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Phylogeny contributes more than site characteristics and traits to the spatial distribution pattern of tropical tree populations

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Abstract

Dispersal mechanism, species height, sexual system, and wood density are potential drivers of the spatial distribution pattern of tropical tree populations. These traits are usually conserved among closely related species, thus populations of these species should have more similar spatial distribution patterns than populations of phylogenetically distant species. Additionally, variation in the abiotic and biotic environment might result in distinct spatial distribution patterns of local populations of the same species. We employed variation partitioning to determine the degree to which traits, shared evolutionary history, site characteristics, and their joint effects govern the degree of overdispersion or aggregation of tree populations at different spatial scales within fourteen 1-ha plots of the Atlantic Rainforest in SE Brazil. We quantified the degree of overdispersion or aggregation with a new standardized index err(r) based on standardized effect sizes of the pair correlation function. Variation in err(r) was mostly explained by phylogenetic relationships among species (70–95%, depending on spatial scale), indicating that traits not included in our analysis are important drivers of the spatial distribution pattern. Site characteristics explained a smaller part of the variation, indicating context-dependence. Finally, the traits studied here provided the smallest explanation of the variation, suggesting a minor role of seed dispersal. Residual variation in err(r) ranged from 5–29%, indicating that stochasticity and/or variables not included in the models (e.g. direct measures of post-dispersal processes) also influence the spatial distribution pattern of the populations. Our results suggest that many ecological processes act in concert at the study site and that their importance changes with spatial scale. Additionally, the relative importance of these processes differs from that previously described for other tropical forests. Determining why a given ecological process is more important in some tropical tree communities than in others are promising venues for further research.

Keywords: Atlantic rainforest, coexistence mechanism, context-dependence, pair correlation function, spatial structure

Introduction

Biodiversity patterns result from the interplay of several processes operating at regional and local scales (Ricklefs 2004). At the local scale, high biodiversity such as that of tropical forests is hypothesized to be maintained by environmental filtering (*e.g.*, Hubbell 1979, Condit et al. 2000, Parmentier et al. 2014, Velázquez et al. 2015), interspecific competition among nearby trees (*e.g.*, Hubbell et al. 2001, Kraft et al. 2014, Velázquez et al. 2015), neutral processes such as dispersal limitation and stochastic recruitment (*e.g.*, Hubbell 2001, Wiegand et al. 2017), and negative density-dependence due to intraspecific competition and species-specific enemy attack (*e.g.*, Janzen 1970, Uriarte et al. 2005, Murphy et al. 2017). Most of these coexistence mechanisms have a strong spatial component, which means that understanding the ecological processes that govern the spatial distribution pattern of populations of tree species can also contribute to a better comprehension of the high biodiversity of tropical forests (He et al. 1996).

Previous studies have suggested that the spatial distribution pattern of tropical trees at small spatial scales (*i.e.* < 50 m) is influenced by seed dispersal (*e.g.*, Condit et al. 2000, Seidler and Plotkin 2006), number of seed sources (*e.g.*, Hubbell 1979, Bleher et al. 2002), wood density (*e.g.*, Réjou-Méchain et al. 2011, Flügge et al. 2012), and post-dispersal processes such as competition, enemy attack and environmental filtering (*e.g.*, Plotkin et al. 2000, Uriarte et al. 2005, Parmentier et al. 2014, Velázquez et al. 2015). A major aspect of the spatial distribution pattern of tree populations is their relative neighbourhood density, which indicates if trees have on average more (aggregation) or less (overdispersion) neighbours at a given distance than expected from a completely random distribution (Condit et al. 2000, Wiegand and Moloney 2004).

A review on the influence of species traits on the spatial distribution pattern of tree populations can be found at Supplementary material Appendix 1. Local seed dispersal usually results in a high degree of aggregation, whereas large dispersal distances scatter seeds in the environment and generate a less aggregated spatial distribution pattern (Bleher et al. 2002). One surrogate for dispersal distance is the species seed dispersal mechanism (Seidler and Plotkin 2006). Species whose diaspores (*i.e.* functional units of dispersal such as seeds and fruits) are equipped for dispersal by wind or by the parent plant itself tend to have their seeds deposited near the adult in dense vegetation due to physical obstacles or reduced air movement (Nathan and Katul 2005). On the other hand, animal-dispersed species usually have their seeds deposited further away from the parent plant. Among animals, birds and bats can generate the most scattered seed distribution because of their flying abilities (Hubbell 1979, Condit et al. 2000, Seidler and Plotkin 2006). Additionally to dispersal mechanism, plant height can affect dispersal distance (Thomson et al. 2011). Taller trees presumably release diaspores at greater heights and, because they have wider crowns (King 1990), they also release seeds further from the parent plant base than do shorter individuals, thus increasing dispersal distance. Moreover, taller species may show adaptations to long-distance dispersal (Thomson et al. 2011) as a mechanism to escape the reduced survival under the parent plant's broad canopy (Janzen 1970). Nevertheless, many tall species are dispersed by wind (Réjou-Méchain and Cheptou 2015), which results in short-distance dispersal (Condit et al. 2000, Seidler and Plotkin 2006).

The second factor influencing the spatial distribution pattern of tree populations is the number of seed sources, which is determined both by the number of adults in a given area and the species sexual system (Bleher et al. 2002). Populations with few adults are expected to be more aggregated under limited seed dispersal than populations with many adults (Hubbell 1979, Bleher et al. 2002). Because dioecious species (*i.e.* species in which individuals produce only feminine or masculine flowers) present lower densities of seed sources when compared to homoecious (*i.e.* species in which individuals produce hermaphroditic flowers) or monoecious species (*i.e.* species in which individuals produce both feminine and masculine flowers), they also tend to be more aggregated than either one of them (Bleher et al. 2002, but see Hubbell 1979). Nevertheless, Plotkin et al. (2000) argued that the correlation between population density and spatial distribution pattern might be spurious.

