



Linking trait similarity to interspecific spatial associations in a moist tropical forest

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Keywords

Co-occurrence; Habitat filtering; Mantel test; Niche differentiation; Point pattern; Recruits; Traits

Abbreviations

BCI = Barro Colorado Island; FDP = Forest Dynamics Plot; GoF = Goodness of Fit (test); LHS traits = leaf–height–seed traits

Nomenclature

Croat (1978), as updated by Condit et al. (1996)

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Abstract

Aim: Community assembly theory predicts that niche differentiation promotes the spatial clustering of functionally dissimilar species, whereas habitat filtering has the converse effect. We used these predictions to assess the relative effects of habitat filtering and niche differentiation on recruit community assembly over spatial (5- and 30-m neighbourhoods) and temporal (20-yr) scales in the Forest Dynamics Plot at Barro Colorado Island.

Location: Barro Colorado Island, Panama.

Methods: We integrated data on the spatial patterns of ≥ 1 cm DBH (diameter at 1.3 m above ground) recruits with data on seven functional traits for 64 species. First, we quantified the interspecific association patterns of all species pairs i and j using the K-function $K_{ij}(r)$ and the nearest-neighbour distribution function $D_{ij}(r)$. Second, for those pairs with significant spatial associations, we calculated an index of interspecific spatial association using the results of these two summary statistics. Finally, we examined the relationship between interspecific spatial association and trait similarity using simple and partial Mantel tests.

Results: In all censuses, almost one-half of species pairs had no spatial associations, but for pairs that were significantly spatially associated, positive relationships between trait similarity and spatial association occurred in 5-m and 30-m neighbourhoods, whereas significant negative relationships only appeared in 5-m neighbourhoods. This suggests that habitat filtering was more important than niche differentiation in assembling recruit communities at 5- and 30-m scales. Habitat filtering mainly acted upon traits related to topographic habitat preferences and dispersal mode, whereas spatial association was inversely related to similarity in terms of wood specific gravity and shade tolerance.

Conclusions: Our findings suggest that both stochastic and deterministic processes operate in species-rich ecological communities, but the role of habitat filtering and niche differentiation as determinants of community assembly vary over spatial and temporal scales. Species co-occurrence was driven by habitat filtering at small and large scales, but also by a combination of niche differentiation and weaker-competitor exclusion effects at small scales. Temporal variations in the importance of habitat filtering and niche differentiation could be related to the occurrence of disturbances such as tree falls. Our results emphasize the role of trait-based processes in plant community assembly.

Introduction

Explaining co-occurrence patterns of plant species in diverse tropical forests is one of the primary challenges in ecology (Wright 2002). Currently, it is widely accepted that these patterns are mainly explained by chance events

associated with seed dispersal and demographic stochasticity (Volkov et al. 2009; Wiegand et al. 2012), but also by deterministic processes such as habitat filtering and niche differentiation (Leibold & Peek 2006). Habitat filtering results from the interaction of plants with their abiotic environment, whereas niche differentiation (also termed

within-site niche differentiation; Cingolani et al. 2007), results from biotic interactions among neighbouring individuals (Chase & Myers 2011). Habitat filtering and niche differentiation can occur simultaneously in a plant community, but their relative importance usually varies at different spatial scales (Götzenberger et al. 2012; Adler et al. 2013; May et al. 2013). Habitat filtering appears to be more important at larger scales, at which predictable environmental and topographic gradients occur (Shipley et al. 2012). Niche differentiation, on the other hand, is often more important at smaller scales at which competitive interactions and pathogen transfer among neighbours increase in frequency and intensity (Kraft & Ackerly 2010).

The extent of habitat filtering and niche differentiation can be evaluated through the measurement of the functional traits of co-occurring species (Cornwell & Ackerly 2009; Shipley et al. 2012). Habitat filtering is expected to limit the range of trait values among neighbouring individuals, such that co-occurring species express similar functional trait values (i.e. trait convergence; Paine et al. 2011). Conversely, niche differentiation should lead to ecological differentiation of species along small-scale abiotic gradients, leading co-occurring species to exhibit dissimilar functional trait values (i.e. trait divergence; Kraft et al. 2008). To understand the relative importance of habitat filtering and niche differentiation by examining trait similarity, we must select the appropriate traits. To study the role played by habitat filtering in the assembly of diverse tropical forests, it is necessary to select traits such as dispersal mode and seed mass, which affect dispersal and establishment limitation (i.e. the failure of seeds to arrive, or to establish as seedlings, respectively; Wright et al. 2005), and the light, soil moisture and nutrient preferences of the species (John et al. 2007). Regarding niche differentiation, we need to select traits such as wood density, leaf mass per unit area, maximum height and seed mass, which affect resource competition through the growth–survival trade-off (Baraloto et al. 2007). Wood density, leaf mass per area and seed mass also affect resistance to pests and pathogens and are thus related to niche differentiation (Westoby et al. 2002).

It is also important to note that functional traits are not independent of each other. Indeed, seed dry mass is generally considered a good proxy of dispersal mode (Westoby et al. 1996), wood specific gravity is associated with shade tolerance (Muller-Landau 2004) and leaf mass per area is significantly related to wood specific gravity and seed dry mass (Wright et al. 2010). Moreover, the majority of these traits are involved in more than one trade-off (Lavorel & Garnier 2002), contributing to both habitat filtering and niche differentiation (Adler et al. 2013). For all these reasons, when studying the relationships between species

co-occurrence and trait similarity it is necessary to analyse the effects of each trait alone, the combined effects of all traits together and the joint effects of correlated groups of traits (Westoby 1998). Some functional traits such as plant height and leaf mass per area also contribute to variation in relative fitness differences among species (Chesson 2000). These traits are strongly related to biotic effects leading to weaker competitor exclusion (Grime 2006), and may show similar (i.e. convergent) values among co-occurring species at small spatial scales (Mayfield & Levine 2010). Moreover, species are not phylogenetically independent of each other, thus, we need to exclude species trait similarities that derive simply from shared evolutionary history (Legendre & Legendre 2012). It is also important to study the relationships between spatial association and phylogenetic relatedness because they contain valuable information on some important characteristics that emerge from suites of traits, such as the susceptibility to natural enemies (Kraft & Ackerly 2010).

