

Stochastic dilution effects weaken deterministic effects of niche-based processes in species rich forests

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Abstract. Recent theory predicts that stochastic dilution effects may result in species-rich communities with statistically independent species spatial distributions, even if the underlying ecological processes structuring the community are driven by deterministic niche differences. Stochastic dilution is a consequence of the stochastic geometry of biodiversity where the identities of the nearest neighbors of individuals of a given species are largely unpredictable. Under such circumstances, the outcome of deterministic species interactions may vary greatly among individuals of a given species. Consequently, nonrandom patterns in the biotic neighborhoods of species, which might be expected from coexistence or community assembly theory (e.g., individuals of a given species are neighbored by phylogenetically similar species), are weakened or do not emerge, resulting in statistical independence of species spatial distributions. We used data on phylogenetic and functional similarity of tree species in five large forest dynamics plots located across a gradient of species richness to test predictions of the stochastic dilution hypothesis. To quantify the biotic neighborhood of a focal species we used the mean phylogenetic (or functional) dissimilarity of the individuals of the focal species to all species within a local neighborhood. We then compared the biotic neighborhood of species to predictions from stochastic null models to test if a focal species was surrounded by more or less similar species than expected by chance. The proportions of focal species that showed spatial independence with respect to their biotic neighborhoods increased with total species richness. Locally dominant, high-abundance species were more likely to be surrounded by species that were statistically more similar or more dissimilar than expected by chance. Our results suggest that stochasticity may play a stronger role in shaping the spatial structure of species rich tropical forest communities than it does in species poorer forests. These findings represent an important step towards understanding the factors that govern the spatial configuration of local biotic communities. The stochastic dilution effect is a simple geometric mechanism that can explain why species' spatial distributions in species-rich communities approximate independence from their biotic neighborhood, even if deterministic niche processes are in effect.

Key words: coexistence theory; forest dynamics plot; functional dissimilarity; habitat filtering; individual species–area relationship; null model; pattern reconstruction; phylogenetic dissimilarity; point pattern analysis; species interaction; stochastic dilution hypothesis.

INTRODUCTION

A fundamental goal of ecology is to understand the mechanisms that determine the spatial distribution of

species and the assembly and dynamics of communities (Ricklefs 1990, Brown et al. 1995). Coexistence theory (e.g., Chesson 2000, Mayfield and Levine 2010, HilleRisLambers et al. 2012) predicts that deterministic niche processes such as habitat filtering and competition should lead to distinct spatial patterns in the placement of species with respect to their neighbors (Table 1A).

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For example, under the action of habitat filtering, ecologically similar species are expected to co-occur locally because species with traits less suitable for that environment will be more vulnerable to local environmental stressors (e.g., Weiher and Keddy 1995, Cavender-Bares et al. 2006, Mayfield and Levine 2010). However, as recently shown by Mayfield and Levine (2010), competitive exclusion can yield the coexistence of either ecologically dissimilar or similar species, depending on how trait differences relate to stabilizing niche differences and/or differences in average competitive ability (“average fitness differences” *sensu* Chesson 2000).

Studies using statistical neighborhood models have found that survival and growth of trees are often associated with the composition of local tree neighborhoods and the phylogenetic or functional similarity to neighbors (e.g., Webb et al. 2006, Uriarte et al. 2010, Paine et al. 2012, Lebrija-Trejos et al. 2014). Thus, if some combinations of habitat filtering and competitive exclusion (among other processes) shape spatial patterns, we might expect to observe systematic differences between the observed local biotic neighborhood of a given species (characterized by a typical set of species) and that of other species. If the effects of the different processes do not cancel each other out (Table 1B; Kraft and Ackerly 2010), species should be surrounded by functionally or phylogenetically more similar or dissimilar species than expected by chance (Table 1A).

Neutral theory, in contrast, assumes that tree species are essentially functionally equivalent (Hubbell 2001, 2006) and that species are independently placed with respect to their local biotic neighborhood (McGill 2010, Table 1B). Despite the remarkable success of neutral theory in approximating several fundamental macroscopic patterns of species rich forests such as the species abundance distribution (SAD) or the species–area relationships (SAR; Hubbell 2001, Rosindell et al. 2011), neutral theory remains unsettling for some ecologists because it suggests that many of the niche based processes that are at the heart of decades of ecological theory (Chase and Leibold 2003) may be inconsequential for understanding the dynamics of some communities. An important limitation in reconciling neutral theory and deterministic coexistence theory is that coexistence theory typically focuses on relatively species-poor communities (e.g., Lieberman and Lieberman 2007), while neutral theory applies best to species rich communities (Hubbell 2006). In order to understand the connection between these two perspectives, we therefore seek to identify a mechanism linked to the effects of high species richness. Ideally such a mechanism would generate identifiable neighborhood patterns in the case of species-poor communities, but also produce patterns expected by neutral theory as species richness increases.

We argue that independent placement of species with respect to their local biotic neighborhoods may emerge in species-rich systems for two reasons (Bell 2001). First, spatial independence may occur if species approximate

functional equivalence (as assumed in neutral theory and other dispersal assembly models of community structure; Table 1). Second, statistically neutral patterns could be a consequence of stochastic effects despite of the action of deterministic niche-based processes (e.g., Hurtt and Pacala 1995, Volkov et al. 2009, McGill 2010, Wiegand et al. 2012). The key mechanism for reconciling these perspectives is “stochastic dilution” (e.g., McGill 2010, Wiegand et al. 2012). The foundation of the dilution hypothesis is the observation that in species rich systems, the identities of the nearest neighbors of individuals of a given species are largely unpredictable (e.g., Hubbell and Foster 1986), and that each individual may be surrounded by a different set of competitors (Goldberg and Werner 1983, Hubbell and Foster 1986, Hubbell 2006). Unpredictability may be introduced, for example, by dispersal limitation, where the best adapted species are not always able to colonize newly available gaps. While the outcome of biotic interactions for individuals of a given species can be indeed governed by deterministic mechanisms outlined by coexistence theory, spatial heterogeneity in biotic neighborhoods generated by dispersal and recruitment limitation (e.g., Hurtt and Pacala 1995) may produce situations where some individuals are surrounded by “favorable” neighbors and show a higher probability of survival, whereas others are surrounded by less favorable neighbors and may show a lower probability of survival. If this demographic heterogeneity is strong, as expected for communities with high species richness, it will not allow for uniform responses at the species level that would generate neighborhood patterns predicted by coexistence theory (Hurtt and Pacala 1995). Thus, the dilution hypothesis postulates that large variability in biotic neighborhoods inhibits emergence of detectable signatures of existing niche differences at the species level. As a consequence, the emerging neighborhood patterns match predictions of niche-free models such as neutral theory. Here, we empirically test this hypothesis by comparing the phylogenetic and functional neighborhoods of species in spatially explicit forest communities with that of randomly generated distribution patterns of the focal species.

