

Habitat filtering drives the local distribution of congeneric species in a Brazilian white-sand flooded tropical forest

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Abstract

The investigation of ecological processes that maintain species coexistence is important in harsh environments, as they act as strong drivers of species selection. Congeneric species are a good model to investigate the relative importance of such processes, as closely related species tend to have similar niches. We aim to find evidence for the action and relative importance of different ecological processes hypothesized to maintain species coexistence in a tropical forest subject to seasonal flooding, using the spatial structure of populations of three congeneric species. We collected data on a 1-ha plot of a Brazilian white-sand flooded tropical forest, where individuals of three *Myrcia* species were tagged, mapped, and measured for diameter at soil height. We also sampled seven environmental variables in the plot. We employed several spatial point pattern models to simultaneously investigate habitat filtering, interspecific competition, stochasticity, and dispersal limitation. Habitat filtering was the most important process driving the local distribution of the species, as they showed associations, albeit of different strength, to environmental variables related to flooding. We did not detect spatial patterns consistent with interspecific competition, i.e. spatial segregation and smaller size of nearby congeners. The three species do not seem to show evidence of stochasticity even though congeners were spatially independent, since they responded to differences in the environment. Last, dispersal limitation only led to spatial associations of different size classes for one of the species. Using data from congeneric species in a harsh environment as a model, we demonstrated that habitat filtering to areas subject to flooding is the most important ecological process driving the local distribution of the species studied in a white-sand forest. Even though many studies on topo-edaphic variation in tropical forests have shown that habitat filtering is an important ecological process, other processes that drive community structuring may have gone undetected.

Introduction

Understanding the ecological processes that maintain high species diversity in natural environments, such as tropical forests, is fundamental in community ecology (He *et al.*, 1996). The main processes maintaining species coexistence in tropical forests are deterministic or stochastic (Chase and Myers, 2011). The deterministic processes of interspecific competition and habitat filtering are based on the species' niche. Species that explore the same limiting resources or that have similar tolerance limits to the same environmental conditions compete intensely, especially in the case of sessile organisms such as trees. In a two-species model with asymmetric competition, the stronger species exclude the weaker species (Schluter, 2000) or constrains the spatial distribution of the weaker species to less favourable environments (Baraloto *et al.*, 2007). Thus, if these deterministic processes are important forces structuring a community, species coexistence is possible when each species has a different niche or when environmental heterogeneity is high enough so that species with similar niches are restricted to somewhat different environments (Silvertown, 2004). On the other hand, according to neutral theory (Hubbell, 2001), species diversity is the balance between stochastic

emergence and disappearance of species at the regional scale (Hubbell, 2005). Locally, seed arrival in vacant space is unpredictable, considering the spatio-temporal variation in availability (stochasticity). However, dispersal and recruitment limitation, common in tropical forests (Hubbell *et al.* , 1999), prevent the most abundant species from occupying all available recruitment sites and thus dominating the community over time (competition exclusion), i.e. “winning-by-forfeit” (Hurtt and Pacala, 1995; Hubbell, 2001).

The arrangement of plants in space is the result of processes acting on each individual throughout its life, with each ecological process generating a characteristic spatial structure at a given spatial scale (Hubbell *et al.* , 2001). Habitat filtering, for example, is expected to result both in spatial segregation of species with different environmental requirements at spatial scales larger than the patch scale where the environment is approximately similar (Itoh *et al.* , 2003; Getzin *et al.* , 2006) and in spatial association of species with similar environmental requirements at spatial scales smaller than the patch scale (Burns and Strauss, 2011). When these species additionally compete within patches, reduced resource availability should result in a decrease in growth rate (Kenkel, 1988), thereby causing nearby neighbours to be smaller than distant trees (Getzin *et al.* , 2008). Also, in extreme cases, the stronger competitor can eventually cause mortality of the weaker competitor (Kenkel, 1988), resulting in spatial segregation of competing species at the small neighbourhood scale (say < 5 m; Velázquez *et al.* , 2015).

In contrast, if species stochasticity governs community structuring as assumed in neutral theory, conspecific interactions should be stronger than heterospecific interactions, producing an approximate independent spatial relationship between species pairs (Volkov *et al.* , 2007). Additionally, species distribution should not be related to environmental characteristics, as all species are expected to respond to the environment in a similar way (Hubbell, 2005). Also, dispersal limitation is expected to result in aggregation of seeds and small trees, and in spatial associations of seeds and smaller trees to large trees (Murphy *et al.* , 2017), because mortality is usually not as strong, even at high-density patches, as to spatially uncouple seeds from their parent trees (Hubbell, 1980; Hubbell, 2005; but see Getzin *et al.* , 2014).