Previous studies of community assembly have divided permanent plots into non-overlapping quadrats, calculated quadrat-level trait indices, and compared them to the values expected if the community was assembled without regard to traits (Swenson & Enquist 2009; Kraft & Ackerly 2010; Shipley et al. 2012). The effect of scale on the relative importance of habitat filtering and niche differentiation was determined by calculating trait indices in increasingly large aggregations of neighbouring quadrats (e.g. Swenson et al. 2012). An alternative approach is given by recent techniques of spatial point pattern analysis that can quantify pair-wise spatial associations between species (i.e. how the individuals of one species are distributed within circular neighbourhoods around individuals of other species) by contrasting them to suitable null models (Illian et al. 2008; Wiegand et al. 2007, 2012; Wiegand & Moloney 2014). The number of species pairs showing non-significant spatial associations is an indicator of the degree to which community assembly is stochastic (Volkov et al. 2009). For each spatially associated species pair, we can derive an index of spatial association, and studying the relationship between this index and other of trait similarity may reveal the relative importance of habitat filtering and niche differentiation. A positive relationship will indicate that neighbouring plants have similar trait values (i.e. trait convergence) whereas a negative relationship will indicate that they have dissimilar trait values (i.e. trait divergence).

In this study, we assess the relative effects of habitat filtering and niche differentiation on the assembly of recruit communities in the moist tropical forest of Barro Colorado Island, Panama, by examining the relationship between spatial association and trait similarity. In contrast to previous studies of larger trees, we focused on the distribution of individuals recruiting into the 1-cm DBH size class, as

their reduced access to resources makes them more sensitive to shading, drought and pathogen attack (Comita & Hubbell 2009). The spatial distribution of recruits is strongly affected by stochastic processes, habitat filtering and niche differentiation (Grubb 1996; Wright et al. 2005), which in turn influences forest composition and dynamics. To examine the scale dependence of recruit community assembly we focused on neighbourhoods of 30 and 5 m in radius because they are the scales at which habitat preferences become evident (Harms et al. 2001) and plant–plant interactions among saplings occur (Casper et al. 2003), respectively. We characterized community structure at three censuses over a 20-yr period, since biotic and abiotic conditions in old-growth tropical forests fluctuate through time (Metz et al. 2008) and we suspect that they could affect recruit community assembly.

We hypothesize that; (1) at all spatial scales, stochastic processes will influence co-occurrence of species, leading to a large proportion of non-significant spatial association patterns; (2) at 30-m neighbourhoods, habitat filtering will structure communities more than niche differentiation, and we will detect a positive relationship between spatial association and trait similarity. (3) Conversely, at 5-m neighbourhoods community assembly will be primarily driven by niche differentiation, leading to a negative relationship between spatial association and trait similarity. Functional traits may differentially contribute to community assembly; (4) traits related to topographic habitat preferences, dispersal and drought resistance will contribute to habitat filtering, whereas (5) traits that affect resource competition through the growth–survival trade-off such as wood density and shade tolerance will contribute to niche differentiation.

Methods

Study site

Our study was carried out in the 50-ha Barro Colorado Island Forest Dynamics Plot (FDP), Panama (9°9' N, 79°51' W, 120–155 m a.s.l.) and where rainfall averages 2600 mm·yr⁻¹, falling mainly between Apr and Nov. The FDP contains semi-deciduous moist tropical forests, and in the plot, all woody plant individuals ≥1 cm DBH (diameter at 1.3 m height above ground) have been mapped, measured and identified to species in 1982, and every 5 yr since 1985 (Hubbell et al. 2005). Species–habitat associations affect the spatial distribution of adult trees (Harms et al. 2001), but they are diffuse at the sapling stage (Kanagaraj et al. 2011). The canopy of the FDP is more open than in other tropical forests (Metz et al. 2008) and tree-fall gaps and other canopy-opening disturbances are relatively frequent, particularly in years following El Niño events (i.e. 1982–83 and 1998), when dry seasons are

unusually severe (Condit et al. 2004). Overall recruit densities in the FDP are high, especially where canopy openings increase light availability (Comita & Hubbell 2009).

Data collection

In this study we focused on recruits, defined as individuals absent in the first census of each interval but present in the second (Wiegand et al. 2009). They included mainly saplings (tree individuals with 1–4 cm DBH), but also a few juveniles (Kanagaraj et al. 2011). We analysed the 1985, 1995 and 2005 censuses because they spanned the monitoring period of the FDP and much of the among-year climatic fluctuations in the Isthmus of Panama. We analysed only species with ≥40 recruits in each of the three studied censuses. With fewer recruits, stochasticity would have precluded meaningful spatial point pattern analysis. This criterion resulted in the inclusion of 64 species, out of the 320 found in the FDP. However, these 64 species comprised between 85% and 88% of the recruited individuals, depending on the census.

We collected species mean data on functional traits of interest from public data sets and the literature. We obtained wood specific gravity, leaf mass per area, seed dry mass and maximum height (i.e. the mean height of the six largest individuals by DBH) from Wright et al. (2010). We obtained shade tolerance index from Comita et al. (2010), and drought sensitivity index from Engelbrecht et al. (2007). Shade tolerance and drought sensitivity indices were calculated specifically for tree species in the BCI plot, and they were based on the species differences in relative growth and mortality rates (Comita et al. 2010), and in the effectiveness of physiological mechanisms of drought tolerance (Engelbrecht et al. 2007), respectively. We extracted dispersal mode from the Smithsonian Tropical Research Institute online database, and topographical habitat preferences from Harms et al. (2001). The latter two traits are categorical, whereas the others are continuous. The trait data are summarized in Appendix S4. Further details on their sampling methods can be found in the aforementioned references.

Spatial point pattern analysis

We characterized interspecific spatial association patterns in a total of $64 \times 63 = 4032$ species pairs at spatial neighbourhoods from radius $r = 1$ to 50 m, but we focused on that of radius $r = 5$ and 30 m. Note that for species i and j , we differentiate between pairs ij and ji because species interactions are frequently asymmetric (Vázquez et al. 2007), but if reciprocal pairs (i.e. species pairs ij and ji) showed the same coordinates in the two-axis scheme, we selected just one.

We used the approach of Wiegand et al. (2007, 2012) to characterize interspecific spatial association patterns. First, for each pair of species i and j in neighbourhood of radius r , we computed the K -function $K_{ij}(r)$, which measures how individuals of species j are distributed within neighbourhoods of radius r around individuals of species i (Ripley 1981). This function would be sufficient to characterize spatial association patterns if the spatial configuration of recruits of species j around recruits of species i were the same throughout the plot (Getzin et al. 2008). However, the same value of $K_{ij}(r)$ results if all neighbourhoods within radius r around individuals of species i contain the same number of individuals of species j , or if they vary (Wiegand & Moloney 2014). To characterize this variation, we also computed the cumulative nearest-neighbour distribution function $D_{ij}(r)$, which yields the probability that individuals of species i has no neighbour individuals of species j within radius r (Wiegand & Moloney 2004).