Wood density is the third potential driver of the spatial distribution pattern of tree populations at small scales (Réjou-Méchain et al. 2011, Flügge et al. 2012). This trait is hypothesized to have two opposite effects on the degree of overdispersion or aggregation of populations. First, because low-wood density species tend to grow fast, be shade intolerant (Muller-Landau 2004, Chave et al. 2009), and better colonizers than high-wood density species, they quickly occupy forest gaps (Nascimento et al. 2005) and are likely to be more aggregated than high-wood density species (Réjou-Méchain et al. 2011, Flügge et al. 2012). Alternatively, populations of high-wood density species might be more aggregated because, as individuals grow more slowly (Muller-Landau 2004, Chave et al. 2009), they remain at the sapling stage (non-reproductive) for a longer time. Therefore, the relative number of adults is lower than in low-wood density species (Condit et al. 1998), which may result in a higher degree of aggregation (Flügge et al. 2012).

Last, post-dispersal processes, which include a myriad of biotic and abiotic interactions that take place at the neighbourhood scale, *i.e.* a few meters (< 10–15 m) from focal plants (Hubbell et al. 2001, Uriarte et al. 2005), can also affect the spatial distribution pattern of tree populations (Plotkin et al. 2000, Uriarte et al. 2005, Velázquez et al. 2015). For instance, environmental filtering and positive interactions, such as facilitation and associations with mycorrhizal fungi, usually increase population aggregation through plant development, as only the seedlings that emerge in favourable patches should establish and reach the adult stage (Hubbell 1979, Condit et al. 2000, Dickie et al. 2007). Conversely, negative biotic interactions, such as intraspecific competition and enemy attack, are more pronounced at high-density patches, which lead to density-dependent mortality and a decrease in aggregation through plant development (Janzen 1970, Hubbell 1979, Condit et al. 2000). The type and strength of the biotic and abiotic interactions might change among different sites and spatial scales within tropical forests due to heterogeneity in both environmental conditions and species distributions (Montoya et al. 2009, Soininen 2016). Additionally, stochasticity in seed dispersal, recruitment, and establishment of new individuals (Hubbell 2001, Wiegand et al. 2017), and distinct disturbance regimes such as gap dynamics (Montoya et al. 2009) contribute to the high variability among sites. As a result, local populations of the same species might show distinct properties (*e.g.*, density and degree of overdispersion or aggregation), which is known as context-dependence (Réjou-Méchain et al. 2011).

Dispersal mechanism, sexual system, and wood density are species traits that are known to be phylogenetically conserved (*e.g.*, Chazdon et al. 2003, Chave et al. 2006, Judd et al. 2007), *i.e.* they differ less among closely related species than might be expected if ecological diversification had occurred in an unconstrained manner. Additionally, phylogenetically close species are likely to share similar traits due to the presence of a near common ancestor (*i.e.* their traits present phylogenetic signal; Losos 2008). As a result, populations of closely related species tend to show more similar spatial distribution patterns than populations of phylogenetically distant species (Réjou-Méchain et al. 2011). Not accounting for shared evolutionary history in community-wide studies is likely to result in pseudoreplication, which inflates the degrees of freedom in statistical analysis and can lead to results that are significant when they should not be (*i.e.* type I error; Seidler and Plotkin 2006, Li and Ives 2017). Despite that, to the best of our knowledge, only few studies accounted for shared evolutionary history when unveiling the contribution of species traits to the spatial distribution pattern of tree populations (*i.e.* Seidler and Plotkin 2006, Réjou-Méchain et al. 2011, Flügge et al. 2012).

Another complication is that different drivers of the spatial distribution pattern (represented by traits) can have synergetic effects. For example, species height and dispersal mechanism may be correlated traits (Thomson et al. 2011, Réjou-Méchain and Cheptou 2015); dispersal mechanism and sexual system have been shown to be correlated in tropical tree species (Chazdon et al. 2003, Réjou-Méchain and Cheptou 2015). Analysing traits separately might then result in misleading significant effects for two reasons: the analysed variable is correlated with another variable that exerts the real influence on the spatial distribution pattern (Legendre and Legendre 1998) and the same data set is being tested against many explanatory variables separately, which increases the probability of significant results just by chance (Bonferroni 1935).

Here we circumvent these caveats by employing variation partitioning analysis (Borcard et al. 1992) to determine the degree to which traits, shared evolutionary history, site characteristics, and their joint effects govern the degree of overdispersion or aggregation of tree populations at different spatial scales within fourteen 1-ha plots of the Atlantic Rainforest in SE Brazil. We predict that the amount of variation explained by the trait component will increase if dispersal mechanism, species height, sexual system, and wood density are strong drivers of the spatial distribution pattern. If the shared evolutionary history component better explains the response variable, other traits that were not explicitly included in the trait component are important to the spatial distribution pattern of populations. Finally, if the spatial distribution pattern is context-dependent, characteristics of the plots where populations were sampled should increase the amount of variation explained by the site component.

Material and methods

Study site

The Brazilian Atlantic Forest biome has only ca. 12% of its original cover remaining in fragments (Ribeiro et al. 2009). Due to its high species richness and endemism, the forest along the coast was classified as a hotspot for biodiversity conservation (Myers et al. 2000). The largest continuous remnant includes the state park “Parque Estadual da Serra do Mar” (PESM; 23°34’ - 23°17’ S and 45°02’ - 45°11’ W), which encompasses the mountain range of “Serra do Mar” along the coast of the State of São Paulo, SE Brazil. PESM comprises 332,000 ha (Parque Estadual da Serra do Mar 2016) ranging from 0 m to 1,200 m above sea level (Alves et al. 2010). The geological and topological complexity of “Serra do Mar” results in extremely heterogeneous habitats and microclimates that are reflected in the different vegetation types present at the study site (Alves et al. 2010, Joly et al. 2012). We used data from a forest inventory conducted at 14 non-contiguous, permanent 1-ha plots established at the four main forest types present along the elevation gradient of the northern portion of PESM: Restinga Forest, Lowland Atlantic Rainforest, Submontane Atlantic Rainforest, and Montane Atlantic Rainforest (Joly et al. 2012; Table A1 in Supplementary material Appendix 2).