Even though habitat filtering and dispersal limitation both result in aggregation and spatial association of individuals, the former leads to species distribution related to local environmental variables, whereas the latter causes high density of small trees centred on conspecific large trees (Wang *et al.* , 2015). Additionally, the spatial pattern of individuals of different sizes indicates which ecological process has acted more strongly on the population (Comita *et al.* , 2007; Shen *et al.* , 2009). Species-habitat association might change through plant development, possibly resulting in spatial dissociation between size classes. Moreover, species-habitat association is expected to be stronger for large than for small trees (Comita *et al.* , 2007; but see Baldeck *et al.* , 2013). On the other hand, aggregation of individuals of different sizes and spatial association between size classes are expected under strong dispersal limitation (Wiegand *et al.* , 2007).

Investigating ecological processes with spatial point process models may be especially important in harsh environments, such as areas of rocky soils (Pollock *et al.* , 2012) and areas subject to periodic flooding (Baraloto *et al.* , 2007; Colmer and Voesenek, 2009), as these environments can act as strong drivers of species selection (Chapin *et al.* , 1993; Reich *et al.* , 2003). Selective pressures on plants, such as gradients in soil moisture, can change functional traits and the niche relationship of co-occurring species (Werner and Platt, 1976). However, few studies have evaluated the spatial structure of trees in environments with seasonal flooding (e.g. Baraloto *et al.* , 2007; Oliveira *et al.* , 2014), even though habitat filtering is commonly associated to topographic and edaphic variation in tropical forests (Bagchi *et al.* , 2011; Baldeck *et al.* , 2012). Thus, species with different flooding tolerances should show different species-habitat associations according to the local environmental heterogeneity (Baraloto *et al.* , 2007).

Congeneric species are a good model to investigate the relative importance of ecological processes that maintain high species diversity because they tend to have similar niches due to their close phylogenetic relationship (Losos, 2008). Therefore, strong interspecific competition within the same tolerable environment should be easily detected, resulting in spatial association between species at large scales (< 30 m) due to habitat filtering and dissociation at small scales (< 5 m) due to interspecific competition (Velázquez *et al.* , 2015). However, congeneric species may show niche differentiation due to selective pressures acting on

each one of them at the evolutionary scale, including competition within the same tolerable environment (Wiegand *et al.* , 2007). This “ghost of competition past” results, at present day, in each species specialized in a different environment (Stubbs and Wilson, 2004; Yamada *et al.* , 2005) or in different use of resources within the same tolerable environment (Schluter, 2000). Alternatively, species’ niche may not be important, and so the spatial structure of populations should reflect dispersal limitation and stochasticity (May *et al.* , 2014).

The present study aims to find evidence for the action and relative importance of different ecological processes hypothesized to maintain species coexistence in a tropical forest subject to seasonal flooding, using the spatial structure of populations of three congeneric species. Specifically, we ask: (1) which environmental variables are associated with the spatial distribution of the different size classes of each species? (2) What is the spatial relationship between congeners in the same size class? (3) Is the size of an individual influenced by the proximity to congeners in the same size class? (4) What is the spatial relationship between small and large conspecific trees? The combination of different spatial patterns will indicate which ecological processes are more important to the maintenance of species coexistence (see Table 1).

Material and methods

Study site

The Brazilian Atlantic Forest covers today only about 12% of its original extension and is distributed in fragments (Ribeiro *et al.* , 2009). Because it also presents high species richness and endemism, the forest along the coast was classified as a hotspot for biodiversity conservation (Myers *et al.* , 2000). The vegetation closest to the beach, covering sandy soils, is called *restinga* . It can vary from sparse herbaceous to forest communities (i.e. white-sand tropical forest; Oliveira *et al.* , 2014). The low altitude (< 10 m; Joly *et al.* , 2012) and high permeable soil result in periodic water table flood, especially during the rainy season. Microtopographic variation forms dry sandy cords between flood channels, which, when dry, hold high quantities of organic matter (Diniz, 2009). While some plant species are flood-tolerant, others are restricted to the sandy cords (Oliveira *et al.* , 2014). Due to its proximity to the beach, *restinga* communities are highly threatened in Brazil by the real estate market (Alho *et al.* , 2002).

In the present study, we collected data in a 1-ha, permanent plot (23° 21’ 22” S and 44° 51’ 03” W) installed at a protected *restinga* forest in the northern coast of the state of São Paulo, southeastern Brazil. The *restinga* forest is composed of dense vegetation, but light levels are high in the understory (Joly *et al.* , 2012), resulting in developed shrub and herbaceous strata. Epiphytes and lianas are also common (Fernandes and Queiroz, 2015). This forest was recently formed from the downward movement of some species from the Atlantic Forest of the interior of the state of São Paulo (Eisenlohr *et al.* , 2013; Sanchez *et al.* , 2013).