Second, to distinguish significant spatial associations from those which arise by chance, we compared the observed bivariate point patterns with those generated by a null model in which the spatial locations of individuals of the species i remained unchanged while those of the species j were distributed randomly and independently of the locations of species i (i.e. a homogeneous Poisson process; Wiegand et al. 2012). For each species pair, we evaluated significant departures from the null model by means of the fifth lowest and the fifth highest values of 199 Monte Carlo simulations in order to generate 95% simulation envelopes, up to $r = 50$ m. We also determined whether departures from the null model were significant by performing a goodness-of-fit (GoF) test (Loosmore & Ford 2006). This test quantifies the fit of the null model in the $K_{ij}(r)$ or $D_{ij}(r)$ functions over the 1–50-m interval at a 5% error rate; however, if we use both functions together the true error rate may vary between 5% and 10%. Thus, only species pairs that showed clearly significant spatial association patterns (i.e. GoF > 190) were subsequently used to analyse the relationships between the degree of spatial association and trait similarity.

Third, we centered $D_{ij}(r)$ and $K_{ij}(r)$ by subtracting their expected values under the null model; $D_{ij}(r) = 1 - \exp(-\lambda_j \pi r^2)$ and $K_{ij}(r) = \pi r^2$. We log-transformed $K_{ij}(r)$ so that $D_{ij}(r)$ and $K_{ij}(r)$ departure from the null model in the same way (Wiegand et al. 2007, 2012; Wiegand & Moloney 2014). We then classified each species pair at each neighbourhood scale, using the centered and log-transformed statistics as positions on two axes:

$$\begin{aligned} \hat{P}(r) &= \hat{D}_{ij}(r) - (1 - \exp(-\lambda_2 \pi r^2)) \\ \hat{M}(r) &= \ln(\hat{K}_{ij}(r)) - \ln(\pi r^2) \end{aligned} \quad (1)$$

where the hat symbol indicates the observed value of each species pair. These two axes allowed us to classify the species pairs that departed significantly from the null model into four interspecific spatial association patterns (Figs 1, Appendix S6 and Appendix S7a). Species pairs located in the upper-right quadrant have a positive spatial association (mixing) because here recruits of species j occur more often within neighbourhoods of radius r around recruits of species i [$M(r) > 0$], and recruits of species i have more neighbours of species j [$P(r) > 0$] than expected under the null model. Conversely, species pairs located in the lower-left quadrant have a negative spatial association (segregation) because there are fewer recruits of species j within neighbourhoods of radius r around the recruits of species i than expected under the null model [$M(r) < 0$ and $\hat{P}(r) < 0$]. Species pairs located in the upper-left quadrant show a type of spatial association (partial overlap) in which some individuals of species i contain more neighbours of species j than expected by chance and others contain less [$\hat{M}(r) > 0$ and $\hat{P}(r) < 0$]. Species pairs located in the lower-right quadrant show the opposite type of association (opposite to partial overlap) [$\hat{M}(r) < 0$ and $\hat{P}(r) > 0$] but they occur rarely (Wiegand et al. 2007, 2012).

Indices of interspecific spatial association and trait similarity

To analyse the relationships between the degree of spatial association and trait similarity, first, we calculated an 'index of spatial association' (hereafter; A_{ij}), as the loadings on the first axis of a PCA of the axes $\hat{P}(r)$ and $\hat{M}(r)$ for each species pair (ij). The first axis of the PCA explained >75% of the variance in the spatial association metrics in each census and spatial scale considered. Positive and negative values of A_{ij} correspond to species pairs located in the upper-right and lower-left quadrants of the classification scheme, respectively (Appendix S7b). Thus, species pairs with positive spatial association show large positive values of A_{ij} , whereas species pairs with negative spatial association show large negative values of A_{ij} . Species pairs located in the upper-left and the lower-right quadrants, in contrast, have intermediate A_{ij} scores.

Second, we estimated the trait similarity of species pairs by calculating the S_{ij} index of similarity (Appendix S1; Podani 1999; Pavoine et al. 2009). To do so, we first computed the Gower dissimilarity coefficient (D_{ij} ; Laliberté & Legendre 2010) with the *gowdis* function of R package *FD* (R Foundation for Statistical Computing, Vienna, AT) and then converted it to a similarity coefficient by using $S = 1 - D$ (Laliberté et al. 2014). The S_{ij} index can be used for both numeric and categorical traits. If it is used for only