Recent advances in spatial point-pattern analysis (Law et al. 2009, Wiegand and Moloney 2014) combined with the availability of large fully mapped forest plots and information on functional and phylogenetic relationships between species (Webb et al. 2002, McGill et al. 2006, Kraft et al. 2008, Swenson 2013) have produced an inspiring new perspective on the structure of diverse communities (e.g., Shen et al. 2013, Wang et al. 2013, 2015, Yang et al. 2013, Wiegand and Moloney 2014, Punchi-Manage et al. 2015). These tools also can be used to test predictions of the stochastic dilution hypothesis. For example, the biotic neighborhood of a focal individual of a given species can be quantified as the mean pairwise phylogenetic (or functional) dissimilarity of the focal species to all other

TABLE 1. Summary of different mechanisms and hypotheses on patterns in the placement of species with regard to their biotic neighborhoods.

Name	Mechanisms	Expectation	References
A) Mechanisms generating nonrandom patterns in placement of species with regard to their biotic neighborhood			
Coexistence theory	Deterministic effects of habitat filtering and species interactions lead to local exclusion of species if stabilizing niche differences are smaller than is needed to overcome relative performance differences.	Species are either surrounded locally by ecologically more similar or more dissimilar species.	Chesson (2000), HilleRisLambers et al. (2012)
B) Mechanisms generating independent placement of species with regard to their biotic neighborhood			
Opposing influences of multiple mechanisms	Particular combinations of ecological processes may erase each other's signature.	Positive and negative interactions with neighbors equilibrate and species appears to be placed independently with regard to their biotic neighborhood.	Kraft and Ackerly (2010), PUNCHI-Manage et al. (2015)
Neutral theory	All species are functionally equivalent and stochastic births, deaths, and dispersal limitation drive community dynamics.	Species are placed independently with regard to their biotic neighborhood.	Hubbell (2001)
Dilution hypothesis	Large variability among the biotic neighborhoods of individuals of a given species does not allow for directed responses of the species with respect to their biotic neighborhood.	The proportion of species that are placed independently with regard to their biotic neighborhood increases with species richness.	Wiegand et al. (2007b, 2012), Volkov et al. (2009), McGill (2010)
Statistical null expectation	Signals of species interactions are more difficult to detect statistically for species-rich communities because sample sizes for individual species become on average smaller if species richness increases.	The proportion of species showing statistically detectable interactions with their neighbors declines if species richness increases.	Lieberman and Lieberman (2007), Volkov et al. (2009), McGill (2010)
C) Mechanisms that can produce functional equivalence of species			
Diffuse coevolution	Species live and evolve against a highly stochastic and averaged competitive environment of all species within the community that does not allow directional selection for niche differentiation.	Lead to evolutionary convergence on similar strategies and functional species equivalence.	Goldberg and Werner (1983), Hubbell and Foster (1986), Hubbell (2006)
Emergent neutrality	An intricate balance between direct and indirect competition effects allows for coexistence of sufficiently dissimilar species and for transient coexistence of sufficiently similar species.	Competing species self-organize into (transient) groups of species similar in their traits.	Scheffer and van Nes (2006)

species within a given neighborhood radius r (e.g., Webb et al. 2006). A suitable summary statistic characterizing the biotic neighborhood of a given focal species is then the average taken over all individuals of the focal species present in the plot. This summary statistic has been termed the r ISAR function (Wiegand and Moloney 2014). An attractive feature of the r ISAR function is that changing the neighborhood radius r allows for a scale-dependent assessment of neighborhood patterns. This provides the means to test if and at which spatial neighborhoods a given focal species is surrounded on average by ecologically more similar or dissimilar species, as indicated by significant departures of the r ISAR function from a null model of spatial independence. Alternatively, if no significant departures occur, the placement of the focal species is independent of the local biotic neighborhood.

The stochastic dilution hypothesis predicts that the proportions of species within communities that show consistent relationships with biotic neighborhoods (i.e., departures of the r ISAR function from the null model of independence) should decrease with increasing species richness (H1) (Table 1B). However, a pattern in agreement with H1 is necessary but not sufficient evidence for the dilution hypothesis. The issue is that patterns compatible with H1 can also arise purely for statistical reasons (Table 1B): if there are more species, each species will have fewer individuals and as a consequence the sample sizes for communities with higher species richness will be smaller on average. This can substantially reduce the power of the null model to detect nonrandom signals against the background of stochastic noise. This leads to the expectation that the likelihood of a species to show departures from independence

should decline with abundance (H2). Nevertheless, we expect that stochastic dilution has effects beyond null expectations of declining statistical power. For example, demographic heterogeneity in the biotic neighborhood of species may allow competitively inferior species to win some sites by forfeit if dominant species are absent (e.g., Hurtt and Pacala 1995). Thus, prediction H1 should remain true after correcting for lower sample sizes in the significance tests (H3). Finally, since we conducted our analyses in communities across a gradient of species richness, we can explore if certain properties of the spatial pattern of the species and certain species traits make them more likely to show departures from the null model. For example, species that are locally dominant (e.g., because they have traits that make them more competitive or because they have shorter dispersal distances) should have more predictable biotic neighborhoods. We therefore expect that species with more predictable neighborhoods should have a greater likelihood of being surrounded by ecologically more similar or more dissimilar species than expected by chance (H4).

In this study we used the *r*ISAR function to compare the observed local biotic neighborhoods of individuals of focal species with those of neighborhoods of random locations taken from the study area. This approach allowed us to test the stochastic dilution hypothesis (Wiegand et al. 2012) from a new angle by considering the functional and phylogenetic compositions of local biotic neighborhoods of individual species. We used data from five fully mapped forest communities, including temperate, subtropical, and tropical forests varying largely in species richness (ranging from 36 species in the temperate Wabikon forest to 304 species in the tropical BCI forest; Table 2). We focused on the communities of large trees with a diameter at breast height (dbh) ≥ 10 cm and tested (1) if more species-rich forests showed a lower proportion of focal species that were surrounded by phylogenetically (or functionally) more similar or more dissimilar species than expected by null models of random locations within the plot (H1), (2) if significant departures from the null models became less likely if the focal species had lower abundance (H2), (3) if H1 held after correcting for the effect of sample sizes in the significance tests (H3), and (4) if positive, negative or no departures from the null models correlated with characteristics of the spatial pattern of the focal species (e.g., local dominance, clustering) and with species traits (e.g., maximum height, wood density, leaf nitrogen) (H4).