Mean temperatures at the Restinga and Lowland Atlantic Rainforest range from 18.4^{o} C in July to 25.5^{o} C in February; mean rainfall ranges from 11 mm in July to 376 mm in January. Mean temperatures at the Montane Atlantic Rainforest range from 16.4^{o} C in July to 23.2^{o} C in February; mean rainfall ranges from 20 mm in July to 278 mm in February. A dry season is absent along the elevation gradient (EMBRAPA 2003; Table A1 in Supplementary material Appendix 2). The Submontane and Montane Atlantic Rainforests are frequently covered by clouds and mist brought by oceanic winds (Silva-Dias et al. 1995), which increase humidity but reduce light availability to plants (Sousa Neto 2008).

Soils along the elevation gradient are shallow and nutrient poor. In particular, the soil of the Restinga Forest is sandier and nutrient-poorer than the soils of the other forest types. Also, it gets waterlogged especially during the rainy period (Martins 2010, Martins et al. 2015; Table A1 in Supplementary material Appendix 2). Soil humidity, total carbon, and nitrogen, ammonia, and nitrate concentrations increase with altitude. Conversely, decomposition rates, and N_2O and CO_2 emissions from the soil to the atmosphere decrease with altitude (Sousa Neto 2008).

Species studied

A forest inventory was conducted in 2006-2007 inside the fourteen 1-ha plots, where every living tree and palm with stem diameter at breast height (DBH) ≥ 4.8 cm was tagged and identified. Approximately 735 species or morphotypes were found. For simplification, we refer here to species and morphotypes collectively as species. Stem DBH and spatial location (accurate to ± 10 cm) were measured for each individual (Joly et al. 2012, data from the Functional Gradient Project Biota/FAPESP 03/12595-7 – available upon request). For more information on the species, please refer to Joly et al. (2012) and Eisenlohr et al. (2013).

We excluded populations with less than 30 individuals per plot because stochastic effects obscure the characterization of the spatial distribution patterns for such low sample sizes (Wiegand et al. 2016). We also excluded populations of species without trait data. For both categorical traits and site variables, we demanded that at least five populations presented 0 or 1 value of a given variable. The trait and site variables included in our analysis can be found at Supplementary material Appendix 2. Our final data set consisted of 101 populations belonging to 46 species along the elevation gradient. More than half of the species occurred in only one plot, with the more broadly distributed species occurring in 10 of the 14 plots (Fig. A1 in Supplementary material Appendix 2).

Potential drivers of the spatial distribution pattern of tropical tree populations

Sexual system, dispersal mechanism, species height, and wood density

We determined the sexual system and dispersal mechanism of each species studied. We characterized the dispersal mechanism through the use of seed dispersal syndromes, as did other authors (*e.g.*, Hubbell 1979, Condit et al. 2000, Seidler and Plotkin 2006, Réjou-Méchain et al. 2011). We classified the dispersal syndromes using the hierarchical levels proposed by Martins et al. (2014) (details in Supplementary material Appendix 3).

To calculate the maximum height of each tree species, we inserted the 98th percentile value of stem DBH of the species in height-diameter Weibull models built for each forest type (Scaranello et al. 2012; Supplementary material Appendix 3). We obtained the 98th percentile value of height of palm species from field surveys conducted by Scaranello et al. (2012) at the study site. Last, we attributed a value of wood density to each species or genus according to Chave et al. (2006), Alves et al. (2010), and L.F. Alves (unpublished data).

Shared evolutionary history

We characterized the shared evolutionary history of the species studied through their phylogenetic relatedness. To do this, we used the phylogenetic hypothesis and clade age estimates of Magallón et al. (2015). These authors built a phylogenetic tree for 87% of angiosperm families based on five molecular markers and 137 fossil-based calibrations of phylogenetic nodes. We then incorporated genus relationships based on molecular markers on the megatree. Last, we inserted the species studied and built a tree with populations as tips (sampling unit of the spatial distribution pattern; Supplementary material Appendix 3).

Site

Because the spatial distribution pattern might be context-dependent (Réjou-Méchain et al. 2011), we included variables measured at each plot where populations were sampled in our analysis. The variables were related to plot identity, forest type, stand structure and richness, disturbance, and topography (see Table A1 in Supplementary material Appendix 2 for details). We also included population density as a site characteristic, as it can differ among distinct environments (Soininen 2016).

Data analysis

Spatial distribution pattern

We measured the degree of overdispersion or aggregation of tree populations with the pair correlation function $g(r)$, which gives the relative density of conspecifics at a given distance of the "typical" tree of the population (Wiegand and Moloney 2014). More technically, $g(r)$ is the mean density of conspecifics within a ring of radius r and width dw centred at the individuals of the pattern, divided by their overall density λ (= number of individuals divided by the area of the study site) (Stoyan and Stoyan 1994).

The pair correlation function $g(r)$ describes the characteristics of the pattern over a range of interpoint distances r and can be intuitively interpreted as a relative neighbourhood density (Condit et al. 2000, Stoyan and Penttinen 2000, Wiegand and Moloney 2014): values of $g(r) = 1$ indicate that individuals are randomly distributed at the study site at distance r, whereas $g(r) > 1$ indicates population aggregation (*e.g.*, $g(r) = 3$ means that the neighbourhood density at distance r is three times higher than that expected from a random pattern), and $g(r) < 1$ indicates overdispersion of individuals. Due to its straightforward characteristics, $g(r)$ is considered the most informative summary function for point pattern data (Illian et al. 2008, Wiegand et al. 2013).

