} D_{ii}(r). \quad 6.$$

Supplemental Figure 2 (Supplemental Appendix 1) shows a summary scheme of the *ISAR* index family. The *ISAR* function can be used to address objective A3 by assessing if and at which spatial neighborhoods a given target species is mostly located in areas of locally higher (or lower) than expected species richness.

To obtain a metric analogous to the phylogenetic mark correlation function $k_i(r)$ (Equation 4), we first replace δ_{ii} with δ_{ii}^P to obtain the phylogenetic *ISAR* function (*PISAR*) as $PISAR_t(r) = \sum_{i=1}^S \delta_{ii}^P D_{ii}(r)$ (cf. Equation 2). To remove the effect of the underlying species richness pattern we then divide the *PISAR* with the *ISAR* and normalize with the corresponding nonspatial metric $\Delta_t^P = \frac{1}{S-1} \sum_{i=1}^S \delta_{ii}^P$ (the analog to *MPD* in Equation 1; Webb et al. 2006) and obtain the *rISAR* function:

$$rISAR_t(r) = \frac{1}{\Delta_t^P} \frac{PISAR_t(r)}{ISAR_t(r)}, \quad 7.$$

the mean pairwise dissimilarity between the individuals of the target species and all other species in a neighborhood with radius r , normalized with Δ_t^P . The *rISAR* function can be used to address objective A3 by assessing if and at which spatial neighborhoods a given target species is surrounded on average by more ecologically similar or dissimilar than expected species (see Section 5.3).

4. QUADRAT-BASED ANALYSIS

Many important reviews have been published and methodological studies have been done on quadrat-based community analysis, including Colwell & Winkler (1984), Webb et al. (2002), Hardy & Senterre (2007), Kraft et al. (2007), Kembel (2009), Swenson (2011), Miller et al. (2017), and Tucker et al. (2017). Following early work by Kembel & Hubbell (2006), these methods are also often applied to fully mapped plots. To this end, the community in W is divided into a grid of quadrats q (**Figure 1b**) and the full spatially explicit information is reduced into a species–quadrat community matrix f_{qs} , representing the relative abundance of species s in quadrat q . The arbitrary quadrats cause edge effects (Peters 2003). The species present in W then usually form the regional pool, and the analysis uses standard metric–null model combinations of phylogenetic analysis to test if species co-occurring in a quadrat are more (or less) related than expected (objectives A1 and A2) (Hardy 2008, Miller et al. 2017). Because these methods are exhaustively described in the literature and discard local within-quadrat spatial structure that can be essential to understanding the process, we do not consider them here in detail (for more details, see **Supplemental Appendix 2**).

5. SPATIALLY EXPLICIT NULL MODELS AND DYNAMIC SIMULATION MODELS

The fully mapped data considered here allow for two types of null models, those that randomize the dissimilarity matrix δ_{ij}^P and those that randomize the locations of the individuals in W . The methods to randomize δ_{ij}^P are those of standard phylogenetic analysis (e.g., Hardy 2008); however, for randomization of the locations of individuals, we can take advantage of abundant techniques of point process modeling (Shen et al. 2009, Wiegand & Moloney 2014, Baddeley et al. 2016, Wang et al. 2015). In principle, all point pattern null models can also be applied together with

 Supplemental Material

quadrat-based metrics (e.g., the toroidal shift null communities in Kraft et al. 2008) instead of conventional matrix shuffle null models.

5.1. Detection of Phylogenetic Spatial Structure

This task involves detection of small-scale spatial correlations in the dissimilarities of neighbored individuals, independent of the overall functional or phylogenetic community structure represented by *MPD* (Equation 1). The phylogenetic mark correlation function $k_d(r)$ is especially suitable for this task because it is normalized with *MPD* (Equation 4) (Shen et al. 2013).

Two null models represent the null hypothesis of no small-scale spatial correlations in the dissimilarities of neighbored individuals. The first null model (termed the 1s null model in Hardy 2008) randomly shuffles species names in the dissimilarity matrix δ_{ij}^P (for species with abundances >0). However, if abundant species are nonrandomly distributed across the phylogeny, this can lead to bias if this null model is used with quadrat-based metrics (Hardy 2008). The second null model is the pairwise species independence null model that randomizes each species pattern to remove (smaller and larger scale) co-occurrence patterns but conserves univariate structures (e.g., aggregation among conspecifics). This approach can be implemented by random toroidal shifts of species patterns (Wiegand & Moloney 2014), but refined methods involve pattern reconstruction (Wiegand et al. 2013, Wang et al. 2015).