METHODS

Study areas

Five large Forest Dynamics Plots (FDP) with areas larger than 20 ha were utilized in the present study. The forest plots are located in Asia and the Americas ranging in latitude from 9.15° N to 45.55° N. Species

TABLE 2. Characteristics of the five plots.

Plot	Latitude	Elevation (m)	Species richness	Individuals ≥ 10 cm dbh	Basal area (m ² /ha)	Area	Mean temperature, <i>T</i> (°C)	Mean precipitation <i>P</i> (mm)
Wabikon lake, Wisconsin, USA (WAB)	45.55	483–514	36	14 021	27.68	25.2 ha (300 × 840 m)	4	800
Changbaishan, China (CBS)	42.40	791–808	52	10 418	43.1	25 ha (500 × 500 m)	2.9	700
Gutianshan, China (GTS)	29.25	446–715	159	18 215	36.91	24 ha (600 × 400 m)	15.3	1964
Fushan, Taiwan China (FS)	24.76	600–733	110	19 261	38.19	25 ha (500 × 500 m)	18.2	4271
Barro Colorado Island, Panama (BCI)	9.15	120–155	304	21 456	31.02	50 ha (1000 × 500 m)	27	2500

richness among the plots ranges from 36 to 304 (Table 2). All free-standing individuals with diameter at breast height (dbh) ≥ 1 cm were mapped, measured, and identified to species. Because we wanted to explain patterns predicted by neutral theory, which focuses on individuals of adult reproductive age (Rosindell et al. 2011), we restricted our analysis to the community of larger individuals with dbh ≥ 10 cm. This size threshold excludes most of the saplings and enables comparisons with previous analyses (e.g., Wiegand et al. 2007a,b, 2012, Wang et al. 2010, 2013, 2015).

Phylogenetic and functional dissimilarity

Estimation of the *rISAR* function requires a measure δ_{fm}^{phy} of phylogenetic or functional dissimilarity between all pairs of species f and m . Several of the plots contain many species without molecular data, so we could not derive matrices δ_{fm}^{phy} of phylogenetic dissimilarity consistently across plots. Instead we utilized the informatics tool Phylomatic (Webb and Donoghue 2005) with the Angiosperm Phylogeny Group III (APG III 2010) phylogeny as a backbone to construct a phylogenetic tree for each of the five forest plots. Branch lengths were estimated for each phylogenetic tree using the BLADJ algorithm with estimated node dates from Bell et al. (2010). The phylogenetic tree was used to calculate phylogenetic dissimilarity using the R function *cophenetic* in the package *picante* (Kembel et al. 2010).

Six functional traits for tree species were collected at each plot: maximum height, leaf area, specific leaf area, wood density, leaf nitrogen, and leaf phosphorus. These traits indicate several major axes of plant functional strategy, including the adult light niche (maximum height), light capture (leaf area), leaf economics spectrum (specific leaf area, leaf nitrogen, and leaf phosphorus), and trade off between structural investment and demographic rates (wood density) (Westoby and Wright 2006, Swenson et al. 2012). Trait collections generally followed the protocols of Perez-Harguindeguy et al. (2013). While intraspecific variation in traits may be important in some circumstances (e.g., Messier et al. 2010, Swenson 2013), it is generally unfeasible to measure traits for all individual trees on plots of sizes of 25–50 ha. We therefore focused on using mean trait values for each species, though we acknowledge that it may be valuable to repeat these analyses with intraspecific trait variation data in the future. The species traits were used to estimate matrices δ_{fm}^{phy} of functional dissimilarity between species f and m (H1), and to correlate the occurrence of positive, negative or no departures from the null models with respect to individual species traits (H4).

The functional dissimilarity matrix δ_{fm}^{phy} was estimated as follows. Because some traits were correlated, we calculated the principal components (PCs) of functional traits between all species at each plot. Measured traits were standardized by subtracting the mean value of

each trait of all species and then dividing by one standard deviation. Because the first five PCs (but not the first four PCs) explained more than 90% of the total variance in traits among the five plots, we used the first five PCs for the calculation of Euclidean functional trait dissimilarity δ_{fm}^{phy} between species.

Quantification of the local phylogenetic or functional neighborhood of individual species

For a given forest community, we assigned each species a number from 1 to S , where S is the total number of species in the plot. In the following, the number of a given focal species is indicated by the index f and the number of neighboring species is indicated by the index m . The function *rISAR_f(r)* yields for a given focal species f the mean pairwise phylogenetic (or functional) dissimilarity between the typical tree of the focal species f and all other species m surrounding it within distance r . To embed the *rISAR_f(r)* function into existing point pattern theory (Wiegand and Moloney 2014), we considered first the individual species–area relationship *ISAR_f(r)* that yielded the expected species richness in the neighborhood with radius r around the typical tree of the focal species f (Wiegand et al. 2007a). The *ISAR_f(r)* can be estimated as

$$\text{ISAR}_f(r) = \sum_{m=1}^S \delta_{fm} D_{fm}(r) \quad (1)$$

where $D_{fm}(r)$ describes the probabilities that the nearest species m neighbor of the typical tree of the focal species f is located within distance r . The δ_{fm} yields a value of zero if $f = m$ and a value of one otherwise. The δ_{fm} can be interpreted as a dissimilarity measure that only distinguishes between conspecifics (i.e., $f = m$) and heterospecifics (i.e., $f \neq m$). By considering instead of δ_{fm} an index δ_{fm}^{phy} of phylogenetic (or functional) dissimilarity between species f and m we obtained the phylogenetic individual species area relationship *PISAR_f(r)* (Wiegand and Moloney 2014)

$$\text{PISAR}_f(r) = \sum_{m=1}^S \delta_{fm}^{\text{phy}} D_{fm}(r) \quad (2)$$

that quantifies the expected phylogenetic (or functional) diversity of species within the neighborhood with radius r around the typical individual of the focal species f (see also Yang et al. 2013 for a similar approach). To yield a function that is independent of local species richness within the neighborhood r we divided the *PISAR* function by the *ISAR* function

$$\text{rISAR}_f(r) = \frac{\sum_{m=1}^S \delta_{fm}^{\text{phy}} D_{fm}(r)}{\sum_{m=1}^S \delta_{fm} D_{fm}(r)} \quad (3)$$

If the placement of the focal species f is unrelated with functional or phylogenetic relationships with their neighbors, the $rISAR_f(r)$ will approximate the mean pairwise functional (or phylogenetic) dissimilarity $\Delta_f^P = \sum_m \delta_{fm}^{phy} / (S-1)$ between an individual of the focal species f and all other species in the plot. The constant Δ_f^P is also the asymptote of the $rISAR_f(r)$ function for large neighborhoods r (i.e., no spatial effects) because in this case all $D_{fm}(r)$'s in Eq. 3 approach a value of 1.