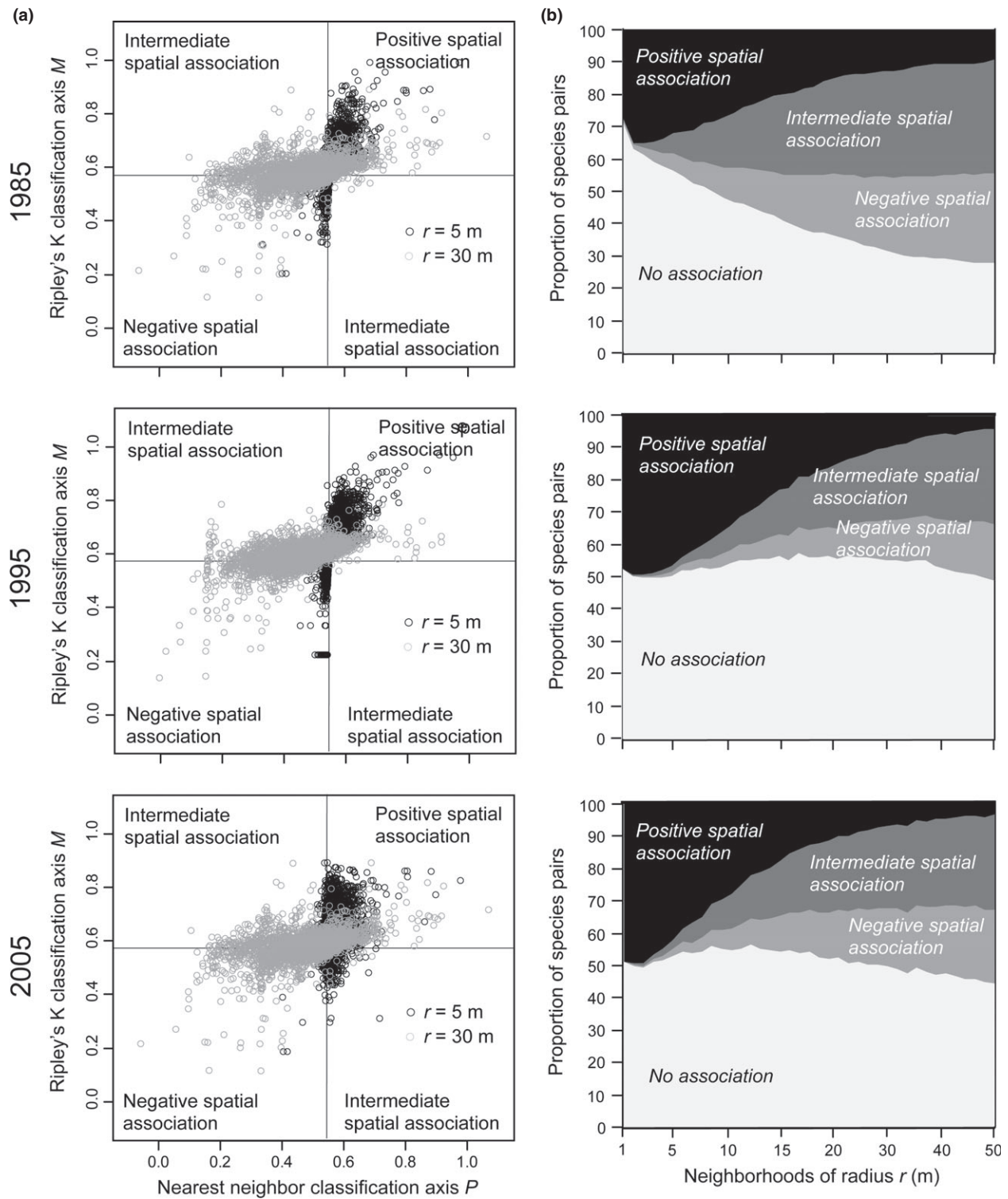


Fig. 1. (a) Classification schemes of interspecific spatial association patterns of recruit species pairs in Barro Colorado Island Forest Dynamics Plot (Panama) in the 1985, 1995 and 2005 census periods. Black and grey circles indicate species pairs at 5- and 30-m radius neighbourhoods, respectively. The distribution of the three types of spatial association patterns considered in the scheme; positive, negative and intermediate spatial association is also indicated. (b) Number of species pairs showing the variation in incidence of non-significant spatial association and the three types of significant spatial association patterns over all spatial scales in the 1985, 1995 and 2005 census periods.

one categorical trait, it yields binary 0–1 values, which express similar or dissimilar values of such trait, respectively. This index was calculated for each particular species pair (ij) considering each trait individually, but also for all traits together and for the leaf–height–seed (LHS) group of traits (Appendix S2). This group is based on three traits that are thought to represent the key axes of ecological strategies among vascular plants; specific leaf mass area index (calculated as the inverse of leaf mass per area), maximum height and seed mass (Westoby 1998; Appendix S1).

Simple and partial Mantel tests

To examine the relationships between the indices of interspecific spatial association and trait similarity, we compare spatial association and trait similarity matrices using simple Mantel tests (Legendre & Legendre 2012). Here, the Mantel correlation coefficient r_M indicates the strength of the relationship between spatial association and trait similarity among species pairs. A positive correlation would be consistent with habitat filtering, whereas a negative correlation would indicate niche differentiation (Appendix S7c). To account for the potential phylogenetic signal in species traits, we also performed partial Mantel tests between interspecific spatial association and trait similarity while controlling the effect of pair-wise phylogenetic relatedness. To calculate phylogenetic relatedness between pairs of species we first assembled our species list to a master phylogeny using the Phylomatic online tool (Webb & Donoghue 2005). Second, we calculated the matrix of phylogenetic distances (measured in millions of years down to the common ancestor of two species) using the *phydist* procedure of the Phylocom 4.1 software (Webb et al. 2008). Third, we calculated the inverse pair-wise distances as a metric of phylogenetic relatedness (Vamosi et al. 2009). The significance of the relationships in simple and partial Mantel tests was tested with 10 000 permutations. In each test we calculate the one-tailed P -values for the null hypotheses of $r_M \leq 0$ (trait convergence) and $r_M \geq 0$ (trait divergence).

Point pattern analyses were performed with Programita (Wiegand & Moloney 2014), which can be accessed at www.programita.org. Trait similarity indices were calculated with the R package *FD* (Laliberté et al. 2014), and Mantel tests were performed using the R package *vegan* (Oksanen et al. 2012). We calculated the two-one-tailed P -values of the Mantel coefficients with the function *permustats* (Appendix S3).

Results

The two-axis classification schemes showed a large proportion of spatially associated species pairs in 1985, however,

across the 1995 and 2005 census periods, regardless of spatial scale, roughly half of the species pairs did not show significant associations. In all census periods, however, the number of species pairs showing positive spatial association (mixing) was highest in small neighbourhoods, whereas the number of species pairs showing patterns of negative spatial association (segregation) increased in neighbourhoods >20 m in radius (Fig. 1b).

Results of Mantel tests were similar with and without controlling for pair-wise phylogenetic relatedness, so we only present the results without phylogenetic information (Fig. 2, Appendix S5). Simple Mantel tests showed that there were more positive relationships at 30- than at 5-m neighbourhoods in all censuses. Additionally, there were more negative relationships at 5- than at 30-m neighbourhoods in all censuses, but many of them were not significant.

Results for the different traits slightly differed between the three census periods but there were a few consistent trends. At 30-m neighbourhoods, the spatial association index was significantly and positively related to topographic habitat preferences and dispersal mode across all censuses, to shade tolerance index in 1985 and 2005, and to maximum height in 1995 (Fig. 2, Appendix S5), which indicates trait convergence. At 5-m neighbourhoods, the Mantel correlation coefficients were also significantly positive for topographic habitat preferences across all censuses and for leaf mass area index in 1985 and 2005 (Fig. 2a, c). Conversely, the spatial association index was significantly and negatively related to shade tolerance index and wood specific gravity in 5-m neighbourhoods in 1995, which indicates trait divergence (Fig. 2b). The combination of all traits together and LHS traits were significantly and positively related to the spatial association index only at 5 m in 2005 and at 30 m in 1995, respectively (Fig. 2, Appendix S5). The Mantel correlation coefficients were generally weak (i.e. 46 of 60 ≤ 0.10 ; Appendix S5).