Our power test, based on the communities of Miller et al. (2017), revealed excellent performance of the phylogenetic mark correlation function $k_d(r)$ over the 1–30 m distance interval for both null models with the exact type I error rate ($\alpha = 0.05$) and very low type II error rates (Figure 2a,c).

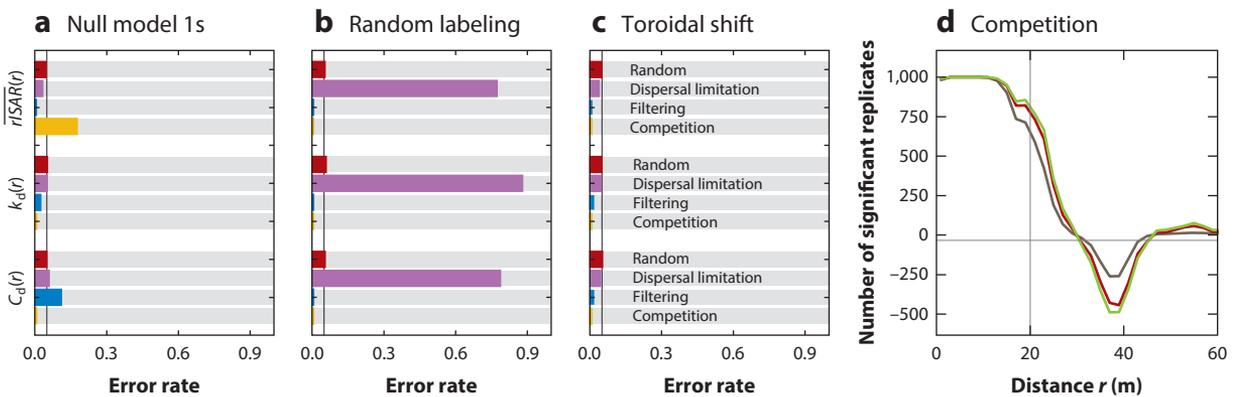


Figure 2

Power test of several point pattern null model–metric combinations based on 1,000 random, habitat filtering, and competition communities used in Miller et al. (2017). Additionally, to represent dispersal limitation we included a community in which species are independently superposed and each species follows a Thomas cluster process with parameters $\sigma = 5$ m (radius 10 m) and $\rho = 0.0002/\text{m}^2$ (20 clusters) (Wiegand & Moloney 2014). The metrics include the phylogenetic mark–correlation function $k_d(r)$ (Equation 4), the cumulative version $C_d(r)$ of the non-normalized $c_d(r)$ (Equation 4), and the community-level $rTSAR(r)$. (a–c) Type I and type II errors based on a global envelope test (Velázquez et al. 2016) over the 1–30 m distance interval. The random (red) and dispersal limitation (magenta) communities do not contain spatial phylogenetic structure (used for assessment of type I errors), and habitat filtering (blue) and competition (yellow) communities show phylogenetic overdispersion and clustering, respectively (used for assessment of type II error rates). The significance level was $\alpha = 0.05$. (d) Scale-dependent assessment of significant effects for the competition communities. The curves show the number of replicates for which the observed metric was outside the simulation envelopes of the null models (gray curve, null model 1s; red curve, random labeling null model; green curve, toroidal shift null model). Negative departures are indicated by negative values.

The toroidal shift null model also showed excellent performance with the community averaged *rISAR* function and the cumulative version of the non-normalized $c_d(r)$ (**Figure 2c**). However, maintenance of species aggregation in the null model is essential to avoid type I error. To show this, we assembled dispersal limitation communities with strong species clustering but no phylogenetic structure and tested the type I error of the random labeling null model that randomly shuffles the species identities among all individuals. This randomization maintains local density but removes species aggregation. Indeed, random labeling showed high type I error rates for the dispersal limitation communities but performed well for the other three community types (i.e., random, filtering, and competition) (**Figure 2b**). Note that random labeling approximates the regional null model of Miller et al. (2017) that randomly assigns each individual in W a species identity taken randomly from a predefined regional pool (e.g., composed of all individuals in W). In quadrat-based analyses, this null model shows mostly high type I error rates for the dispersal limitation communities (**Supplemental Figures 1 and 2 in Supplemental Appendix 3**).