However, $g(r)$ itself is not well suited as an index of the strength of overdispersion or aggregation because stochastic effects may result in values of $g(r) > 1$ or $g(r) < 1$, even if individuals were distributed in a completely random manner. This is especially true for populations with few individuals and for $g(r)$ at small distances r (Wiegand et al. 2016). To derive an index $err(r)$ of the strength of overdispersion or aggregation, we first estimated standardized measures of the strength of departures of $g(r)$ from the null model of Complete Spatial Randomness (CSR; Wiegand and Moloney 2014), namely the standardized effect sizes SES (also called z-scores):

$$SES(r) = [g_{\mathrm{obs}}(r) - g_{\mathrm{exp}}(r)]/\sigma_g(r), \qquad (1),$$

where $g_{\mathrm{obs}}(r)$ is the observed $g(r)$, $g_{\mathrm{exp}}(r) = 1$ is the expectation of $g(r)$ under CSR, and $\sigma_g(r)$ is the corresponding standard deviation (Wang et al. 2018). Significant departures from CSR occur at a given distance r if $SES(r) < -z_\alpha$ (overdispersion) or $SES(r) > z_\alpha$ (aggregation) (Wiegand et al. 2016). For a significance level of $\alpha = 0.05$, we have $z_\alpha = 1.96$. We used the analytical formula for $\sigma_g(r)$ given in Wiegand et al. (2016) to estimate $SES(r)$ without simulation of the null model. Finally, because $SES(r)$ values of (-1.96, 1.96) correspond to a zero effect (*i.e.* no significant departure from CSR), we defined our final index $err(r)$ of the strength of overdispersion or aggregation of populations as

$$err(r) = \begin{cases} SES(r) - z_\alpha & \text{if } SES(r) > z_\alpha \quad \text{aggregation} \\ SES(r) + z_\alpha & \text{if } SES(r) < -z_\alpha \quad \text{overdispersion} \\ 0 & \text{otherwise} \quad \text{CSR} \end{cases} \qquad (2)$$

Our new index *err*(*r*) is similar to an index of Wang et al. (2018) designed to capture the absolute strength of departures from a null model over an entire distance interval. However, our index captures the strength and direction of departures from a null model for a given distance *r*.

We used *err*(*r*) at distances of 1 m, 10 m, 20 m, 30 m, 40 m, and 50 m as measures of the spatial distribution pattern of the 101 tree populations, and evaluated the contribution of traits, phylogenetic relationships, site, and their joint effects in explaining the variation in *err*(*r*) among the populations at these distances. Note that the results for the largest distances (*i.e.* 40 m and 50 m) should be interpreted with caution since the plots are relatively small (100 m × 100 m) and therefore typical spatial structures at these scales cannot be fully captured (Wiegand and Moloney 2014).

We calculated *g*(*r*) with the software *Programita* (Wiegand and Moloney 2014), which can be accessed at www.programita.org. Estimators of *g*(*r*) and the edge correction used in *Programita* are detailed in Wiegand et al. (2016). For populations with few individuals, *g*(*r*) may show fluctuations that do not have biological meaning. To avoid this, we selected a ring width of *dw* = 9 m for the estimation of *g*(*r*), which was the smallest one that produced reasonably smooth curves (Illian et al. 2008). For all populations studied, we used the same *dw*.

Variation partitioning

We partitioned the variation of *err*(*r*) at the distances previously described into a trait component (*T*), a phylogenetic relationship component (*P*), a site component (*S*), and their joint effects by using variation partitioning analysis (Borcard et al. 1992). Variation partitioning is commonly employed to explore community variation in species composition and abundance across space (*e.g.*, Soininen 2016). It has received some criticism because it fails to correctly model the spatial and environmental components of community variation (*e.g.*, Gilbert and Bennet 2010). Nevertheless, Diniz-Filho et al. (2012) showed that the analysis can be efficiently applied, and so it is still widely employed in community variation investigation (*e.g.*, Punchi-Manage et al. 2014 and references in Soininen 2016) and also in other types of study (*e.g.*, Liu et al. 2013, Duarte et al. 2014). Additionally, we did not include a spatial distance matrix as a component in our analysis, which should decrease any possible error in the modelling of variation partitioning.

We included eigenvectors of the phylogenetic distance matrix in the *P* component, and traits and site variables selected by forward selection in the *T* and *S* components respectively (see Supplementary material Appendix 3 for details). We performed forward selection of site variables with and without population density in the site dataset. This is because we are uncertain about its biological meaning (see Plotkin et al. 2000). After selecting the phylogenetic eigenvectors, and trait and site variables, we computed a sequential regression of *err*(*r*) on *T*, *P*, *S*, and their joint effects $T + P$, $T + S$, $P + S$, and $T + P + S$. The adjusted coefficient of multiple determination R^2_{adj} from each part indicates the proportion of the variance in *err*(*r*) that is explained exclusively from an individual component or by the interaction of multiple components (Borcard et al. 1992). We performed the variation partitioning and significance tests with the package Vegan v. 2.0-2 (Oksanen et al. 2011) of the R Statistical Environment (R Core Team 2017) using 9999 permutations and $\alpha = 0.05$.

Phylogenetic signal

To obtain more information on how similar closely related species are, which would help us to interpret the explanation of *err*(*r*) by the *P* component, we conducted a phylogenetic signal analysis of the traits included in our final dataset (see Supplementary material Appendix 2). The only trait not analysed was monoecy, because just one species, *Euterpe edulis* Mart. (Arecaceae), presents this sexual system. For the continuous-valued traits, we used Blomberg's *K* statistics (Blomberg et al. 2013); for the categorical traits, we used *D* statistics (Fritz and Purvis 2010). We performed the analysis with the packages picante v.1.6.2 (Kembel et al. 2010) and caper v.0.5.2 (Orme et al. 2013) of the R Statistical Environment (R Core Team 2017).