Discussion

We quantified the relative contributions of habitat filtering and niche differentiation to the assembly of recruit communities in the moist tropical forest of Barro Colorado Island, Panama, by examining the relationships between spatial association and trait similarity for species pairs over a 50-m range of spatial scales, and over a 20-yr period. We detected a large proportion of no significant spatial association patterns, indicating an important role of stochastic processes in structuring this forest. However, our results for spatially associated species indicated that habitat filtering and niche differentiation operate on the recruit community. Habitat filtering was important at both large and small spatial scales, whereas niche differentiation only

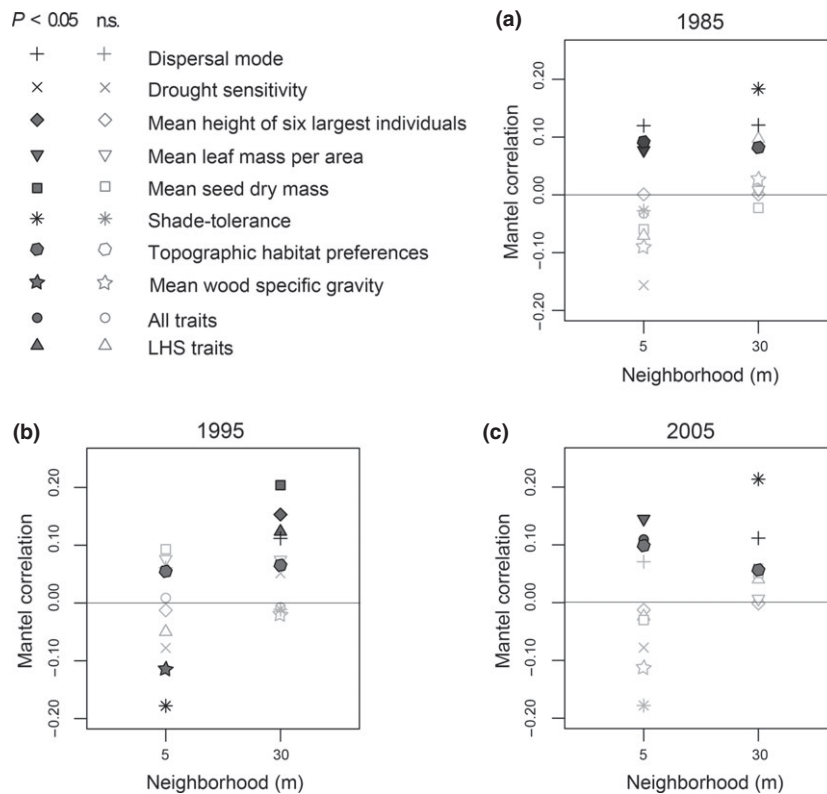


Fig. 2. Mantel correlations between interspecific spatial association and trait similarity matrices at Barro Colorado Island Forest Dynamics Plot (Panama) in the 1985 (a), 1995 (b) and 2005 (c) censuses, at 5- and 30-m neighbourhoods, i.e. from small to large spatial scales. Positive correlations indicate that spatially associated species are similar in terms of a given trait or trait combination (trait convergence), which suggests mainly habitat filtering. Negative correlations indicate dissimilarity between spatially associated species (trait divergence), which suggests niche partitioning. The full results indicating the number of species pairs and the exact values of the Mantel correlation coefficient r_M and their one-tailed P -values for the null hypotheses of $r_M \leq 0$ (trait convergence) and $r_M \geq 0$ (trait divergence) in each Mantel test are presented in Appendix S5.

occurred at small spatial scales. Habitat filtering is associated with traits related to topographic habitat preference and dispersal mode of the species, and niche differentiation is associated with traits related to the growth–mortality trade-off across a gradient of light availability. We also determined that the relative importance of niche differentiation and habitat filtering varied over the 20-yr period studied.

Independent patterns and stochastic processes

Notably, across the 1995 and 2005 census periods and at spatial neighbourhoods up to 50 m, roughly half of species pairs showed non-significant spatial association patterns (Fig. 1b). These findings indicate that, as we predicted in our first hypothesis, stochastic processes play the most important role in determining the assembly of recruit communities in the BCI plot, particularly in 1995 and 2005. According to Getzin et al. (2014), more than three quarters of the species present in the BCI plot showed an independent placement of recruits with respect to conspecific

adults. A large proportion of non-significant spatial association patterns have also been recently found in the tropical forests of Costa Rica (Lieberman & Lieberman 2007), Sri Lanka and BCI (Wiegand et al. 2012), and also in semi-arid shrublands of southwest Australia (Perry et al. 2013). These authors attributed non-significant spatial association patterns to the fact that in species-rich communities, the population density of individual species decreases and the probability that trees of a given species combination will occur as neighbours is exceedingly small. In that case, chance events associated with seed dispersal and demographic stochasticity would overpower deterministic processes, such as habitat filtering and niche differentiation, to explain species co-occurrence patterns (Volkov et al. 2009).

Spatially associated patterns and deterministic processes

As predicted by our second and third hypotheses, we found mainly positive relationships between spatial association and trait similarity (trait convergence) at 30-m

neighbourhoods, and mainly negative associations (trait divergence) at 5-m neighbourhoods. However, the majority of the negative relationships in 5-m scales were not significant (except for the 1995 census). These results suggest that habitat filtering drives the assembly of recruit communities in the BCI plot at both large and small scales, whereas niche differentiation plays a less important role and only appears at small scales. Our findings support those of Swenson et al. (2012), who found trait convergence at spatial scales of >20 m when inferring the mechanisms responsible for the assembly of trees ≥ 1 cm DBH in BCI. Surprisingly, habitat filtering at all spatial scales is as evident in the BCI forest as in the subtropical wet forest of Luquillo, Puerto Rico (Uriarte et al. 2010) and that of the dry Costa Rican forest of San Emilio (Swenson & Enquist 2009). But BCI is less topographically heterogeneous than Luquillo, and has less variation in soil moisture than San Emilio. This suggests that habitat filtering on BCI is related to factors other than topography and soil moisture, such as spatial variations in soil nutrient availability, which is rather marked in this forest (John et al. 2007). It is also important to note that in 5-m neighbourhoods, trait similarity in topographic habitat preferences was significantly and positively related to the index of spatial association in the 1985 and 2005 censuses. This finding suggests that species habitat associations for recruits may be stronger than previously thought (Kanagaraj et al. 2011).

Habitat filtering and niche differentiation associated to different traits

Species pairs with matching dispersal modes or habitat preferences were more likely to exhibit positive spatial associations than were species pairs with divergent dispersal modes or habitat preferences. These results indicate that, as we predicted in our fourth hypothesis, habitat filtering is principally related to topographic habitat preferences and dispersal mode of the species, which provides support for previous studies in BCI (Wright et al. 2005) and in other Neotropical forests (John et al. 2007).