Testing if species were placed independently on their biotic neighborhood (H1)

In order to test if individuals of the focal species were surrounded by phylogenetically (or functionally) more similar or dissimilar species than expected by chance, we used Monte Carlo tests based on randomization of focal individuals within the entire study area ("plot-wide" displacement null model) or to random locations within a 30 m radius of the original positions ("local" displacement null model; Appendix S1; Wiegand and Moloney 2014). Previous studies have shown that these tests need to conserve the observed spatial aggregation of the focal species; otherwise the variance in the summary statistic under the null model may be too small and cause spurious statistical significance (Lotwick and Silverman 1982). To solve this difficult problem, we used nonparametric techniques of pattern reconstruction (Appendix S2; Wiegand et al. 2013). Briefly, a simulated annealing algorithm was used to generate patterns that minimize the deviations between a set of summary statistics of the observed and reconstructed patterns (Tscheschel and Stoyan 2006). We used for this purpose the pair correlation function, the K function, the distribution function of the distances to the nearest neighbor, and the spherical contact distribution as summary statistics.

While testing the stochastic dilution hypothesis does not require us to link departures from the null models to specific processes, a cautious link may improve the biological interpretation of our results. The plot-wide model offers the best chance to detect signals of habitat filtering because the random samples contain locations of all different habitats in the plot, not only the habitats to which the species is adapted (Kraft et al. 2015). This is especially true for neighborhoods larger than the typical range of competition (say >30–50 m for larger trees). We therefore assessed departures from the plot-wide null model [e.g., by means of a goodness-of-fit (GoF) tests, see section "Testing for departures from each null model (H1)"] over the 30–50 m distance interval.

To study potential smaller-scale effects in the placement of individuals of the focal species within their habitats (e.g., caused by competitive exclusion), we compared the $rISAR$ function of the observed locations of the focal species with functions derived from random

locations restricted to similar environments (e.g., Wiegand et al. 2007a, Kraft et al. 2008). In this case, we assumed that habitats features relevant for the placement of large trees of the focal species should be mostly larger-scale (>30 m) topographic features such as slopes, plateaus, or gullies as identified, for example, by Harms et al. (2001), or Kanagaraj et al. (2011). Local displacement within radii of 30 m, again using pattern reconstruction, ascertained that individuals of the focal species were displaced only to similar environments (Wiegand et al. 2007a). We therefore assessed departures from the local null model (e.g., GoF tests) over the 1–20 m distance interval. In Appendix S1, we checked the validity of the underlying assumption of separation of scales (Wiegand and Moloney 2014).

Testing for departures from each null model (H1)

We used only species as focal species that had more than 50 individuals with dbh ≥ 10 cm. For each focal species, we conducted 199 realizations of the null model and derived simulation envelopes of the $rISAR_f(r)$ bounded by the fifth lowest and highest values estimated from the null model simulations. A significant departure from the null model occurred therefore for a given neighborhood distance r with an approximate 5% error rate if $rISAR_f(r)$ is below or above the simulation envelopes. To test if an empirical $rISAR$ curve agreed with the null model we used a GoF explained in detail in Loosmore and Ford (2006). This test collapses the scale-dependent information from the $rISAR$ curves into a single test statistic, which represents the accumulated deviation of the observed $rISAR$ from the expected $rISAR$ under the null model, summed over distance interval r_{min} to r_{max} to estimate a P value.

Impact of abundance on departures from the null models (H2)

To test if significant departures from the null models were less likely if the focal species had lower abundance, we conducted rarefaction tests for each null model for abundant species that showed strong departures from the null model (i.e., the lowest possible P value of the GoF test). To this end we randomly selected n_r individuals of the observed pattern of the focal species and of the null model patterns and repeated the $rISAR$ analysis 20 times. This procedure was conducted for abundances of $n_r = 50, 100, 200, 400, 800, 1000$, and 1200.

Correcting for the effect of sample size on the significance of the $rISAR$ function (H3)

To assess significance of the observed $rISAR$ function we switched from the simulation envelopes to an equivalent representation based on standardized effect sizes (Getzin et al. 2014; also called z scores)

$$\text{SES}_f(r) = [\text{obs}_f(r) - \text{exp}_f(r)] / \text{SD}_f(r), \quad (4)$$

where $\text{obs}_f(r)$ is the observed r ISAR for focal species f , $\text{exp}_f(r)$ the mean of the r ISAR $_f(r)$ estimated for the 199 patterns generated by the null model, and $\text{SD}_f(r)$ the corresponding standard deviation. The sample size n_f influences $\text{SD}_f(r)$, but $\text{exp}_f(r)$ only weakly. For each forest, we can therefore determine for a given neighborhood radius r how $\text{SD}_f(r)$ depends on sample size n_f (e.g., Appendix S3: Fig. S1). As detailed in Appendix S3, we found a good approximation to a power law $\text{SD}(n_f) = c n_f^p$ with exponents close to $p = -0.5$. Based on this empirical relationships we can approximately correct for the effect of sample size on the significance of the r ISAR function by multiplying $\text{SES}_f(r)$ with factor $(n_f/1000)^p$ to obtain standardized effect sizes that are scaled to the equivalent of a sample size of e.g., $n_f = 1000$. If hypothesis H3 is true, we expect that the distribution of the sample size corrected $\text{SES}_f^*(r) = \text{SES}_f(r) (n_f/1000)^p$ (e.g., Fig. S2) should become narrower for forests with increasing species richness. As measures of the width of this distribution we used the mean absolute value and the standard deviation of the $\text{SES}_f^*(r)$ values, taken over all focal species f in the given forest community. We derived these distributions by using a neighborhood radius of $r = 40$ m for the plot-wide displacement null model and $r = 10$ m for the local displacement null model. For details, see Appendix S3.