Degree of overdispersion or aggregation of populations in relation to trait and site variables

We performed t tests and simple linear regressions to explore the relationship between *err*(*r*) and the trait and site variables included by forward selection in the *T* and *S* components at most distances tested. We performed the analyses with the software SigmaPlot Version 12 (Systat Software, San Jose, CA) with $\alpha = 0.05$.

Results

Degree of overdispersion and aggregation of populations

At small distances (< 20 m), approximately 40% of the 101 tree populations showed spatial distribution patterns indistinguishable from a random spatial pattern (CSR). This proportion increased with distance to some 67% at 40–50 m (Fig. 1a). Most populations were aggregated at small distances (maximum of 61% at 10 m), but almost no population was overdispersed at these distances. However, with increasing distance, the proportion of populations showing aggregation declined and the proportion of populations showing overdispersion increased to a maximum of 31% at 50 m (Fig. 1a). At the same time, the strength of aggregation declined with distance whereas overdispersion became stronger with distance (Fig. 1b).

Variation partitioning

The variation partitioning analysis (with and without population density in the site dataset) of *err*(*r*) calculated at different distances *r* showed that the spatial distribution pattern of the populations studied was mostly explained by the *P* component, and to a lesser extent by the *S* and *T* components (Fig. 2). There was no clear trend in the proportion of the variation in *err*(*r*) explained by the three components in relation to distance (details in Tables A1-A4 in Supplementary material Appendix 4). Below, we only present the detailed results of variation partitioning analysis without population density in the site dataset, as the R^2 of the relationship between population density and *err*(*r*) were very small, indicating spurious correlations as demonstrated by Plotkin et al. (2000) (results shown in Table A5 in Supplementary material 4).

The variation in *err*(*r*) explained by the whole *P* component and by the pure *P* fraction was significant at all distances tested. The explanation of the whole *P* component ranged from 70–95% and of the pure *P* fraction, from 53–84%. The variation explained by the whole *S* component was significant for *err*(*r*) at all distances, with the exception of 20 m, and ranged from 4–12%. However, the pure *S* fraction explained very little of *err*(*r*) (< 2.6%) at only two distances (Fig. 2). The site variable included by forward selection in the *S* component at most distances was one of the study plots, namely plot I, indicating that populations at this plot showed different spatial distribution patterns than populations at the other plots (Table A2 in Supplementary material Appendix 4). Last, the variation in *err*(*r*) explained by the whole *T* component was significant at all distances tested, with the exception of 1 m, and reached a maximum value that is a little lower than the maximum explanation provided by the whole *S* component (10%). Additionally, the variation explained by the pure *T* fraction was not significant at any distance (Fig. 2). The trait included by forward selection in the *T* component at most distances was biotic seed dispersal (Table A2 in Supplementary material Appendix 4).

Phylogenetic signal and degree of overdispersion or aggregation of populations in relation to trait and site variables

The phylogenetic signal analysis showed that only one trait, species height, was randomly distributed among the 46 species studied. Wood density and winged diaspores were overdispersed, while the other 10 traits evaluated were clumped among species (Table 1). This means that the species studied present a large set of traits that are phylogenetically conserved.

Populations of species dispersed by birds and mammals (*i.e.* biotic agents; Supplementary material Appendix 2) were less aggregated than populations of species dispersed by wind (*i.e.* abiotic agent; Supplementary material Appendix 2) at small distances (Fig. 3a; t = -3.046, d.f. = 99, p = 0.003 at 10 m; t = -2.754, d.f. = 99, p = 0.007 at 20 m). However, we found an opposite pattern at larger distances (Fig. 3a; t = 3.083, d.f. = 99, p = 0.003 at 40 m; t = 3.510, d.f. = 99, p = 0.001 at 50 m). Populations were more aggregated at plot I than at other plots altogether at 30 m (Fig. 3b; t = 2.219, d.f. = 99, p = 0.029), but were less aggregated at larger distances (Fig. 3b; t = -3.224, d.f. = 99, p = 0.002 at 40 m; t = -2.957, d.f. = 99, p = 0.004 at 50 m).

Discussion

The two main approaches for quantifying ecological differences among species are to use their functional differences based on traits and their phylogenetic differences based on genetic relationships (Swenson 2013). In this study, we extended these approaches by incorporating context-dependence so as to investigate the influence of traits, shared evolutionary history, site characteristics, and their joint effects on the degree of overdispersion or aggregation of tropical tree populations. Unexpectedly, most of the variation in the spatial distribution pattern of populations (as measured by $err(r)$) was explained by phylogenetic relationships among species, followed by site variables collected in each plot, and then by traits. This is surprising, considering that previous studies reported strong effects of the traits included in our trait component on the spatial distribution pattern of tree populations (*e.g.*, Hubbell 1979, Condit et al. 2000, Bleher et al. 2002, Seidler and Plotkin 2006). However, we obtained the same overall result for two other summary functions commonly used to characterize the spatial distribution pattern of populations, *i.e.* the untransformed pair correlation function $g(r)$ and the cumulative L-function $L(r)$ (Tables A6-A9 in Supplementary material Appendix 4), which confirms the robustness of our results.

The influence of traits on the spatial pattern of populations

Previous studies identified seed dispersal as a major driver of the spatial distribution pattern of tropical tree populations (*e.g.*, Hubbell 1979, Condit et al. 2000, Bleher et al. 2002, Seidler and Plotkin 2006). In accordance with this, we found that seed dispersal, specifically by birds and mammals, contributes to the variation in the degree of overdispersion or aggregation of tree populations of the Brazilian Atlantic Rainforest. However, the contribution is small (< 10%) and entirely shared with the phylogenetic relationship component, *i.e.* dispersal syndromes present strong phylogenetic constraint, as also shown by Chazdon et al. (2003). At small distances, populations of animal dispersed species were less aggregated than populations of species dispersed by wind, as also found by other authors (*e.g.*, Condit et al. 2000, Seidler and Plotkin 2006, and others at Supplementary material Appendix 1). At larger distances (40 m and 50 m), however, we found an opposite pattern, which may be explained by the small size of the study plots that prevents the larger-scale spatial structure from being fully captured (Wiegand and Moloney 2014).