The relationships between the index of spatial association and the indices of trait similarity in mean wood specific gravity and shade tolerance were consistently negative at 5-m neighbourhoods across all census periods (although they were significant only in 1995). This result is explained by the close dependence between these two traits (Muller-Landau 2004) in the BCI forest and suggests that, as we predicted in our fifth hypothesis, niche differentiation is mainly related to the growth–mortality trade-off across a gradient of light availability. On BCI, this gradient is mainly related to the occurrence of tree-fall gaps and canopy openings (Rüger et al. 2009). Therefore, our results also support the prediction of Grime (2006) that

traits that diverge among co-existing species should be related to regeneration and the tolerance of disturbance.

The index of spatial association was mainly positively associated with the indices of trait similarity in maximum height and leaf mass per area. In the case of leaf mass per area, these relationships were significant at 5-m neighbourhoods in the 1985 and 2005 censuses. These results confirm that, as we predicted, these two traits, and particularly leaf mass per area, contributed more to fitness than to niche differences among the 64 finally selected species and were, therefore, responsible for the exclusion of weaker competitors at small scales (Mayfield & Levine 2010). It is also important to note that the relationships between spatial association and phylogenetic relatedness were not predominantly positive or negative, but either positive or negative, and none of them significant, across all censuses and spatial scales (Appendix S5). This finding highlights the existence of a random phylogenetic structure among recruits. As most functional traits are known to be phylogenetically conserved among trees at BCI (Swenson et al. 2007), this random structure reflects stochastic drift or a mixture of phylogenetic clustering and overdispersion.

Temporal effects

We also detected interesting temporal trends. Shade tolerance were significantly and positively associated with interspecific spatial association in censuses 1985 and 2005 at 30-m neighbourhoods, but significantly and negatively associated in 1995 at neighbourhoods of 5 m, together with wood specific gravity (Fig. 2, Appendix S5). We suspect that this stems from two unusually severe droughts associated with El Niño events, which occurred in 1983 and 1999 and increased mortality rates of adult trees >10 cm DBH by $>70\%$ (Condit et al. 2004). Canopy openings resulting from this mortality augmented light availability and recruit emergence, particularly of those of light-demanding species (Rüger et al. 2009), which provoked the spatial association of species with similar shade tolerance in 1985 at the scale at which canopy openings occur (i.e. 30 m). According to Lobo & Dalling (2014), 83% of the tree-fall gaps in the BCI plot have an area of ≤ 50 m², which provides support for this hypothesis. However, in these canopy openings, recruits of light-demanding species have better access to light, grow faster and experience strong competition for light among each other. Ten years later, in 1995, mortality of recruits rose as an outcome of this process, and species with differing values of shade tolerance and wood specific gravity, which are both involved in the growth–mortality trade-off, appeared spatially associated at the small scales (i.e. 5 m; Casper et al. 2003) at which plant–plant interactions occur. The fact that significant negative relationships between spatial association and trait similarity at 5-m neighbourhoods

appeared only in the 1995 census, and for traits related with resource competition, indicates that the relative importance of niche differentiation at small scale can change over time in relation to the occurrence of tree falls associated to unusually severe droughts.

Limitations

Our quantification of the relative contributions of habitat filtering and niche differentiation to community assembly, via an examination of the relationship between spatial association and trait similarity, has several limitations. First, it can be argued that our approach, which considers 64 species, could miss important aspects of species interactions, which in turn would influence the detection of niche differentiation (Swenson 2013). Had we included all species in our analyses, however, the frequency of interspecific encounters would have been so low that we would have observed even more non-significant spatial association patterns (Lieberman & Lieberman 2007; Wiegand et al. 2012). Therefore, it is unlikely that the exclusion of these species affected the detection of habitat filtering and niche differentiation. Second, it can be also argued that our findings are not representative of the entire tree community since they consider only recruits. However, similar analyses focusing on juvenile (T. Wiegand, unpubl.) and adult trees (Wiegand et al. 2012) showed higher proportions of species pairs without significant interspecific spatial association patterns. This fact, together with our findings, indicates that deterministic processes such as habitat filtering and niche differentiation drive community assembly mainly at the recruitment phase. Finally, it is also important to point out that relationships between the indices of spatial association and trait similarity were weak, perhaps because some functional traits are not independent of one another and because any trait difference is likely to influence both habitat filtering and niche differentiation (Adler et al. 2013). However, traits that are supposedly related, such as dispersal mode and seed dry mass (Westoby et al. 1996), and leaf mass per area, wood specific gravity and seed dry mass (Wright et al. 2010), showed relationships of opposing sign with interspecific spatial association. Moreover, the combinations of all and LHS traits had relationships of differing strength, sign and significance over all censuses and spatial scales considered (Fig. 2, Appendix S5). These findings imply that selected traits acted independently to determine recruit community assembly.

Conclusions

Our results indicate that in the absence of strong top-down forcing, stochastic processes are the most important determinants of recruit community assembly in species-rich

tropical forests such as that of Barro Colorado Island (Chase & Myers 2011). This process, however, is also simultaneously influenced by deterministic processes, such as habitat filtering and niche differentiation, whose relative roles vary over spatial and temporal scales. Our study confirms that at both larger and smaller spatial scales, species co-occurrence is mainly driven by habitat filtering, but at smaller scales it may also be explained from a combination of niche differentiation and weaker competitor exclusion effects. Changes in the importance of habitat filtering and niche differentiation over time are apparently influenced by the occurrence of disturbances such as tree falls. Similar conclusions were recently reported from a study conducted in temperate grasslands (De Bello et al. 2013), which suggests that our findings could apply to markedly different plant communities. Our study points toward the existence of multiple trait-based processes and emphasizes their importance to determine species co-existence (Cornwell & Ackerly 2009; Götzenberger et al. 2012).

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References

- Adler, P.B., Fajardo, A., Kleinhesselink, A.R. & Kraft, N.J.B. 2013. Trait-based tests of coexistence mechanisms. *Ecology Letters* 16: 1294–1306.