The study plot was divided into 100 subplots of 10 m × 10 m (Joly *et al.* , 2012). The regional climate is tropical humid, with mean annual precipitation of 2634 mm and mean annual temperature around 22 °C (Morellato *et al.* , 2000). The plot presents 84 tree and palm species, being Myrtaceae and Fabaceae the richest families, and Myrtaceae, Arecaceae, and Euphorbiaceae the most abundant ones (Joly *et al.* , 2012).

Species studied

The three species studied belong to the genus *Myrcia* , family Myrtaceae, subfamily Myrtoideae. Myrtaceae presents the highest number of species in tropical rainforests (Oliveira-Filho and Fontes, 2000) and is considered a characteristic family in the Brazilian Atlantic coastal forest (Lucas and Bünger, 2015). In the study plot, there are 21 Myrtaceae species, seven belonging to *Myrcia* (Joly *et al.* , 2012). The three species studied have 50 or more individuals in the plot (individuals with stem diameter at breast height [?] 4.8 cm; data from the Functional Gradient Project Biota/FAPESP 03/12595-7 – available upon request).

The three species are not geographically restricted to the *restinga* forest and are widely distributed in the Atlantic Forest (Fig. 1). In the study plot, they occupy different canopy strata. *Myrcia brasiliensis* occupies the first stratum and also occurs as an emergent tree; *M. multiflora* occupies the first and second strata, and *M. racemosa* occupies the first stratum (Pedroni, 2001). The three species increase water capitation

in the soil at 50 cm depth and reduce the use of topsoil water (10 cm depth) from the flooded to the dry period. In the dry period, the species show a similar use of water sources, but *M. racemosa* capitates a higher proportion of water at 30-cm depth (Antunes, 2018). The similar water use suggests that the three *Myrcia* species are restricted to similar environments in the periodically flooded *restinga* forest studied here, but we lack knowledge on other traits to hypothesize whether the species present similar niches.

Data collection

Between 2016 and 2017, we marked with individually numbered tags all free stems with diameter at soil height (DSH) ≥ 1.5 mm (minimum size at which taxonomic identification was possible) of the three species studied. We also measured the DSH and mapped (x, y) all individuals in the study plot. We sampled soil moisture, canopy opening at two different moments (2008 and 2017), elevation, terrain slope, flooding height, and litterfall height, which are variables that are likely related to different species requirements in a *restinga* forest. Details can be found in Appendix S1.

Data analysis

Size classes

To investigate ecological processes throughout species development, we divided the individuals of each species into three size classes based on DSH and taking into account the minimum number of individuals in each class for spatial point pattern analysis (n ≥ 30 , Martins *et al.*, 2018). Small trees were defined as individuals with DSH ≤ 0.2 cm for *M. brasiliensis*, and DSH ≤ 0.5 cm for *M. multiflora* and *M. racemosa*. Medium-sized trees had $0.2 < \text{DSH} \leq 10.0$ cm for *M. brasiliensis*, and $0.5 < \text{DSH} \leq 10.0$ cm for *M. multiflora* and *M. racemosa*. Large trees were those with DSH > 10.0 cm for the three species. We conducted all the following analyses separately for the three size classes of each of the three species studied.

Analysis 1: Relationship between species distribution and environmental variables

To test for species habitat-association through plant development, we first used the variance inflation factor (VIF) to check whether our seven environmental variables were multicollinear (VIF > 10 , Zuur *et al.*, 2007). None of them showed multicollinearity and thus all were included in our models.

Without habitat association, the intensity function λ is spatially constant and given by the mean number of points (i.e. individuals) per unit area of the study plot. However, under habitat association, the intensity differs at different positions x, y in the study plot, thus $\lambda_{\eta}(x, y)$. To determine the relationship between species distribution and environmental variables, we modelled the intensity function $\lambda_{\eta}(x, y)$ at the location (x, y) as a function of the sum of the variables on a log scale. The corresponding log-linear regression model yields:

$$\log(\lambda_{\eta}(x, y)) = \beta_0 + \beta_1 v_1(x, y) + \dots + \beta_7 v_7(x, y),$$

where β_0 is the intercept and β_i is the coefficient of the i^{th} environmental variable $v_i(x, y)$ to be estimated (Waagepetersen, 2007), with v_1 being flooding height, v_2 soil moisture, v_3 terrain slope, v_4 elevation, v_5 litterfall height, v_6 canopy opening in 2017, and v_7 canopy opening in 2008.