 Supplemental Material

5.2. Example for Detection of Scales of Spatial Phylogenetic Structure

A special strength of point pattern techniques is the ability to precisely reveal spatial scales of clustering or overdispersion. To demonstrate this ability, we apply the phylogenetic mark correlation function $k_d(r)$ to the competition communities by Miller et al. (2017) that show scale-dependent spatial structures (**Figures 2d and 3a**). To mimic competition, they considered an interaction range of 20 m and repeatedly removed one of two closely related individuals within this distance and replaced it by a randomly located individual from the pool. Analysis with the $k_d(r)$ -toroidal shift combination reveals phylogenetic overdispersion for distances up to 20 m and a weak signal of phylogenetic clustering at distances of approximately 33 m (**Figure 3a**). Phylogenetic clustering arises because two neighbors B and C, located at the edge of the zone of influence of a focal individual A, will tend to be ecologically similar because AB and AC are dissimilar, as depicted by $k_d(r)$.

Application of the phylogenetic co-occurrence function $c_{\text{phy}}(r, P^b)$ (Equation 5) showed that closely related species were segregated within the competition range (i.e., distances less than 20 m) (**Figure 3b**), and species pairs with the largest phylogenetic distance (63.05 Ma) showed attraction at short distances ($r < 10$ m) (**Figure 3d**). This produced the overall pattern of phylogenetic overdispersion. More complicated situations arise if different processes cause phylogenetic clustering and overdispersion simultaneously. However, such effects likely occur at different spatial scales or phylogenetic depths (Parmentier et al. 2014) that can be detected using the phylogenetic co-occurrence functions.

5.3. Point Pattern Null Models Randomizing the Species Locations

To find out if the assemblages surrounding the target species show nonrandom spatial diversity patterns (objective A3), the observed *ISAR* and *rISAR* functions are compared with those of a stochastic null model. Two features in species distribution patterns can be manipulated in null models: the observed first-order structure of the pattern (i.e., variation in local point density, mostly driven by the environment) and the observed second-order structure (i.e., small-scale correlation structures among conspecific individuals, driven by demographic processes such as dispersal or plant interactions). Maintaining or removing first- or second-order structures results in four types of null models (Shen et al. 2009, Wang et al. 2013, Wiegand & Moloney 2014):

- (i) homogeneous Poisson processes (i.e., no first- or second-order structures),