- Baraloto, C., Morneau, F., Bonal, D., Blanc, L. & Ferry, B. 2007. Water stress tolerance and habitat associations within four Neotropical tree genera. *Ecology* 88: 478–489.
- Casper, B.B., Schenk, H.J. & Jackson, R.B. 2003. Defining a plant's belowground zone of influence. *Ecology* 84: 2313–2321.
- Chase, J.B. & Myers, J.A. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. *Philosophical Transactions of the Royal Society of London Series B* 366: 2351–2363.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- Cingolani, A.M., Cabido, M., Gurvich, D.E., Renison, D. & Daz, S. 2007. Filtering processes in the assembly of plant communities: are species presence and abundance driven by the same traits? *Journal of Vegetation Science* 18: 911–920.
- Comita, L.S. & Hubbell, S.P. 2009. Local neighbourhood and species' shade tolerance influence survival in a diverse seedling bank. *Ecology* 90: 328–334.
- Comita, L.S., Muller-Landau, H.C., Aguilar, S. & Hubbell, S.P. 2010. Asymmetric density dependence shapes species abundances in a tropical tree community. *Science* 329: 330–332.
- Condit, R., Hubbell, S.P. & Foster, R.B. 1996. Assessing the response of plant functional types to climatic change in tropical forests. *Journal of Vegetation Science* 7: 405–416.
- Condit, R., Aguilar, S., Hernández, A., Pérez, R., Lao, S., Angehr, G., Hubbell, S.P. & Foster, R.B. 2004. Tropical forest dynamics across a rainfall gradient and the impact of an El Niño dry season. *Journal of Tropical Ecology* 20: 51–72.
- Cornwell, W.K. & Ackerly, D.D. 2009. Community assembly and shifts in functional traits distributions across an environmental gradient in coastal California. *Ecological Monographs* 79: 109–126.
- Croat, T.B. 1978. *Flora of Barro Colorado Island*. Stanford University Press, Redwood City, CA, US.
- De Bello, F., Vandewalle, M., Reitalu, T., Leps, J., Prentice, H.C., Lavorel, S. & Sykes, M. 2013. Evidence for scale- and disturbance-dependent trait assembly patterns in dry semi-natural grasslands. *Journal of Ecology* 101: 1237–1244.
- Engelbrecht, B.M.J., Comita, L.S., Condit, R., Kursar, T.A., Tyree, M.T., Turner, B.L. & Hubbell, S.P. 2007. Drought sensitivity shapes species distribution patterns in tropical forests. *Nature* 447: 80–82.
- Getzin, S., Wiegand, T. & Hubbell, S.P. 2014. Stochastically driven adult–recruit associations of tree species on Barro Colorado Island. *Proceedings of the Royal Society of London Series B* 279: 20140922.
- Getzin, S., Wiegand, T., Wiegand, K. & He, F. 2008. Heterogeneity influences spatial patterns and demographics in forest stands. *Journal of Ecology* 96: 807–820.
- Götzenberger, L., de Bello, F., Brathen, K.A., Davison, J., Dubuis, A., Guisan, A., Leps, J., Lindborg, R., Moora, M., (...) & Zobel, M. 2012. Ecological assembly rules in plant communities – approaches, patterns and prospects. *Biological Reviews* 87: 111–127.
- Grime, J.P. 2006. Trait convergence and trait divergence in herbaceous plant communities: mechanisms and consequences. *Journal of Vegetation Science* 17: 225–260.
- Grubb, P.J. 1996. Rainforest dynamics: the need for new paradigms. In: Edwards, D.S., Booth, W.E. & Choy, S.C. (eds.) *Tropical Rainforest Research – Current Issues*, pp. 215–233. Kluwer Academic, Dordrecht, NL.
- Harms, K.E., Condit, R., Hubbell, S.P. & Foster, R.B. 2001. Habitat associations of trees and shrubs in a 50-ha neotropical forest plot. *Journal of Ecology* 89: 947–959.
- Hubbell, S.P., Condit, R. & Foster, R.B. 2005. *Barro Colorado Forest Census Plot Data*. URL <https://ctfs.arnarb.harvard.edu/webatlas/datasets/bci>.
- Illian, J., Penttinen, A., Stoyan, H. & Stoyan, D. 2008. *Statistical analysis and modelling of spatial point patterns*. Wiley, Chichester, UK.
- John, R., Dalling, J.W., Harms, K.E., Yavitt, J.B., Stallard, R.F., Mirabello, M., Hubbell, S.P., Valencia, R., Navarrete, H., Vallejo, M. & Foster, R. 2007. Soil nutrients influence spatial distributions of tropical tree species. *Proceedings of the National Academy of Sciences of the United States of America* 104: 864–869.
- Kanagaraj, R., Wiegand, T., Comita, L.S. & Huth, A. 2011. Tropical tree species assemblages in topographical habitats change in time and with life stage. *Journal of Ecology* 99: 1441–1452.
- Kraft, N.J.B. & Ackerly, D.D. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs* 80: 401–422.
- Kraft, N.J.B., Valencia, R. & Ackerly, D.D. 2008. Functional traits and niche-based tree community assembly in an Amazonian forest. *Science* 322: 580–582.
- Laliberté, E. & Legendre, P. 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91: 299–305.
- Laliberté, E., Legendre, P. & Shipley, B. 2014. FD: Measuring Functional Diversity from Multiple Traits, and Other Tools for Functional Ecology. R package version 1.0-12. Available at <http://cran.r-project.org/web/packages/FD/index.html> (accessed 20 November 2014).
- Lavorel, S. & Garnier, E. 2002. Predicting changes in community composition and ecosystem functioning from functional traits: revisiting the Holy Grail. *Functional Ecology* 16: 545–556.
- Legendre, P. & Legendre, L. 2012. *Numerical ecology*, 3rd edn. Elsevier, Amsterdam, NL.
- Leibold, M.A. & Peek, M.A. 2006. Coexistence of the niche and neutral perspectives in community ecology. *Ecology* 87: 1399–1410.
- Lieberman, M. & Lieberman, D. 2007. Nearest-neighbor tree species combinations in tropical forest: the role of chance, and some consequences of high diversity. *Oikos* 116: 377–386.
- Lobo, E. & Dalling, J.W. 2014. Spatial scale and sampling resolution affect measures of gap disturbance in a lowland tropical forest: implications for understanding forest regeneration