We could only capture the spatial signature of seed dispersal syndromes belonging to the first hierarchical level of classification proposed by Martins et al. (2014), *i.e.* biotic and abiotic dispersal. This reinforces the finding that more specific dispersal syndromes are not necessarily correlated to dispersal agents (Jordano 1995, Howe 2016) and thus might show a wide variation in realized dispersal patterns at the local scale (Muller-Landau et al. 2008). Additionally, our results outline the importance of evaluating the patterns generated by seed dispersal within dispersal syndromes belonging to hierarchical levels of similar variation in diaspore morphology, as proposed by Martins et al. (2014).

The influence of phylogenetic relationships on the spatial distribution pattern of populations

The unexpected high proportion of variation in the degree of overdispersion or aggregation of populations explained by phylogenetic relationships among species indicates that individual traits, or a set of traits, that were not studied here play an important role in governing the spatial distribution pattern of tree populations of the Brazilian Atlantic Rainforest. We suspect for several reasons that these traits are conserved among closely related species. First, most of the traits included in our analysis are conserved. Even wood density should be conserved within congeneric species, as found by Chave et al. (2006). We probably found wood density to be weakly overdispersed because most of the genera included in our analysis present only one species. Therefore, our phylogenetic signal results actually show overdispersion or clustering of traits among phylogenetically close genera, not species. As also found by Chave et al. (2006), phylogenetic signal for wood density is not strong above the genus level. Other reasons why we suspect that traits not included in our analysis are conserved are that trait (Chazdon et al. 2003, Chave et al. 2006, Judd et al. 2007) and niche (Prinzing et al. 2001) conservatism is common in plants, and that taxonomic groups above species level present more similar spatial distribution patterns (Condit et al. 2000, Réjou-Méchain et al. 2011).

Further studies are needed to identify the traits that govern the spatial distribution pattern of the tree populations studied and to confirm that they are indeed phylogenetically conserved. Promising candidates are traits related to the acquisition and usage of resources such as nutrients, water and light, factors that have all been shown to limit the distribution of individuals (*e.g.*, Svenning et al. 2006, Engelbrecht et al. 2007). These traits include leaf mass per area, photosynthetic capacity, leaf nitrogen, leaf phosphorus, dark respiration rate, and leaf lifespan, which are also related to leaf vulnerability to herbivory and physical hazards (Wright et al. 2004). Reproductive traits such as floral displays could also play an important role in community assembly (Sargent and Ackerly 2008). Other good candidates are traits related to establishment success, such as germination strategies (Lönnberg and Eriksson 2013). Last, attributes of diaspores that are related to secondary dispersal may affect the spatial distribution pattern of populations.

Context-dependence of the spatial distribution pattern of populations

The characteristics of the plots where populations were sampled (*i.e.* plot identity, forest type, stand structure and richness, disturbance, and topography) were slightly more important than seed dispersal to the degree of overdispersion or aggregation of populations of the Brazilian Atlantic Rainforest. Most of the explanation of the site component was shared with the phylogenetic relationship component. This again suggests that traits not included in our models are important to the spatial distribution pattern of populations, as they are related to the way species interact with their biotic and abiotic environment (Svenning et al. 2006, Engelbrecht et al. 2007, John et al. 2007). The contribution of the site component indicates that the degree of overdispersion or aggregation of populations is context-dependent, as also found by Réjou-Méchain et al. (2011). Context-dependence of population properties might be a widespread phenomenon and future studies should include different sampling units so as to tease apart overall patterns and the influence of sites where populations are sampled.

In our study system, characteristics of plot I that were not explicitly included in the site component left a signature on the spatial distribution pattern of populations sampled at this plot in relation to populations sampled at the other 13 plots. Populations of plot I were more aggregated at 30 m and less aggregated at larger distances (40 m and 50 m), perhaps due to stronger environmental heterogeneity at different spatial scales in the plots.

Spatial distribution pattern at different distances from focal trees

As expected (*e.g.*, Condit et al. 2000), most of our 101 populations showed aggregation at small distances and the strength of aggregation declined with increasing distance. Nevertheless, the contribution of traits, phylogenetic relationships among species, and site variables to the degree of overdispersion or aggregation of populations did not show a clear trend in relation to distance. Even though a neighbourhood radius of 10 m is regarded as the scale where interactions of trees with their biotic and abiotic neighbourhood typically occur (Uriarte et al. 2004), Hubbell et al. (2001) showed that neighbourhood effects can propagate to much larger distances (up to 50 m), which seems to be the case in the Brazilian Atlantic Rainforest.

The unexplained variation in *err*(*r*) also showed no pattern in respect to distance. The unexplained variation represents stochasticity or missing variables that are drivers of the spatial distribution pattern of populations (He et al. 1996), *e.g.*, environmental filtering and effects of intra- or interspecific interactions (Bleher et al. 2002). Importantly, the unexplained variation was low (5–29%), which shows that our models captured much of the explanation of the spatial distribution pattern of tree populations of the Brazilian Atlantic Rainforest.

Our results suggest that many ecological processes act in concert at the study site. At all spatial scales (< 50 m), the most important process by far is the interaction of trees with their biotic and abiotic environment mediated by as yet unknown traits, followed by stochasticity and/or post-dispersal processes, and to a lesser extent tree responses to environmental characteristics and seed dispersal. The diversity of forces acting at local scales is regarded as key to the formation of highly complex, megadiverse tropical communities (Janzen 1970, Hubbell 1979, He et al. 1996).