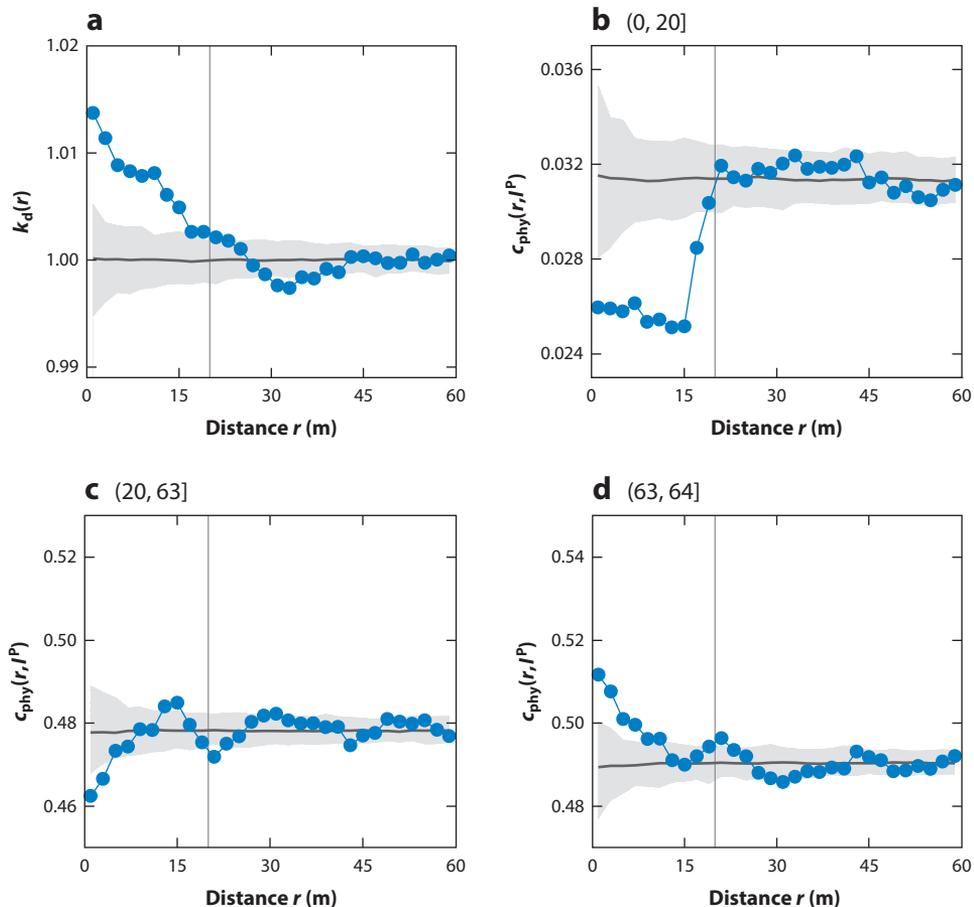


Figure 3

Results of the (a) phylogenetic mark correlation function $k_d(r)$ and (b–d) the phylogenetic co-occurrence function $c_{\text{phy}}(r, I^P)$ for different phylogenetic intervals I^P for a competition community of Miller et al. (2017). The $k_d(r)$ is the (normalized) expected dissimilarity between two randomly selected heterospecifics that are distance r apart, and the $c_{\text{phy}}(r, I^P)$ is the probability that two heterospecifics distance r apart have dissimilarities within interval I^P , which is provided on top of panels b–c. Note that the lower endpoint of the interval I^P is excluded (e.g., the value 0 in panel b) but the higher endpoint is included (e.g., the value 20 in panel b). Blue circles indicate observed functions, and gray shaded areas indicate simulation envelopes of the toroidal shift null model, which are the fifth lowest and highest values of the 199 null model simulations.

- (ii) heterogeneous Poisson processes (i.e., only a first-order structure),
- (iii) null models with only a second-order structure (e.g., homogeneous Thomas cluster point processes), and
- (iv) null models with first- and second-order structures (e.g., inhomogeneous Thomas cluster point processes and pattern reconstruction null models).

Maintenance of second-order structure is important to avoid type I error, and inference on processes typically requires the assumption of separation of scales (i.e., species interactions occur over shorter spatial scales than habitat filtering; Wiegand & Moloney 2014). Null model iv reveals selectively interspecific species interactions (because the effect of habitat filtering is accounted for), whereas larger-scale departures from null model iii can be attributed to habitat filtering.

5.4. Point Pattern Null Communities

Point pattern null communities are constructed by independently superposing one realization of a given null model for each species present in the community (Plotkin et al. 2000, Shen et al. 2009). They therefore assume absence of interspecific interactions (McGill 2010b). The null communities based on null model type i correspond to the random placement hypothesis, the point of reference without any spatial structure. By progressively adding first- and/or second-order effects, their relative importance in explaining spatially explicit diversity patterns can be studied (objectives B1–B4). Together with additional hypotheses, this allows for inference on the relative strength of different processes at different spatial scales in generating species and phylogenetic or functional alpha and beta diversity (objectives C1 and C2; e.g., Shen et al. 2009; Wang et al. 2011, 2013, 2015).

Communities based on null model type ii correspond to the habitat filtering hypothesis in which species distribution patterns are only driven by local habitat suitability, and communities based on null model type iii correspond to the dispersal limitation hypothesis because only intrinsic demographic factors such as dispersal limitation (or conspecific negative density dependence) govern the species patterns. Finally, null model type iv generates null communities that are expected in the absence of smaller-scale interspecific species interactions (independent placement hypothesis; Wang et al. 2015) because both first- and second-order effects in the patterns are conserved but the different species patterns are independently superimposed.

5.5. Dynamic Simulation Models

Ultimately even refined point pattern null community approaches are limited in detecting processes because they are static and do not describe the underlying dynamical (spatial) mechanisms and processes directly. An alternative is given by recent reconciliation of dynamic and individual-based community simulation models with methods of statistical inference for stochastic simulation models (e.g., Hartig et al. 2011, Lehmann & Huth 2015).