Relating r ISAR results to species properties (H4).— We used several indices to test if the spatial pattern of the focal species (e.g., local dominance) affects the likelihood that a focal species is surrounded by phylogenetically (or functionally) more similar or dissimilar species than expected by chance. These indices quantify aspects of the inter- and intraspecific spatial patterns in the 20-m neighborhood of the focal species (the approximate range of direct species interactions of large trees; Wang et al. 2010). The indices included the neighborhood density M_{ff} of the focal species, the neighborhood density M_{fo} of heterospecific individuals, an aggregation index A_f of the focal species $\alpha\lambda_p$, an index L_f of local dominance of the focal species, and the species abundance n_f (see Appendix S4).

To find out if species with predominantly positive, negative, or no departures from the null models shared certain properties, we condensed the information contained in the full r ISAR $_f(r)$ function and the simulation envelopes into three indices that count the number of negative, positive, and no departures from the null model, taken over the distance interval $(r_{\text{min}}, r_{\text{max}})$ of interest (see Appendix S4). We then used Spearman rank correlation coefficients to relate a given species property to these indices (n_f , M_{ff} , M_{fo} , A_f , L_f) and to functional traits of species (maximum height, wood density, leaf N, leaf P, leaf area, and specific leaf area). In all correlation analyses, we pooled the data of the focal species of all five forests.

TABLE 3. Summary of the results of the goodness-of-fit tests for the different plots.

Plot	No. focal species	FD non	PD non	FD negative	PD negative	FD positive	PD positive
A) Plot-wide null model							
Wabikon	14	0.36	0.29	0.43	0.43	0.21	0.29
CBS	15	0.53	0.73	0.27	0.27	0.20	0.00
GTS	33	0.61	0.68	0.39	0.21	0.00	0.12
Fushan	34 (30) [†]	0.67	0.82	0.20	0.15	0.13	0.03
BCI	77 (68) [†]	0.84	0.79	0.15	0.17	0.01	0.04
Percentage of focal species		0.69	0.73	0.24	0.20	0.07	0.07
No. focal species	173 (160) [†]	110	126	39	35	11	12
B) Local null model							
Wabikon	14	0.57	0.57	0.29	0.14	0.14	0.29
CBS	15	0.67	0.67	0.13	0.07	0.20	0.27
GTS	33	0.76	0.85	0.09	0.03	0.15	0.12
Fushan	34 (30) [†]	0.87	0.82	0.00	0.09	0.13	0.09
BCI	77 (68) [†]	0.93	0.81	0.04	0.13	0.03	0.06
Percentage of focal species		0.83	0.79	0.07	0.10	0.10	0.11
No. focal species	173 (160) [†]	132	136	12	17	16	20

Notes: The columns headed FD (results of functional analyses) and PD (results of phylogenetic analyses) report the proportion of species per plot that showed no significant departures ($P > 0.5$) from the null model (non), that showed positive departures from the null model (positive), and that showed negative departures from the null model (negative). The test was conducted for the plot-wide null model over the 30–50 m distance range and for the local null model over the 1–20 m distance range.. [†]The number of focal species used for the functional analysis is shown in parentheses.

RESULTS

Plot-wide displacement null model

The overwhelming majority (>66%) of focal species among the five forest plots did not show consistent relationships with the functional or phylogenetic composition of their local biotic neighborhoods; 69% and 73% of the species did not show significant departures from the plot-wide null model based on functional and phylogenetic dissimilarity, respectively (Table 3). Approximately 20% of all focal species were surrounded by functionally or phylogenetically more similar species, whereas less than 10% of all focal species were surrounded by functional or phylogenetically more dissimilar species (Table 3).

As expected by the dilution hypothesis (H1), the proportion of species that did not show departures from the plot-wide model for functional dissimilarity increased monotonically from the plot with the lowest species richness (Wabikon, 36 species, 29%) to the plot with the highest species richness (BCI; 304 species, 84%; Table 3). Similar results were observed for phylogenetic dissimilarity, but here the CBS and GTS plots showed a somewhat higher proportion of non-significant focal species (Table 3). The majority of the departures from the plot-wide null model were negative, indicating that species were located in functionally or phylogenetically more similar biotic neighborhoods than expected by chance (Table 3).

To test if the significance of the plot-wide displacement null model was dependent on the abundance of the focal species (hypothesis H2) we conducted a rarefaction test. To this end we randomly “thinned” the observed and the null model patterns of several abundant species that showed strong departures from the null model and repeated the null model test several times with the thinned data. The results showed threshold behavior, with a substantially reduced ability to detect significant departures from the plot-wide

displacement null model if the abundance of the species was below 200 individuals (Fig. 1a). However, even for the lowest abundance used here (i.e., 50 individuals) the rarefaction test still detected departures from the null model in 40% of all replicates. Thus, the null model has a reduced ability to detect significant effects only for low abundance species (say below 200 or 100 individuals/25 ha). This indicates that the potential signals of habitat filtering are only weakly influenced by sample size.

To test if hypothesis H1 holds after correcting for the effect of sample size on the significance of the r ISAR function (hypothesis H3), we analyzed the distribution of the sample-size-corrected standardized effect sizes $SES_f^*(r)$ (Eq. 4), taken over all focal species f of a given forest (Fig. C2). If H1 holds, this distribution should become narrower if species richness increases. Indeed, as expected by hypothesis H3, we found that the standard deviation and the mean absolute values of $SES_f^*(r)$, our measures of the width of the distribution, declined with increasing species richness (Fig. 2a, c).

In hypothesis H4, we tested whether the r ISAR results were correlated with properties of the focal species (e.g., local dominance or species traits). Indeed, the index neg_r (that yields for a given focal species f the number of neighborhoods r with negative departures from the null model; Eq. D.3) was significantly correlated with properties of the spatial pattern of the focal species when estimated for functional dissimilarity (Appendix S5: Table S1). A species tended to be surrounded by functionally more similar species if the focal species was more aggregated (A_f), locally more dominant (L_f), and had more conspecific neighbors (M_{ff}). However, in accordance with the rarefaction test, the correlation with abundance (n_f) was weak. Negative departures from the null model correlated also with species traits and were more likely if the focal species had a lower leaf P, leaf N, and specific leaf area (Table S1). Almost exactly opposite properties were