Conclusions

This study shows that several ecological processes contribute to the degree of overdispersion or aggregation of tree populations of the Brazilian Atlantic Rainforest in SE Brazil. More importantly, the relative importance of these processes differs from that previously described for other tropical forests (*e.g.*, Hubbell 1979, Condit et al. 2000, Bleher et al. 2002, Seidler and Plotkin 2006, Réjou-Méchain et al. 2011, Flügge et al. 2012). Ecologists have been particularly interested in understanding the importance of environmental filtering, dispersal limitation, and intra- and interspecific competition so as to better comprehend the high biodiversity of tropical forests. It is now clear that the mechanisms maintaining high species richness differ in their relative importance among forests. Determining why a given ecological process is more important in some tropical tree communities than in others and which species trait mediates these processes offer promising avenues for further research. In particular, future investigations of the spatial distribution pattern of populations should include new traits, phylogenetic relationships among species, and context-dependence so as to better understand the ecological processes maintaining coexistence in species-rich communities.

Data deposition

Data available at The Knowledge Network for Biocomplexity (KNB):

<https://knb.ecoinformatics.org/#view/knb.711.3>

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Supplementary material (Appendix oik. OIK-03326 at LÄNK). Appendix 1–4.

Figure legends

Figure 1. Analyses of the degree of overdispersion or aggregation of tree populations of the Atlantic Rainforest in SE Brazil, as measured by the standardized pair correlation function index *err*(*r*). (a) The proportion of populations showing aggregation (*err*(*r*) > 0) (continuous line), overdispersion (*err*(*r*) < 0) (dashed line) or following a random pattern (*err*(*r*) = 0) (dotted line) at different distances *r* from focal trees; (b) the 85th percentile (continuous line), the 15th percentile (dashed line), and the median (dotted line) of *err*(*r*) for the 101 populations studied.

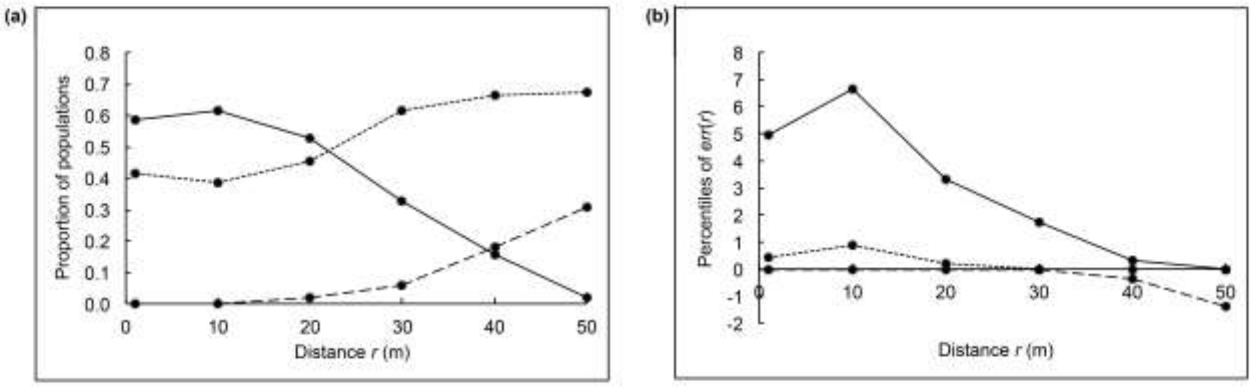

Figure 2. Variation partitioning of the degree of overdispersion or aggregation of tree populations of the Atlantic Rainforest in SE Brazil, as measured by the standardized pair correlation function index $err(r)$, including variable sets representing traits, phylogenetic relationships, and site characteristics. The standardized index $err(r)$ was calculated at distances of (a) 1 m, (b) 10 m, (c) 20 m, (d) 30 m, (e) 40 m, and (f) 50 m from focal trees. “Traits”, “Phylo”, and “Site” represent the whole variation explained by the trait, phylogenetic relationship, and site components respectively; the portion inside the circles represents the pure variation explained by traits, phylogenetic relationships, and site where populations were sampled. “***$p < 0.001$”; “**$p < 0.01$”; “*$p < 0.05$”.