We used the Z value to evaluate the significance and direction of the effect of the different environmental variables on each species' pattern. For a significance level of $\alpha = 0.05$, we have a significant and positive association with a given variable if $Z > 1.96$ (and a negative if $z < -1.96$) and the larger the absolute value of Z, the stronger the association. We considered habitat effects to be strong when $|Z| \geq 4$. We fitted $\lambda_{\eta}(x, y)$ using maximum likelihood estimation to determine the values of the coefficients β_i (Shen *et al.*, 2009; Wang *et al.*, 2011) in the package "spatstat" (Baddeley *et al.*, 2015) of the software R (R Core Team, 2018).

Analysis 2: Spatial relationship between congeners

To assess the spatial relationship between two congeners in the same size class, we used the bivariate pair correlation function $g_{12}(r)$ as the summary function (Stoyan and Stoyan, 1994) and a null model of inde-

pendence. The pair correlation function $g(r)$ is based on the distribution of distances r between pairs of points belonging either to the same pattern (e.g. same species) or to two different patterns (e.g. species 1 and species 2). Therefore, $g(r)$ can describe the dependence between points on multiple spatial distances r . It determines the expected density of points of the same pattern (e.g. species 1; univariate) or of the other pattern (e.g. species 2; bivariate) within a ring of radius r and width d centred on an arbitrary focal point of species 1. In the univariate $g(r)$, this value is divided by the overall intensity λ_1 of species 1 in the study site, whereas in the bivariate function, it is divided by λ_2 of species 2 (Wiegand and Moloney, 2014).

We compared the observed values of $g_{12}(r)$ to those calculated during simulations of the independence null model. To detect species associations, either caused by species interactions, or by shared or opposed habitat associations, the independence null model breaks the potential associations between species but conserves the observed aggregation of each one of them. To simplify this task, we fixed the original location of points of pattern 2 and randomized the point pattern of species 1. To generate null model patterns of species 1 with the desired properties, we used the technique of pattern reconstruction (Wiegand *et al.*, 2013) based on non-parametric optimization. It reconstructs the point pattern of the species based on information provided by several summary functions calculated from the observed pattern. We conducted (homogeneous) pattern reconstruction based on $g_{11}(r)$, the univariate L -function $L_{11}(r)$ (a transformed K -function, which is a cumulative version of $g_{11}(r)$), and several univariate nearest neighbour distribution functions. As a result, the spatial structure of the reconstructed pattern very closely matches that of the observed pattern (Wiegand *et al.*, 2013), but because the location of species 1 was reconstructed without regard of that of species 2, the locations of the species are spatially independent. Positive departures of the observed $g_{12}(r)$ indicate species association, negative departures indicate species dissociation, and values within the simulation envelope indicate no significant departure from independence (Wiegand and Moloney, 2014).

To find out if spatial associations were caused by the location of congeners within the same environmental patches, we used the intensity function $\lambda_n(x, y)$ of species 1 to parameterize the pattern reconstruction of species 1 (Wiegand *et al.*, 2013; Wang *et al.*, 2015). In this case, observed values of $g_{12}(r)$ should lie within the simulation envelopes, whereas departures suggest species interactions not explained by habitat-association (Wiegand and Moloney, 2014).

Analysis 3: Spatial distribution of size between congeners

For the analysis of the plant size as a function of the distance between individuals, we attributed the quantitative mark DSH to points of plants location. Mark correlation functions are designed to detect correlations in the marks of pairs of points i and j that are separated by distance r (Stoyan, 1984). For example, they allow us to find out if trees of species 1 tend to be smaller than expected if a tree of species 2 is located nearby (Wiegand and Moloney, 2014).

For bivariate patterns, there are type v (e.g. species 1) and type w (e.g. species 2) points. The bivariate r -mark correlation function $\kappa_{\mu_1}(r)$ measures the mean mark of type v points located at distance r from type w points. The dot (".") in the subscript " m_1 ." indicates that the mark of the second point ($= m_2$) is not used for estimation of $\kappa_{\mu_1}(r)$. This function is normalized by μ , the mean mark of type v points. If $\kappa_{\mu_1}(r) = 1$, the marks m_1 of type v points that have a type w point at distance r are similar to μ ; if $\kappa_{\mu_1}(r) < 1$, they are smaller on average than the mean μ , indicating interspecific competition; if $\kappa_{\mu_1}(r) > 1$, they are larger on average, indicating facilitation or location of individuals at resource-rich patches. Because the r -mark correlation function is evaluated at different interpoint distances r , we can observe how spatial effects decline with increasing distance between individuals (Wiegand and Moloney, 2014).

In order to generate the null model values representing the absence of interactions for comparison of $\kappa_{\mu_1}(r)$, we randomly shuffled the marks within type v points while keeping unchanged the marks of type w points; additionally, the original location of all individuals was kept fixed. This "random marking" null model assumes that the size of type v points is independent of the size of nearby type w points (Wiegand and Moloney, 2014).