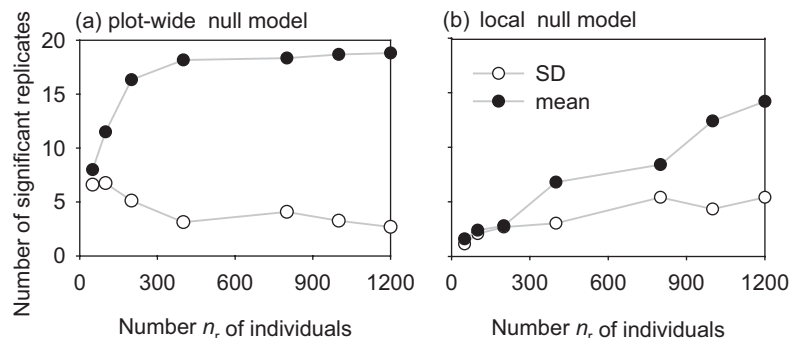


FIG. 1. Results of the rarefaction test. We selected species with strong departures from the null models (i.e., rank = 200 in the goodness-of-fit test) and randomly selected n_r (where r is the neighborhoods radius) individuals of the focal species from both the observed and null model patterns and repeated the r ISAR analysis 20 times with the reduced data sets. The graphs show the mean and the standard deviation (SD) of the number of significant results for different values of n_r .

found for focal species that did not show significant departure from the plot-wide null model (index non_j; Table S1). However, positive departures from the plot-wide displacement null model (i.e., the index pos_j) did not show stronger correlations with properties of the focal species, probably because positive departures occurred only for less than 7% of the focal species. Most of the correlations found for functional dissimilarity disappeared when using phylogenetic dissimilarity, although species that tended to agree with the plot-wide model had fewer conspecific neighbors, were less aggregated and were locally less dominant (Table S1).

Local displacement null model

The majority of focal species (83% and 79% for the phylogenetic and functional analysis, respectively) did not show departures from the local null model within local neighborhoods of 1–20 m (Table 3). Again, as expected by hypothesis H1, the percentages of species showing no significant departures increased systematically with species richness; for the two temperate forests, these percentages ranged between 57% and 67%, but for all other forests, the percentages were equal to or larger than 76% (Table 3). Thus, the small-scale (<20 m) placement of most species was independent of its immediate biotic neighborhood for both functional and phylogenetic dissimilarity.

In contrast to the plot-wide displacement null model, the significance of the local displacement null model was strongly dependent on sample size. The ability of this null model to detect systematic differences

between the observed biotic neighborhoods of species and randomly selected nearby neighborhoods was substantially reduced if the abundance of the focal species dropped below 1200 individuals/25 ha (Fig. 1b). In accordance with this result, we found that the distribution the $SES_j^*(r)$ (Eq. 4) did not become wider for more species-poor forests (Fig. 2b). Thus, the pattern H1 (the percentages of species with no significant departures from this null model increased with species richness; Table 3) can be attributed to a statistical sampling effect, and hypothesis H3 was not confirmed for the local displacement null model. This indicates that potential effects of species interactions are more strongly overpowered by stochastic effects, compared with the potential effects of habitat filtering (Fig. 1a).

As expected by the rarefaction test, less abundant focal species tended to show little or no consistent relationship with their phylogenetic neighborhoods (i.e., the indices n_j vs. non_j; Appendix S5: Table S2). Additionally, we found that this lack of relationship tended to apply if the focal species had fewer conspecific neighbors (M_{ff}), was less locally dominant (L_j), and less clumped (A_j). Almost exactly the opposite properties were shared by species with positive and negative departures from the local model (Table S2). However, species that tended to be surrounded by functionally more similar species (i.e., more negative departures; the index neg_j) tended to have more heterospecific neighbors and a smaller stature (Table S2). Generally, the above correlations were also found when analyzing functional instead of phylogenetic dissimilarity. However, the focal species with positive departure

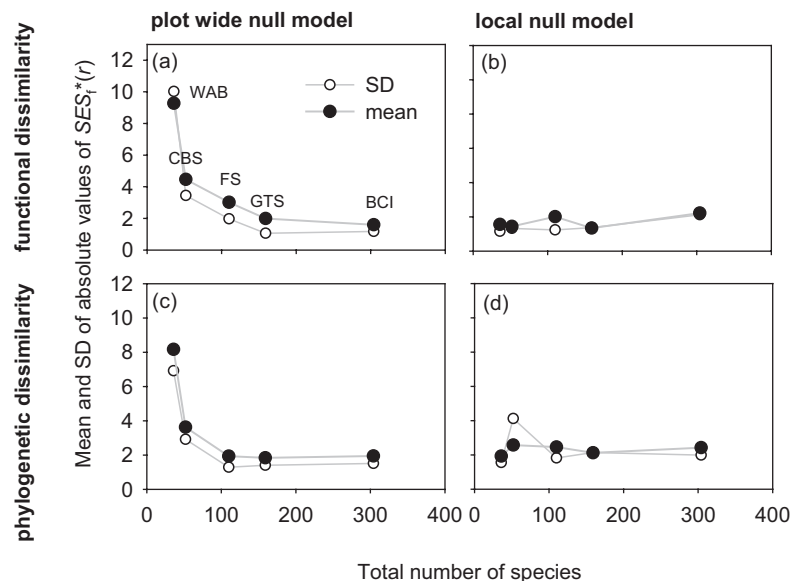


FIG. 2. The mean and the standard deviation of the distribution of the absolute values of the sample-size corrected effect sizes $SES_j^*(r)$ of the focal species for each forest plot plotted over the total species richness of the forest plots. The dilution hypothesis is supported if the mean of the absolute values declines with species richness. Forest plots are identified in Table 2.

from the local model (the index ρ_{pos}) for functional dissimilarity exhibited no correlation with properties of the spatial pattern of the focal species, but were strongly correlated with functional traits (Table S2).

DISCUSSION

Phylogenetic and functional diversity are increasingly recognized as important aspects of biodiversity (e.g., Swenson 2013). Consideration of these additional axes of biodiversity has produced substantial advances in our understanding of the co-existence and assembly mechanisms in ecological communities (Kraft et al. 2008, Kraft and Ackerly 2010, Swenson et al. 2012). Here we present a novel approach that uses data on fully mapped communities to quantify functional or phylogenetic properties of the biotic neighborhoods of focal species. Comparisons of simulations with spatially explicit field data allow us to infer if individuals of a focal species show consistent relationships with their phylogenetic (or functional) neighborhood, as expected by coexistence theory, and if the incidence of such relationships declines with species richness as expected by stochastic dilution (Wiegand et al. 2012). We applied this methodology to data from five 25–50 ha forest-dynamics plots ranging from temperate, subtropical, to tropical forests to test predictions derived from the stochastic dilution hypothesis. Our results support the dilution hypothesis in that the proportion of species that were surrounded by phylogenetically or functionally more similar or dissimilar species (i.e., patterns expected by coexistence theory) decreased with species richness. We also found that species showing consistent relationships with their neighbors tended to be more abundant, more clustered, and locally more dominant. Thus, they showed spatial patterns that were similar to the patterns typically observed in relatively species poorer forests.