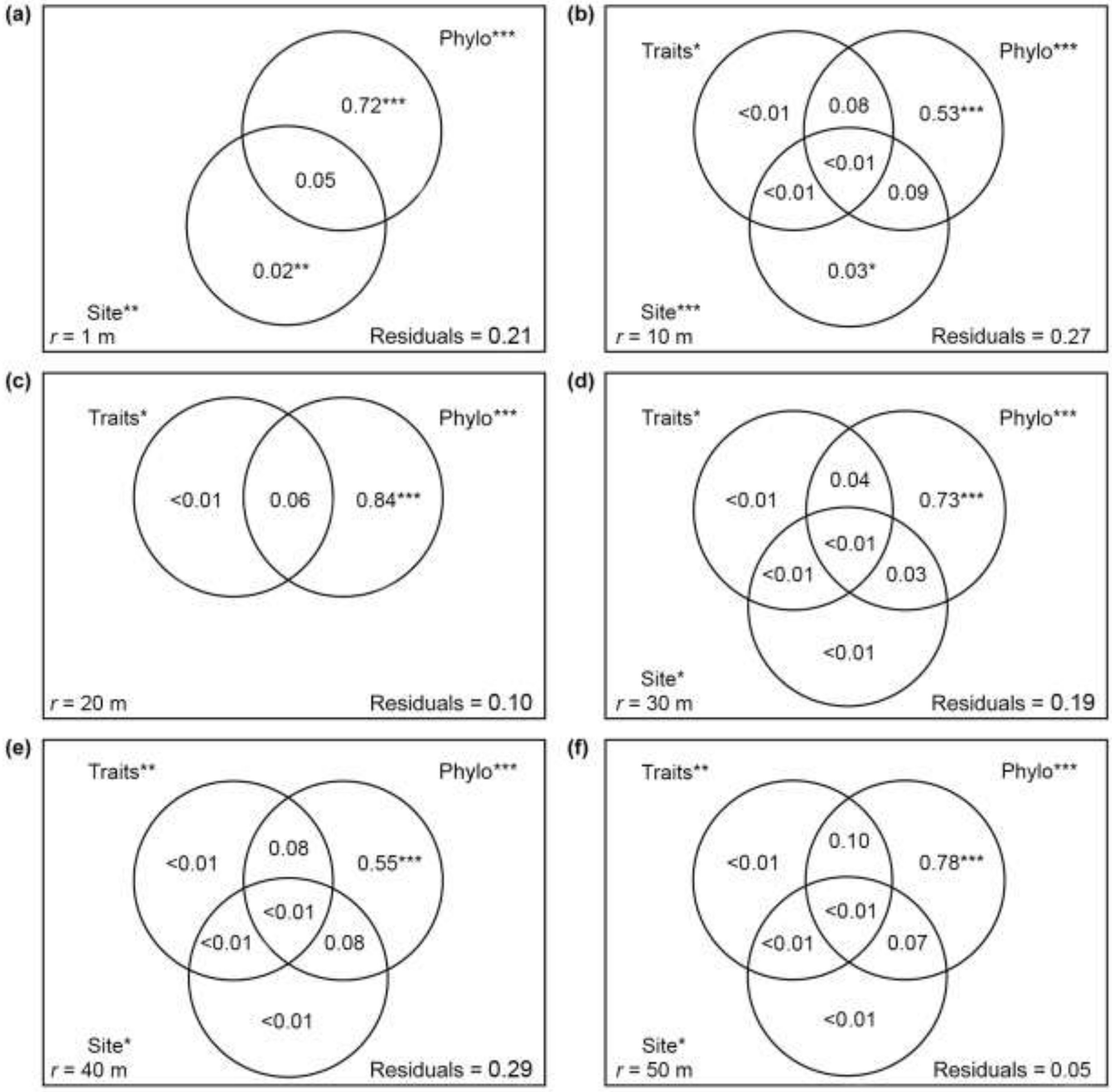

Figure 3. The degree of overdispersion or aggregation of tree populations of the Atlantic Rainforest in SE Brazil, as measured by the standardized pair correlation function index *err*(*r*), in relation to trait and site variables. (a) Boxplots containing the median (solid line), mean (dotted line), 10%, 25%, 75%, 90%, and outlier values of *err*(*r*) calculated at different distances *r* from focal trees of species dispersed by biotic (B) and abiotic (A) agents; (b) boxplots of *err*(*r*) calculated at different distances *r* from focal trees at plot I (I) and at other plots altogether (O).

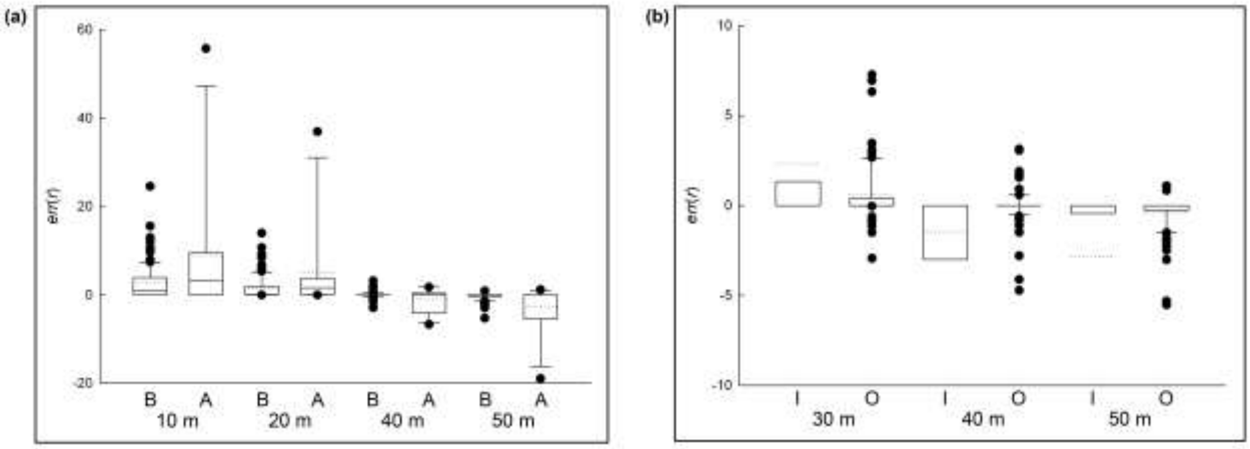

Table Legend

Table 1. Results of phylogenetic signal analysis for traits of tree species of the Atlantic Rainforest in SE Brazil. K values ≈ 1 indicate random distribution of traits among species; $K < 1$ implies that species resemble each other less than expected under Brownian motion evolution, whereas $K > 1$ implies that closely related species are more similar than expected. D values ≈ 0 indicate strong phylogenetic signal, whereas D values ≈ 1 indicate random distribution of traits among species; values in between indicate moderate phylogenetic signal; $D > 1$ implies that species resemble each other less than expected under Brownian motion evolution. "*Low phylogenetic signal"; "**strong phylogenetic signal".

Trait	Blomberg's K statistics		D statistics		
	K	p	D	p ($D > 0$)	p ($D < 1$)
Species height	0.033	0.381			
Wood density*	0.261	0.001			
Dioecy**			- 0.166	0.677	< 0.001
Homoecy**			- 0.166	0.678	< 0.001
Biotic seed dispersal*			0.398	0.337	0.165
Abiotic seed dispersal*			0.408	0.334	0.171
Bird dispersal**			0.011	0.518	0.001
Mammal dispersal**			- 0.185	0.668	< 0.001
Seeds with fleshy appendage attached**			- 0.309	0.661	0.014
Drupoid diaspores**			- 0.228	0.756	< 0.001
Diaspores with attractive colours**			- 0.184	0.669	< 0.001
Dust diaspores**			- 4.311	0.965	< 0.001
Winged diaspores**			3.464	0.049	0.920