The simulation models include representations of the most important processes hypothesized to affect the fate of individuals during their lifetime (e.g., reproduction, competition, survival, dispersal, migration from a metacommunity) and how they may depend on species traits and, possibly, on environmental covariates (May et al. 2015, 2016; Brown et al. 2016). Usually, a suite of alternative models that represent competing hypotheses on the underlying processes is developed (e.g., May et al. 2016), and the task is to assess which hypothesis is most likely, given multiple summary statistics (e.g., spatial diversity metrics) extracted from a fully mapped data set (Hartig et al. 2011). This approach is only in its emerging phase, but it can already be foreseen that dynamics simulation models of community assembly and trait or phylogenetic structure, in concert with the diversity metrics presented here, may ultimately prove more powerful for detecting specific community assembly processes than null model approaches.

6. STATISTICAL NEIGHBORHOOD ANALYSIS

The overall goal of individual-based neighborhood analysis is to relate plant performance (i.e., growth, mortality, and reproduction) to its biotic and abiotic neighborhood (**Figure 1c**) (Canham & Uriarte 2006). We define a neighborhood as the distance over which interactions among species (and traits or clades) or between species and their physical environment affect demographic processes of a target individual (**Figure 1c**). For trees, the neighborhood typically ranges between 10 and 20 m (Uriarte et al. 2004b). Using this approach, statistical models are built in which the effect of neighborhood interactions (e.g., competition, facilitation, dispersal) on the performance of

individual plants is expressed as a function of species identity, stem size, and spatial configuration of individuals (Canham & Uriarte 2006). These models also provide the tool for synthesizing these processes into spatial and temporal predictions of system dynamics (Phillips et al. 2003, Uriarte et al. 2009).

Neighborhood analysis answers fundamental questions for species coexistence—for example, if neighborhood interactions are independent of species identity or are different for conspecifics versus heterospecifics (Uriarte et al. 2004b), how quickly they decline with distance, or how functional traits or phylogenetic relationships influence the strength of neighborhood effects (Uriarte et al. 2010a, 2016; Kunstler et al. 2012; Lasky et al. 2014; Fortunel et al. 2016). Thus, in contrast to the point pattern or quadrat-based methods that target the emerging average spatial community patterns, statistical neighborhood analysis aims to model the impact of the variation of neighborhood patterns among individuals on tree-scale demographic rates and ecological processes.

6.1. Spatial Diversity Metrics Used in Statistical Neighborhood Analysis

Neighborhood analysis overcomes limitations of quadrat-based analysis (e.g., Connell et al. 1984, Wills et al. 1997) in which the use of arbitrary quadrat size may introduce errors into the analyses (Peters 2003). The applications of neighborhood analysis include studies modeling effects of conspecific versus heterospecific neighborhood crowding on growth and survival of individual trees by adopting neighborhood competition indices (e.g., Hubbell et al. 2001; Peters 2003; Uriarte et al. 2004a,b) and generalized linear mixed-effects models for testing density-dependence effects (e.g., Metz et al. 2010).

Canham et al. (2004) and Uriarte et al. (2004a) generalized the use of neighborhood competition indices (*NCI*) to specify the competitive effect of all neighbors within a given distance *R* of a target individuals *t* of a focal species *f*. An example for such an index is:

$$NCI_t = \sum_{i=1}^s \lambda_{if} \sum_{j=1}^{n_i} \frac{(dbh_{ij})^{\alpha_f}}{r_{ij}^{\beta_f}}, \quad 8.$$

where *dbh_{ij}* is the diameter at breast height (dbh) of the *j*th neighbor of species *i*, and *r_{ij}* is its distance to the target individual *t*. Thus, competition increases with increasing dbh and decreasing distance. The λ_{if} is a species-specific competition coefficient describing the impact of species *i* on the focal species *f*, and α_f and β_f are species-specific model parameters. Neighborhood effects are then translated into actual growth by using, for example, a negative exponential function of the *NCI* (Uriarte et al. 2004a).

When identifying λ_{if} with functional or phylogenetic similarity (Uriarte et al. 2010a), the *NCI* becomes similar to the species-centered version of the phylogenetic or functional diversity metric *D^P* (Equation 1), where $D_i^P = \sum_j d_{ij}^P f_j$ is the mean dissimilarity of the focal individual to all neighbors within distance *r*, but each neighbor is weighted with its size and distance to the target individual. These neighborhood models can also embed the strong size asymmetries in pairwise plant interactions by adding an additional term to Equation 8 (Uriarte et al. 2004a).