The effects of stochasticity

When assessing species coexistence mechanisms, ecologists have traditionally focused on deterministic processes such as niche differentiation or competition (e.g., Chesson 2000). However, we argue here that stochastic dilution effects associated with increasing species richness can mask deterministic processes, thereby approximating spatial independence of species in diverse communities (McGill 2010, Wiegand et al. 2012). Stochastic dilution is a consequence of the stochastic geometry of biodiversity where each individual of a given species is surrounded by a different set of competitors (Hubbell and Foster 1986, Lieberman and Lieberman 2007). A factor that may lead to this stochasticity is dispersal limitation; competitively superior species might by chance fail to colonize appropriate sites before the establishment of competitively inferior species (Hurtt and Pacala 1995). While the outcomes

of local species interactions are governed by mechanisms outlined by coexistence theory, these outcomes also may vary greatly among individuals of a given species (i.e., demographic heterogeneity in biotic neighborhoods); this variation might prevent emergence of uniform responses at the species level that would otherwise generate the neighborhood patterns predicted by coexistence theory. In other words, more unpredictable biotic neighborhood of species in a community should produce weaker signals of neighborhood patterns predicted by coexistence theory.

Our results support several predictions of the dilution hypothesis. First, the proportion of focal species that were surrounded by phylogenetically (or functionally) more similar or dissimilar species decreased with species richness as expected by hypothesis H1. This is a strong result based on data from five fully mapped forest plots ranging from temperate to tropical forests. However, weaker signals of the neighborhood patterns can also be a consequence of lower samples sizes in species richer forests if we assume that stem numbers are roughly similar (e.g., Table 2). This statistical mechanism has been emphasized with respect to pairwise species interactions (e.g., Lieberman and Lieberman 2007, Wiegand et al. 2007b, 2012, Volkov et al. 2009, McGill 2010), but can also apply in the framework presented here. Analysis of hypothesis H2 showed that the power of the plot-wide null model (that most likely depicts effects of habitat filtering) was only weakly affected by sample size, whereas the significance of the local displacement null model (that most likely depicts the effects of species interactions) was strongly impacted by sample size (Fig. 1). We also tested whether our results provide evidence for dilution of ecological interactions beyond the statistical effect of reduced samples size (Appendix S3). Our results showed that hypothesis H1 remained true for the plot-wide null model, but not for the local displacement null model (Fig. 2).

Circumstances under which stochastic dilution may emerge

Our results suggest that stochastic dilution is not only a statistical issue, but a real mechanism of species assembly if species are exposed to at least some stochasticity in the processes determining their biotic neighborhoods. Being surrounded by an unpredictable set of species neighbors is a mechanism that has the potential to maintain diversity because it constitutes a sort of “spreading of risk” with respect to the neighbors. The more different species an individual may encounter in its neighborhood, the higher the chance that some individuals will have “favorable” neighbors and therefore a higher probability of surviving and reproducing (Hurtt and Pacala 1995, Wiegand et al. 2007b). This mechanism works if species do not reach all sites for which they are best adapted (i.e.,

recruitment limitation), which allows inferior competitors to win such sites by forfeit. Remarkably, Hurtt and Pacala (1995) summarized a version of the dilution hypothesis as “Thus, since recruitment limitation is likely to be most common in highly species-rich communities because of the rarity of many species, we suggest that the importance of chance and history in diverse plant communities is not in conflict with strong interspecific competitive differences between plants.”

Stochastic dilution is caused by demographic heterogeneity in the biotic neighborhood of a species; this phenomenon can arise through a variety of mechanisms whereby the identity of the nearest neighbors of an individual of a given species is largely unpredictable. In general, the effects of stochastic dilution will be strongest when the community is characterized by high species richness, low local dominance of species, and dispersal limitation, whereby intermediate dispersal distances leave suitable sites unoccupied. In turn, dispersal distances that are too low may generate local dominance of species (where biotic neighborhoods become more predictable), and too large dispersal distances reduce the patchiness in the species distribution and therefore the potential for demographic heterogeneity.

Analysis of hypothesis H4 supports the notion that particular patterns in the stochastic geometry of biodiversity are responsible for stochastic dilution. For example, we found that the local dominance index of species decreased strongly and systematically with species richness (Fig. 3) and that a focal species was more likely to be surrounded by phylogenetically (or functionally) more similar or dissimilar species than expected by the null models if it showed spatial patterns that more closely resembled the patterns typically found at species poorer forests (i.e., higher

abundance, higher neighborhood density M_{fit} , higher clustering A_j , and higher local dominance L_j ; Table S1, Fig. 3).

We have to emphasize that we consider here spatial scales ranging from the immediate neighborhood scales of plants (where interactions with their neighbors occur) to local scales of tens of hectares (where demographic dispersal of tree species typically occurs; Muller-Landau et al. 2008). It is clear that we would find stronger systematic patterns at larger scales, where additional habitats are added and the biotic environment is more strongly influenced by habitat filtering (e.g., Garzon-Lopez et al. 2014). We also expect effects of stochastic dilution to be visible at demographic time scales of say tens of generations; at evolutionary time scales stochastic dilution is hypothesized to result in functional equivalence of species (Table 1C; Hubbell 2006).

Alternative explanations for the observed patterns.—

Lack of neighborhood patterns as expected by coexistence theory can also arise if species approximate functionally equivalence (Table 1C). A mechanism similar to stochastic dilution has been proposed to explain functional equivalence of species on evolutionary timescales (e.g., Goldberg and Werner 1983, Hubbell and Foster 1986) (Table 1C). For example, Hubbell and Foster (1986) noted that individuals of a given species are often exposed to unpredictable local assemblages of competitors and argued that this may force species, on evolutionary timescales, to converge on similar life-history strategies that are competitively equivalent because the opportunities for directional character displacement among a large number of competing species would be low (Hubbell 2006).