Additionally to distance between individuals, plant size can be influenced by the environment where indi-

viduals are located. Therefore, nearby plants may be smaller in less favourable patches and larger in more favourable patches, independently of the distance between individuals. In order to tease apart the effects of environmental heterogeneity and distance between individuals, we used the local random marking null model. In this variation of the null model, shuffling of the marks is restricted to points separated only up to a given distance R , which represents an approximated size of environmental patches. By doing this, we can check whether departures from the independent marking null model are caused by environmental heterogeneity. Conversely, departures from the local random marking indicate congeners interactions within patches (Wiegand and Moloney, 2014). We stipulated $R = 25$ m (one-quarter of the 1-ha plot) for the local random marking null model after testing for different values of R . The selected value corresponds to an approximate patch size where most distance effects disappear. Additionally, $R = 25$ m is large enough to encompass neighbourhood interactions within patches. In all analyses, we considered the influence of species 1 on species 2 and vice-versa.

Significance of spatial patterns against the null models for analysis 2 and 3

In order to determine whether the observed summary functions indicating spatial associations between congeners ($g_{12}(r)$) and the spatial distribution of size between congeners ($\kappa_{\mu 1.}(r)$) differed from the expected values under the appropriate null models, we first performed 199 Monte Carlo simulations of the point processes underlying the null models. Then we created global simulation envelopes for the 1-50 m distance interval, considering the critical α value as calculated in the Z test statistics. The global envelopes have the convenient property that the null model can be rejected with the prescribed significance level α if the observed summary function falls at least at one distance bin outside the envelopes (Wiegand *et al.*, 2016).

Analysis 4: Spatial relationship between conspecifics of different sizes

In order to assess ecological processes driving spatial relationships between conspecifics of different size classes, we used a suite of alternative point process models that represent competing hypotheses, namely independence, dispersal limitation, habitat filtering, and a combination of dispersal limitation and habitat filtering. In all cases, we fixed the pattern of large trees, and randomized the pattern of small and medium trees according to the point process model used. To conserve the univariate pattern of small and medium trees during the simulations, we again used the technique of pattern reconstruction (Wiegand *et al.*, 2013) with different intensity functions tailored specifically for each point process model.

For the independence hypothesis (lack of small-scale species interactions), we used (as in analysis 2) a spatially constant intensity function λ (i.e. homogeneous pattern reconstruction). To represent dispersal limitation, we used the intensity function $\lambda_d(x, y)$ given by the superposition of Gaussian kernels with parameter σ around large trees. This creates patterns where the distribution of small and medium trees follows a normal distribution around the large conspecific trees (Wiegand and Moloney, 2014). The value of the parameter σ was fitted. For the habitat association hypothesis, we used the parametric intensity function $\lambda_h(x, y)\lambda_h(x, y)$ of small trees. Finally, to represent the combined dispersal limitation and habitat filtering hypothesis, we used the geometric mean of the two intensity functions (i.e. $[\lambda_d(x, y)\lambda_h(x, y)]^{0.5}\sqrt{\lambda_d\lambda_h}$).

To determine the most parsimonious point process model, given the data, we used model selection based on the Akaike information criterion (AIC) and “synthetic” likelihood functions (Wood, 2010). With this method, we reduced the raw point pattern data to three-point pattern summary functions that quantify the spatial structure of the observed bivariate point patterns, namely $g_{12}(r)$, the bivariate L -function $L_{12}(r)$, and the bivariate nearest neighbour distribution function $D_{12}(r)$. We performed 999 simulations of the point process model to obtain the mean and the covariance matrix of these functions for each radius r (in steps of 3 m), given the vector Θ of model parameters. This allows for the construction of the synthetic likelihood to assess model fit. The resulting log-likelihood can then be used to calculate the AIC that balances model fit and model complexity to identify the most parsimonious model (Akaike, 1974; Wiegand and Moloney, 2014). We used here 999 simulations for better estimation of the covariance matrix needed for construction

of the likelihood function.

We performed all point pattern analyses with the software *Programita* (Wiegand and Moloney, 2014), which can be accessed at www.programita.org. Estimators of the summary functions and the edge correction used in *Programita* are detailed in Wiegand, Grabarnik, and Stoyan (2016). We used a spatial resolution of 1 m, which is much smaller than the study plot, fine enough to answer our questions, and larger than the mapping error of the data (Wiegand and Moloney, 2004, 2014). We selected a ring width $d = 3$ m in all analyses.