- and carbon storage. *Proceedings of the Royal Society of London Series B* 281: 20133218.
- Loosmore, N.B. & Ford, E.D. 2006. Statistical inference using the G or K point pattern spatial statistics. *Ecology* 87: 1925–1931.
- May, F., Giladi, I., Ristowa, M., Zivd, Y. & Jeltsch, F. 2013. Plant functional traits and community assembly along interacting gradients of productivity and fragmentation. *Perspectives in Plant Ecology, Evolution and Systematics* 15: 304–318.
- Mayfield, M.M. & Levine, J.M. 2010. Opposing effects of competitive exclusion on the phylogenetic structure of communities. *Ecology Letters* 13: 1085–1093.
- Metz, M.R., Comita, L.S., Chen, Y.-Y., Norden, N., Condit, R., Hubbell, S.P., Sun, I.-F., Supardi, M.N.N. & Wright, S.J. 2008. Temporal and spatial variability in seedling dynamics: a cross-site comparison in four lowland tropical forests. *Journal of Tropical Ecology* 24: 9–18.
- Muller-Landau, H.C. 2004. Interspecific and inter-site variation in wood specific gravity of tropical trees. *Biotropica* 36: 20–32.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H. & Wagner, H. 2012. vegan: Community Ecology Package. R package version, 2.0-5. Available at <http://cran.r-project.org/web/packages/vegan/index.html> (accessed 2 December 2014).
- Paine, C.E.T., Baraloto, C., Chave, J. & Hérault, B. 2011. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rainforests. *Oikos* 120: 720–727.
- Pavoine, S., Vallet, J., Dufour, A., Gachet, S. & Daniel, H. 2009. On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos* 118: 391–402.
- Perry, G.L.W., Miller, B.P., Enright, N.J. & Lamont, B.B. 2013. Stochastic geometry best explains spatial associations among species and plant functional types in species-rich shrublands. *Oikos* 123: 99–110.
- Podani, J. 1999. Extending Gower's general coefficient of similarity to ordinal characters. *Taxon* 48: 331–340.
- Ripley, B.D. 1981. *Spatial statistics*. John Wiley & Sons, New York, NY, US.
- Rüger, N., Huth, A., Hubbell, S.P. & Condit, R. 2009. Response of recruitment to light availability across a tropical lowland rain forest community. *Journal of Ecology* 97: 1360–1368.
- Shiple, B., Paine, C.E.T. & Baraloto, C. 2012. Quantifying the importance of local niche-based and stochastic processes to tropical tree community assembly. *Ecology* 93: 760–769.
- Swenson, N.G. 2013. The assembly of tropical tree communities – the advances and shortcomings of phylogenetic and functional trait analyses. *Ecography* 36: 264–276.
- Swenson, N.G. & Enquist, B.E. 2009. Opposing assembly mechanisms in a Neotropical dry forest: implications for phylogenetic and functional community ecology. *Ecology* 90: 2161–2170.
- Swenson, N.G., Enquist, B.J., Thompson, J. & Zimmerman, J.K. 2007. The influence of spatial and size scale on phylogenetic relatedness in tropical forest communities. *Ecology* 88: 1770–1780.
- Swenson, N.G., Erickson, D.L., Mi, X., Bourg, N.A., Forero-Montana, J., Ge, X., Howe, R., Lake, J.K., Liu, X., (...) & Kress, W.J. 2012. Phylogenetic and functional alpha and beta diversity in temperate and tropical tree communities. *Ecology* 93: S112–S125.
- Uriarte, M., Swenson, N.G., Chazdon, R.L., Comita, L.S., Kress, W.J., Erickson, D., Forero-Montana, J., Zimmerman, J.K. & Thompson, J. 2010. Trait similarity, shared ancestry and the structure of neighbourhood interactions in a subtropical wet forest: implications for community assembly. *Ecology Letters* 13: 1503–1514.
- Vamosi, S.M., Heard, S.B., Vamosi, J.C. & Webb, C.O. 2009. Emerging patterns in the comparative analysis of phylogenetic community structure. *Molecular Ecology* 18: 572–592.
- Vázquez, D.P., Melián, C.J., Williams, N.M., Blütgen, N., Krasnov, B.R. & Poulin, R. 2007. Species abundance and asymmetric interaction strength in ecological networks. *Oikos* 116: 1120–1127.
- Volkov, I., Banavar, J.R., Hubbell, S.P. & Maritan, A. 2009. Inferring species interactions in tropical forests. *Proceedings of the National Academy of Sciences of the United States of America* 106: 13854–13859.
- Webb, C.O. & Donoghue, M.J. 2005. Phylomatic: tree assembly for applied phylogenetics. *Molecular Ecology Notes* 5: 181–183.
- Webb, C.O., Ackerly, D.D. & Kembel, S.W. 2008. Phylocom: software for the analysis of phylogenetic community structure and trait evolution. *Bioinformatics* 24: 2098–2100.
- Westoby, M. 1998. A leaf–height–seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199: 213–227.
- Westoby, M., Leishman, M., Lord, J., Poorter, D. & Schoen, D.J. 1996. Comparative ecology of seed size and dispersal. *Proceedings of the Royal Society of London Series B* 351: 1310–1318.
- Westoby, M., Falster, D.S., Moles, A.T., Vesk, P. & Wright, I.J. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.
- Wiegand, T. & Moloney, K.A. 2004. Rings, circles and null-models for point pattern analysis in ecology. *Oikos* 104: 209–229.
- Wiegand, T. & Moloney, K. 2014. *Handbook of spatial point-pattern analysis in ecology*. CRC Press, Boca Raton, FL, US.
- Wiegand, T., Gunatilleke, S. & Gunatilleke, N. 2007. Species associations in a heterogeneous Sri Lankan dipterocarp forest. *The American Naturalist* 170: 77–95.
- Wiegand, T., Martínez, I. & Huth, A. 2009. Recruitment in tropical tree species: revealing complex spatial patterns. *The American Naturalist* 174: 106–140.
- Wiegand, T., Huth, A., Getzin, S., Wang, X., Hao, Z., Gunatilleke, C.V.S. & Gunatilleke, I.A.U.N. 2012. Testing the independent species' arrangement assertion made by theories of stochastic geometry of biodiversity. *Proceedings of the Royal Society of London Series B* 279: 3312–3320.
- Wright, S.J. 2002. Plant diversity in tropical forests: a review of mechanisms of species coexistence. *Oecologia* 130: 1–14.

- Wright, S.J., Muller-Landau, H.C., Calderón, O. & Hernández, A. 2005. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. *Ecology* 86: 848–860.
- Wright, S.J., Kitajima, K., Kraft, N.J.B., Reich, P.B., Wright, I.J., Bunker, D.E., Condit, R., Dalling, J.W., Davies, S.J., (...) & Zanne, A.E. 2010. Functional traits and the growth–mortality trade-off in tropical trees. *Ecology* 91: 3664–3674.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Calculation of the S_{ij} index of similarity.

Appendix S2. R-code to calculate the multidimensional S_{ij} index of similarity.

Appendix S3. R-code to calculate the two-one-tailed P -values of Mantel correlation coefficients.

Appendix S4. The 64 species included in our analyses and their functional traits.

Appendix S5. Results of the Mantel correlations between matrices of interspecific spatial association and trait similarity.

Appendix S6. Distributions of species pairs that underlie positive and negative spatial association patterns at 5- and 30-m neighbourhoods.

Appendix S7. Overview of the analyses carried out for recruit species pairs on Barro Colorado Island Forest Dynamics Plot, at the 1985, 1995 and 2005 censuses and at 5-m and 30-m neighbourhoods.