Scheffer and van Nes (2006) presented “emergent neutrality” as an alternative mechanism that can produce functional equivalence of species in species rich communities at demographic (and evolutionary) timescales. This idea is based on self-organization that produces transient dynamics in multispecies Lotka-Volterra models that yield for extended periods of time functional equivalence of groups of species (Table 1C). Emergent neutrality requires an intricate balance between direct and indirect competition effects (Scheffer and van Nes 2006), and future research must show if this mechanism persists in a spatially explicit and stochastic setting and if it can generate the systematic patterns H3 and H4 observed here. Fisher and Mehta (2014) found, in a nonspatial context, results similar to the expectations of stochastic dilution. They used a stochastic multispecies Lotka-Volterra model to investigate the effect of stochasticity on the phase transition between a “neutral phase” where the species abundance distributions could not be distinguished statistically from those generated by a neutral model and a “niche phase” where abundance distributions could be distinguished. As expected, the niche

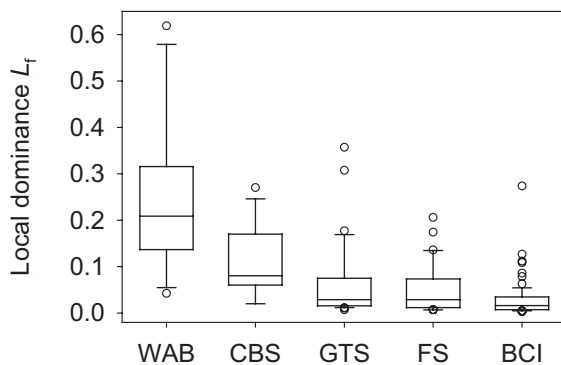


FIG. 3. The distribution of the index L_j of local dominance for all focal species / species analyzed in the five plots. The index L_j is defined as the mean proportion of conspecifics within a 20-m neighborhood around the focal species individuals. The midline inside each box represents the median, and the bottom and top of each box are the first and third quartiles, respectively. The whiskers represent values outside the upper and lower quartiles. The circles are outliers not included between the whiskers.

phase was favored in communities with large population sizes and relatively constant environments, whereas the neutral phase was favored in communities with small population sizes and fluctuating environments.

Another hypothesis to explain lack of neighborhood patterns is that stronger positive and negative interactions of a focal species with other species just average each other out (e.g., Kraft and Ackerly 2010, Punchi-Manage et al. 2015; Table 1B). However, while this mechanism may contribute to the weak observed effects, it is somewhat unlikely that such a delicate balance would occur for many focal species in species rich forests but disappear in forests that are more species poor (Punchi-Manage et al. 2015).

The importance of habitat filtering and species interaction

As expected under habitat filtering, approximately 66% of the species that showed significant departures from the plot-wide null model were surrounded by ecologically more similar species than expected by the plot-wide displacement null model (i.e., negative departures), and in all simulations we found more focal species with negative departures from the plot-wide null model than with positive departures.

Mayfield and Levine (2010) showed that competitive exclusion can result in either more similar or more dissimilar species than expected co-occurring locally. Thus, the roughly 10% of cases with negative departures from the local displacement null model (focal species were surrounded by more similar biotic neighborhoods) could be caused by either competitive exclusion and/or habitat filtering operating at small scales. The latter is also consistent with previous studies showing that abiotic filtering of traits and lineages may also occur on smaller spatial scales (Kraft and Ackerly 2010, Swenson et al. 2012). We found that the plot-wide null model showed additional dilution effects beyond the effects of reduced statistical power in species richer forests. However, the effects of species interactions (most likely revealed by the local displacement null model) degrade basically with sample size as hypothesized before (e.g., Lieberman and Lieberman 2007, Volkov et al. 2009, McGill 2010, Wiegand et al. 2012).

It is nevertheless a surprising result that the overwhelming majority of focal species analyzed here (Table 3) did not show consistent relationships with the functional or phylogenetic composition of their local biotic neighborhoods, given earlier evidence of studies based on statistical neighborhood models that evaluated the performance of individual plants relative to phylogenetic neighborhood (e.g., Webb et al. 2006, Uriarte et al. 2010, Paine et al. 2012, Lebrija-Trejos et al. 2014). We suggest two explanations that are not mutually exclusive. First, our analysis involved large trees whereas previous studies analyzed mostly seedlings (see, e.g., Table 5 in Lebrija-Trejos et al. 2014). It is therefore likely that our method would show more significant effects when applied to

seedlings or saplings (but see Punchi-Manage et al. 2015). Second, statistical neighborhood models relate the performance of individuals of a focal species (e.g., growth or survival) to ecological properties of their neighbors, whereas our approach compares the average biotic neighborhood of individuals of a focal species to that of random locations within the plot. Thus, if interspecific and intraspecific variability in the biotic neighborhoods of individuals is of similar order of magnitude, the signals of deterministic processes may not translate into detectable patterns in species placement. Future research should therefore not only analyze the average biotic neighborhood of species but also its variance.

CONCLUSIONS

In this study, we used a novel point pattern approach based on the plant's eye view of the community (Turkington and Harper 1979) to systematically investigate if individual species were surrounded by phylogenetically (or functionally) more similar or less similar species than expected by chance. Such patterns are expected if deterministic processes such as habitat filtering and competition would operate. Our approach is different from that taken in most studies of community assembly using data of fully mapped plots (e.g., Kembel and Hubbell 2006, Swenson et al. 2006, Kraft et al. 2008) in that it focus not on the entire community, but on individual focal species. This allowed us to use fundamentally different null models that randomized only the individuals of the focal species and not the entire community (e.g., the independent swap algorithm; Kembel and Hubbell 2006, Kraft and Ackerly 2010) or the functional or phylogenetic dissimilarity matrix (e.g., Swenson et al. 2012, Yang et al. 2013).

Our results from the analysis of five forests with largely different species richness showed that the placement of large trees of individual species with respect to their functional and phylogenetic neighborhood were in good agreement with predictions derived from the stochastic dilution hypothesis (Wiegand et al. 2012). The dilution hypothesis allows the outcome of local species interactions to be governed for each individual by deterministic mechanisms outlined by coexistence theory, however, these outcomes may vary greatly among individuals of a given species if they are surrounded by highly variable subsets of competitors. As a result, directed responses failed to emerge at the species level and patterns of independent placement of focal species with respect to their biotic neighborhood appeared. This is a simple mechanism based on stochastic geometry that can explain why species rich forests show neutral patterns in local biotic neighborhoods despite the existence of deterministic niche processes. We purposefully analyzed only communities of large trees, excluding earlier life stages. Future research will be needed to determine if the results found here hold also for other forest communities and if juveniles or seedlings also

tend to be independently distributed with respect to their functional or phylogenetic neighborhoods.

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