6.2. Inference on Processes with Statistical Neighborhood Analysis

The competition coefficients λ_{if} in Equation 8 can be used in different ways to infer about the mechanism underlying plant performance. For example, Kunstler et al. (2012) fitted the λ_{if} values for all species pairs and correlated them with the corresponding trait and/or phylogenetic distances δ_{if}^P . An alternative is to make specific assumptions about the structure of the λ_{if} values and to

compare the statistical support for the resulting alternative models (objective D1; Uriarte et al. 2004a, 2010a). For example, the null model of no species-specific effects on plant performance (Uriarte et al. 2010a), the ecological equivalence hypothesis (Connell 1980, Hubbell & Foster 1986, Hubbell 2006), can be implemented by $\lambda_{if} = 1$. Additionally, assuming two different values of λ_{if} , they can be used to test if plant performance responds differently to conspecific versus heterospecific neighbors (Uriarte et al. 2004b).

The competition coefficients λ_{if} in Equation 8 can also be used to formulate hypotheses on the impact of functional or phylogenetic dissimilarity on plant performance. For example, assuming that functional traits are good predictors of shared resource use or defenses, functionally similar species should compete more intensely or share more natural enemies than functionally dissimilar species (the trait similarity hypothesis; Uriarte et al. 2010a). This can be implemented as $\lambda_{if} = 1 - |F_f - F_i|$, where F_i is the average functional trait value of species i , normalized between zero and one (Uriarte et al. 2010a). If functional traits are phylogenetically conserved, the phylogenetic similarity hypothesis can be tested by using phylogenetic dissimilarity δ^P_{if} instead of $|F_f - F_i|$ (Uriarte et al. 2010a).

However, competition may also work in a hierarchical asymmetric way (Lasky et al. 2014), and a trait hierarchy hypothesis can be implemented as $\lambda_{if} = 1 - (F_f - F_i)$. This hypothesis predicts that competition results in functional clustering because more competitive species will be favored under a given environment (Mayfield & Levine 2010). In contrast, the trait similarity hypothesis predicts that competition or natural enemies lead to functional or phylogenetic overdispersion, whereas environmental filtering leads to clustering (Kunstler et al. 2012).

Neighborhood models can also be used to assess the importance of dispersal limitation in communities. In this case, equations similar to Equation 8 are parameterized with spatially explicit data on the distribution of potential seed sources and seed or flower data collected in baskets, and the equations can then be used to make predictions about seed dispersal limitation (objective D2) (Muller-Landau et al. 2002, Uriarte et al. 2010b). These dispersal and neighborhood models can then be used to simulate community dynamics (Uriarte et al. 2016) or to assess the importance of dispersal or establishment limitation (Uriarte et al. 2010b).

7. DISCUSSION

Spatial dependency in ecological data was once viewed as a nuisance that complicates the analysis by violating the assumption of independence in biotic responses. It took ecologists a while to recognize that there is a great deal of biology buried in spatial patterns and to adopt a research agenda that strives for measuring, understanding, and modeling spatial patterns in biotic responses as a critical aspect of the ecology of organisms and communities (Legendre 1993, McIntire & Fajardo 2009). In this review, we focus on fully mapped plots of plant communities and argue that analysis of spatial structures in species diversity, phylogenetic diversity, and functional diversity can provide important insights into the processes that drive community assembly and dynamics.

7.1. Pattern Detection

The multivariate data structures considered here are an extension and generalization of the point pattern analysis framework introduced by Ripley (1977). Point pattern analysis was designed to extract the maximum information from mapped point data to infer distribution across spatial scales to overcome a drawback of quadrat methods, “their inability to test for interactions at different scales simultaneously” (Ripley 1977, p. 172). Our generalized framework shares the same main

motivation of the original spatial analyses: Infer underlying processes by quantifying the spatial scales at which nonrandom spatial patterns occur.

The analytical tools presented here overcome or alleviate two fundamental problems of pattern–process inference outlined by McIntire & Fajardo (2009): imprecise quantification of patterns and imprecise biological (null) hypothesis on spatial patterns. Associated with the first problem, a major methodological issue of earlier nonspatial approaches is that the signatures of opposing processes may cancel out each other (Colwell & Winkler 1984, Parmentier et al. 2014). Our approach provides a solution to this issue because point pattern metrics such as the phylogenetic mark correlation or co-occurrence functions (Equations 4 and 5) can decompose community patterns at different scales and therefore distinguish processes operating at different spatial scales and phylogenetic depths (e.g., **Figure 3**) (Shen et al. 2013, Parmentier et al. 2014). For the second problem, our analysis framework allows for construction of null models with intuitive interpretation, direct links to biological processes, and deep roots in point process theory.