Results

Number of individuals and distribution of size classes in the plot

Myrcia racemosa showed the highest number of individuals in all size classes in the plot ($n = 574$), followed by *M. brasiliensis* ($n = 192$) and *M. multiflora* ($n = 110$, Appendix S2). Individuals of all size classes of *M. brasiliensis* were well distributed in the study plot. Small and medium trees of *M. racemosa* were distributed as a decreasing gradient from flooded to drier areas (from northwest to southeast of the plot), and large trees were distributed as a decreasing gradient from North to South of the plot. All size classes of *M. multiflora* occurred only in the West part of the plot (Appendix S2).

Relationship between species distribution and environmental variables

The three species occur in similar environments in the plot, that is low flat areas and better-lit patches. For *M. brasiliensis*, there was a positive relationship between small trees and canopy opening in 2017 and 2008, and a negative relationship between large trees and both terrain slope and elevation. However, these relationships were weak. All size classes of *M. multiflora* were negatively related to terrain slope and elevation. Additionally, small and large trees were positively associated with soil moisture, small and medium trees were positively associated with canopy opening in 2008, and large trees were negatively affected by litterfall height. Elevation was the environmental variable that more strongly influenced the distribution of individuals, especially of medium and large trees. Small and mainly medium trees of *M. racemosa* also showed a strong, negative relationship to elevation. Additionally, small trees were strongly and negatively related to terrain slope, and medium trees, weakly and positively related to canopy opening in 2008, which kept influencing the distribution of large trees, but now in a negative fashion (Table 2).

Spatial relationship between congeners

Although the three *Myrcia* species occur in similar environments in the plot, we found no positive associations indicating habitat filtering to the same favourable patches, or negative associations as evidence of interspecific competition. The different size classes of the three species studied were, in most cases, spatially independent, i.e. the observed $g_{12}(r)$ fell within the simulation envelopes. The only exception was medium trees of *M. multiflora* and *M. racemosa*, which were spatially associated (Appendix S3). This association was explained by a shared habitat association of the two congener species, as $g_{12}(r)$ fell within the simulation envelopes when we used the parametric intensity function $\lambda_{\eta}(x, y)$ to parameterize the pattern reconstruction (Fig. 2).

We also found no evidence of interspecific competition in relation to size distribution of the species. The sizes of trees were in most cases not influenced by the presence of nearby congeners of the same size class, as indicated by results of the independent marking null model. The only exception was medium-sized trees of *M. racemosa*, which showed smaller DSH near individuals of *M. brasiliensis* (< 6 m) and of *M. multiflora* (< 13 m). However, this effect was caused by systematic size differences caused by harsh environmental conditions, as the observed $\kappa_{\mu-1}(r)$ fell within the simulation envelopes of the local random marking null model (Fig. 3).

Spatial relationship between conspecifics

Only *M. multiflora* showed spatial associations, which were best explained by dispersal limitation for small in relation to large trees, and the combination of dispersal limitation and habitat filtering for medium in relation to large trees (Table 3). For *M. brasiliensis* and *M. racemosa*, small and medium trees were spatially

independent of large trees, but for the small-large tree combination of *M. racemosa*, the habitat filtering model received similar support as the independence model (Table 3). The parameter σ that resulted in the best fit for the models of dispersal limitation was 20 m for *M. brasiliensis*, 9 m for *M. multiflora*, and 15 m for *M. racemosa*.

Discussion

In our study system, habitat filtering was the most important process driving the local distribution of the species in a *restinga* forest, because species distribution showed associations, albeit of different strength, to environmental variables. We did not detect spatial patterns that are consistent with interspecific competition, i.e. spatial segregation and smaller size of nearby congeners, and the three *Myrcia* species do not seem to show evidences of stochasticity even though congeners were spatially independent, since they responded to differences in the environment. Last, dispersal limitation only led to spatial associations of different size classes for one species studied. Even though many studies on topo-edaphic variation in tropical forests (e.g. Baldeck *et al.*, 2012), including flooded areas (Baraloto *et al.*, 2007; Oliveira *et al.*, 2014), have shown that habitat filtering is an important ecological process, other processes that drive community structuring may have gone undetected (see Wang *et al.*, 2015).