7.2. Macroecological Patterns

Multivariate point pattern analysis of ecological communities takes advantage of powerful point process theory and formulates analytical relationships such as those in Equation 3, which show how the spatial scaling of diversity patterns depends on the key variables: species abundances ($f_i f_j$), species dissimilarities (d_{ij}^P), and the spatial scaling of species co-occurrence [$g_{ij}(r)/g(r)$]. Such formulas can be used as a theoretical yardstick to evaluate the relative strength of different mechanisms of community dynamics in generating species and phylogenetic (or functional) beta diversity. Combinations of this approach with null communities (Shen et al. 2009, Wang et al. 2015) can reveal deep insight on the scale dependency of community assembly. For example, Wang et al. (2015) showed that habitat filtering (i.e., conserving first-order structures in the species patterns) was required in two temperate forests to match the observed levels of species and functional and phylogenetic beta diversity at scales above 150 m, whereas keeping the second-order species structures (e.g., due to dispersal limitation) was required to match the observed levels of beta diversity at the 20–150 m scale. Their analysis also showed that interspecific species interactions contributed only slightly to beta diversity at distances less than 20 m.

7.3. Neighborhood Interactions

Coexistence theory outlines the importance of deterministic biotic and abiotic mechanisms in maintaining community assemblages. Individuals arriving at a site might fail to colonize owing to an inability to tolerate the abiotic conditions or they might be outcompeted by neighbors. This implies that the remaining individuals form nonrandom local assemblages. Collective efforts to quantify how the local biotic neighborhood influences plant performance (objective D1) and how species are embedded into their local neighborhoods (objective A3) have produced interesting new insight into the mechanism of species assembly. Recent neighborhood models have showed that species niche similarities associated with traits influence neighborhood interactions in forests in a variety of settings (Uriarte et al. 2010a, Kunstler et al. 2012, Lasky et al. 2014, Fortunel et al. 2016). However, in species-rich forests this seems to apply only to the most abundant species. Fortunel et al. (2016), for example, analyzed 315 species in a hyperdiverse tropical forest and found that 72% of the species showed no biotic neighborhood effect on growth. These results accord with point pattern analyses (e.g., Lieberman & Lieberman 2007, Wiegand et al. 2012, Perry et al. 2014, Wang et al. 2016) that suggest weaker linkages of species with their biotic neighborhood if species richness increases. The reason for such stochastic dilution is grounded in the stochastic geometry

of biodiversity in which the identity of neighbors becomes increasingly unpredictable if species richness increases (McGill 2010b, Wiegand et al. 2012, Wang et al. 2016, Perry et al. 2017). This causes large variability in the outcome of deterministic species interactions among individuals of a given species and dilutes nonrandom patterns expected from deterministic theory. Consequently, using a metric of local dominance, Wang et al. (2016) found that a target species was more likely to show linkages to its functional or phylogenetic neighborhood if it was locally more dominant. Point process theory deals with the stochastic placement of individuals in space and is therefore predestinated to take the lead in efforts to quantify the role of stochasticity in community assembly. Stochasticity is not inherently uninteresting noise, as has long been perceived in ecology, but an essential ingredient of spatial processes.

Deterministic processes operating via ecological dissimilarities d_{ij}^P provide important assembly mechanisms, and the dissimilarity measures can be incorporated into community-level point pattern or neighborhood analyses to evaluate the relative support for competing hypotheses on the multivariate properties of the neighborhood of species (Uriarte et al. 2010a, Wang et al. 2016). The need for a multivariate perspective was outlined by Kraft et al. (2015b), who found that the outcomes of interactions between multiple species can be very different from predictions of pairwise competition experiments. Nevertheless, we may need even more refined analytical tools to obtain a comprehensive understanding of the complex spatial nature of multispecies interactions. The analysis of the competition community (**Figure 3**) suggests that capturing spatial patterns that emerge from competitive interactions may need metrics of third-order interactions among triplets of individuals. For example, if pairs of nearby species AB and AC co-occur because AB and AC are dissimilar, what happens with the BC pairs that are likely to be more similar? Similarly, neighborhood-based multivariate analyses need to find a way to incorporate intransitive competition (i.e., no single competitor exists like in the rock-paper-scissors game) that has been proposed as a mechanism promoting coexistence among dominant species (Allesina & Levine 2011, Soliveres et al. 2015). Intransitivities in species interactions can result from species effects on their biotic (e.g., microbes; Reed et al. 2008) or abiotic environments (e.g., leaf litter; Uriarte et al. 2015). By explicitly incorporating these feedbacks into analyses (e.g., effects of leaf litter inputs on seedling demography; Muscarella et al. 2013), we can gain insights into the mechanisms that underlie intransitivities in species interactions.

7.4. The Relative Importance of Ecological Mechanisms for Community Assembly and Dynamics

Future work that takes advantage of the dynamic simulation modeling framework (e.g., Brown et al. 2011, May et al. 2015) should involve both forward and backward (inverse) simulations. Inverse simulation modeling (Hartig et al. 2011) can parallel recent approaches of neighborhood analyses (e.g., Uriarte et al. 2010a, Fortunel et al. 2016) to evaluate the relative support of competing hypotheses on the structure of competition coefficients with respect to ecological similarity. The advantage is that the statistical model is replaced by a dynamic model, allowing not only for inference on the collective effects of the biotic neighborhood on plant performance (as done by neighborhood approaches) but also for more direct exploration of the link between processes and the emerged patterns. Forward simulations can do this by systematically varying the parameters governing the processes in the model to evaluate their relative importance in generating spatial patterns in diversity. For example, F. May, T. Wiegand, A. Huth, and J.M. Chase (submitted manuscript) found in such a study that operation of conspecific negative density dependence (on the sapling level) enhances species diversity of mature tree communities only marginally and that its effect is overpowered even under (unrealistically) low levels of species immigration. This is

an example of cases in which mechanisms operate in a system (e.g., as revealed by neighborhood analyses; objective A5) but which may not translate into the theoretically expected patterns because community dynamics are driven by complex interactions of several mechanisms operating simultaneously. Revealing the relative importance of processes may therefore be possible only by using spatially explicit dynamic approaches.

FUTURE ISSUES

1. Point pattern analysis quantifies the average biotic neighborhood of individuals, but analysis of the variance in the biotic neighborhoods among individuals is required to better understand the effects of stochasticity on coexistence in species-rich communities.
2. Although most point pattern analyses deal with static patterns, future efforts should also take the temporal dimension of the census data into account and develop methods of spatiotemporal and multivariate pattern detection and point process modeling.
3. Partitioning the relative importance of biotic interactions, habitat heterogeneity, and stochastic effect in neighborhood diversity remains a general problem in ecology. Statistical neighborhood analysis shows that certain mechanisms operate in a community, but future efforts are needed to place these mechanisms into a dynamic framework (e.g., of spatially explicit simulation models) to evaluate their relative importance with respect to emerging diversity patterns.
4. Species have effects on the microbial communities and nutrient fluxes in their neighborhood. These effects can interact in different ways with the demography of the species and possibly cause intransitive competition. Incorporating these feedbacks into neighborhood analyses may uncover mechanisms underlying intransitive competition.
5. Individual-based stochastic simulations guided by results of spatiotemporal pattern analyses and neighborhood analyses are required to assess the effect of temporal variation in external forcing (e.g., climate) on biotic interactions among species and community assembly.
6. The techniques presented here could also be applied to evolutionary studies, given the fundamental analogies between allele diversity and species diversity and those between allele genealogies and phylogenies (Hardy & Senterre 2007, Matesanz et al. 2011). Additionally, if genetic dissimilarity between all individuals of a population can be determined within an observation window or spatial scale, spatially explicit patterns of genetic variation or genetic neighborhood effects can be assessed.

DISCLOSURE STATEMENT

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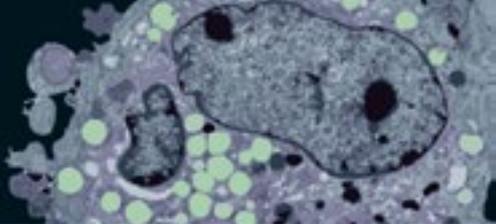
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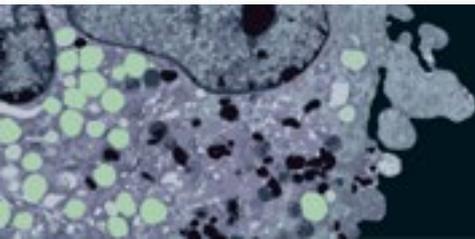
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