Relationship between species distribution and environmental variables

The distribution of the three species studied showed somewhat similar associations to environmental variables, which is expected due to the close phylogenetic relationship among the species (Losos, 2008). In general, the distribution of the three *Myrcia* species was negatively related to elevation and terrain slope, and positively related to canopy opening. Flooding is expected to be more frequent, last for a longer time, and/or reach higher heights at lower parts of the study plot due to periodic water table flood (Diniz, 2009). As shown in Fig. A1, the lower part of the study plot does present higher soil moisture and flooding height. Therefore, we believe elevation is a good surrogate for flooding at the study site. Additionally, we detected positive relationships between the distribution of small and large trees and soil moisture for *M. multiflora*, which reinforces our hypothesis that the three congeneric species are restricted to patches subject to flooding within the plot. We probably did not find more relationships between species distribution and flooding height and/or soil moisture because both variables were measured only once and thus we probably could not capture flooding seasonality properly. The distribution of the three species studied was also restricted to better-lit patches, where individuals are likely to show higher survival probability, growth rate, and fecundity (Dahlgren and Ehrlén, 2009). Interestingly, we were able to detect the influence of temporal changes in the light environment on the distribution of different size classes of the three *Myrcia* species. Although smaller trees were correlated with recent and/or past light environment, large trees were correlated only with the past light environment, which probably reflects more closely the conditions of the time plants were smaller.

Myrcia brasiliensis, which is well distributed in the study plot, showed weak associations to the environmental variables. Conversely, the other two species, whose distributions follow a flood-dry gradient, showed strong associations to elevation. For the three species, environmental requirements shifted through plant development, as also observed for other species (e.g. Comita *et al.*, 2007). For *M. brasiliensis*, the light environment was important during early development (Poorter, 2007). However, as trees reach large sizes, they no longer depend on canopy opening, as the species occupies the first canopy stratum and also occurs as an emergent tree (Valladares *et al.*, 2016). As individuals grow in better-lit environments, some become restricted to patches subject to flooding. On the other hand, *M. racemosa* showed an opposite pattern, whereby smaller trees get restricted to patches subject to flooding and later on development the past light environment becomes detectable on the distribution of large trees. The shift in environmental requirements likely explains the change in distribution from small and medium trees (flood-dry gradient) to large trees (from northwest to southeast of the plot) for *M. racemosa*. *Myrcia multiflora* showed an intermediate pattern, with species distribution restricted to patches subject to flooding from early to late development, and light influencing the distribution of small and medium trees.

Even though flooding is the most important environmental characteristic driving species distribution in the

plot, the fundamental niche of the three *Myrcia* species potentially encompasses a much wider variation of conditions than the environments of the study site, as the species occur in different vegetation types and are not restricted to areas subject to flooding at the geographic scale (Fig. 1). Thus, in the restinga forest studied, the species are capable to use the most common environmental condition (niche position, Marino *et al.* , 2019), and patches subject to flooding may work as areas of refuge from strong competitors and/or natural enemies (Baraloto *et al.* , 2007), which drives the species' realized niche. We suggest future studies should evaluate flood tolerance of the different species of the community and the presence of natural enemies to better understand the spatial distribution constraint in a gradient of soil moisture in flooded forests.

Spatial relationship between congeners

Due to the overall association of the three *Myrcia* species to patches subject to flooding, the spatial association between congeners should be expected. Nevertheless, only medium trees of *M. multiflora* and *M. racemosa* were spatially associated due to the same habitat-association. All other congener spatial relationships were independent, which has been frequently shown for tropical tree species (Wiegand *et al.* , 2012; Wang *et al.* , 2016). One explanation is that positive and negative interactions between species cancel each other's effects out (note that there are many more species competing in our plot with the three species studied), resulting in spatial patterns that appear on overall independent (Punchi-Manage *et al.* , 2015). Also, according to the stochastic dilution hypothesis, independence increases with species richness in rich forests such as in the tropics, due to large variability of neighbour's trees that inhibit the detection of the spatial arrangement of plants directed by interactions between species (Wang *et al.* , 2016). The apparent spatial independence between congeners likely explains the independence between tree size and distance between congeners when we considered environmental heterogeneity in our analysis (i.e. local random marking null model). The evaluation of plant performance in greenhouse experiments and functional traits related to resource acquisition could help to elucidate whether the three *Myrcia* species use resources differently, as expected by niche differentiation of sympatric species with similar environmental requirements due to strong competition in the past (Connell, 1980).

Spatial relationship between conspecifics

Even though dispersal limitation is common in tropical forests (Hubbell, 2005) and habitat filtering is expected to influence species distribution in harsh environments (Baraloto *et al.* , 2007), these processes only drove the spatial associations between small/medium and large trees of *M. multiflora*. Dispersal limitation drives the spatial relationship between small and large trees and, as trees grow, habitat filtering also becomes important for this species, which agrees with the stronger associations (i.e. higher Z values) of medium and large trees to environmental variables. Note that we estimated for this species the smallest width of the kernel function ($\sigma = 9$ m vs. 15 m and 20 m for the other two congeners) of the dispersal limitation model. Although it is consistent with species height (occupation in different canopy strata), we cannot exclude the possibility that the size of our plot is too small to allow for the detection of the effects of dispersal limitation for *M. brasiliensis* and *M. racemosa*.

Spatial independence between small and large trees was also found by Getzin, Wiegand, and Hubbell (2014) in Barro Colorado Island, Panama. The authors suggested that this pattern could be habitat-association masked by unpredictable dispersal events created by disperser movement behaviour or uncoupling the positive association of trees expected from dispersal limitation due to high mortality of seeds and early development stages. Negative density dependence caused by the attack of species-specific natural enemies (Janzen, 1970; Connell, 1971) or by intraspecific competition among seedlings (Wright, 2002) poses high offspring mortality close to parent plants. Additionally, the spread of natural enemies and competition from parents are major mortality causes of seeds and seedlings in tropical forests (Fricke *et al.* , 2014). A future venue is to assess seed distribution around large trees and mortality through size classes in order to better understand intraspecific spatial patterns.

Conclusions

In this study, we employed several spatial point pattern models to simultaneously investigate important

ecological processes that are hypothesized to maintain species coexistence in tropical forests, i.e. habitat filtering, interspecific competition, stochasticity, and dispersal limitation. Using data from congeneric species in a harsh environment as a model, we demonstrated that habitat filtering to areas subject to flooding is the most important ecological process driving the local distribution of the species studied in a *restinga* forest. In this type of vegetation, there seems to be a clear division of tree species into either flood-tolerant or flood-intolerant (Oliveira *et al.* , 2014). Given that *restinga* is highly threatened in Brazil (Alho *et al.* , 2002), the preservation of its different habitats is of utmost importance to the maintenance of high species richness and functional strategies. Additionally, flood-tolerant species present in, but not restricted to *restinga* communities provide an excellent model to the evaluation of niche breadth and position, interpopulation genetic variation, and local adaptation.

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Table 1. Expectations for different ecological processes driving local species distribution. The analyses employed in this study and the results for three size classes of three *Myrcia* species sampled in a 1-ha plot of *restinga* forest, southeastern Brazil, are also shown. The neighbourhood scale (up to some 10 m) represents direct species interactions, the patch scale represents approximately homogeneous (suitable or less suitable) environments, whereas the community scale (100 m – tens of km) comprises several patches.

Hosted file

image2.emf available at <https://authorea.com/users/338985/articles/465319-habitat-filtering-drives-the-local-distribution-of-congeneric-species-in-a-brazilian-white-sand-flooded-tropical-forest>

Table 2. Results of species-habitat association analysis using log-linear regression models for different size classes three *Myrcia* species sampled in a 1-ha plot of *restinga* forest, southeastern Brazil. Bold indicates significant species-habitat association. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

<i>M. brasiliensis</i>	Estimate	Std. Error	z Value	<i>M. multiflora</i>	Estimate	Std. Error
	Small trees				Small trees	
(Intercept)	-5.51	13.70	-0.40	(Intercept)	70.70	21.29
Flooding height	-0.01	0.02	-0.42	Flooding height	0.00	0.02
Soil moisture	0.05	0.03	1.92	Soil moisture	0.09	0.04
Terrain slope	-0.16	1.19	-0.13	Terrain slope	-5.01	1.89
Elevation	-0.43	1.31	-0.33	Elevation	-8.03	2.09
Litterfall height	0.04	0.05	0.85	Litterfall height	0.00	0.07
Canopy opening 2017	0.10	0.05	2.02*	Canopy opening 2017	0.02	0.08
Canopy opening 2008	0.08	0.04	2.29*	Canopy opening 2008	0.11	0.05
	Medium trees				Medium trees	
(Intercept)	-0.89	16.50	-0.05	(Intercept)	171.92	33.27
Flooding height	0.02	0.02	1.35	Flooding height	0.03	0.02
Soil moisture	0.01	0.03	0.26	Soil moisture	0.02	0.04
Terrain slope	1.96	1.41	1.39	Terrain slope	-11.96	2.72
Elevation	-0.64	1.57	-0.41	Elevation	-18.18	3.39
Litterfall height	-0.02	0.06	-0.40	Litterfall height	-0.01	0.07
Canopy opening 2017	-0.03	0.06	-0.49	Canopy opening 2017	0.12	0.07
Canopy opening 2008	0.09	0.05	1.95	Canopy opening 2008	0.26	0.06
	Large trees				Large trees	
(Intercept)	22.95	12.62	1.82	(Intercept)	83.07	20.09
Flooding height	0.00	0.02	-0.20	Flooding height	0.01	0.02
Soil moisture	0.04	0.02	1.51	Soil moisture	0.08	0.04
Terrain slope	-2.57	1.15	-2.23*	Terrain slope	-4.25	1.78
Elevation	-2.92	1.21	-2.42*	Elevation	-8.86	1.97
Litterfall height	0.02	0.04	0.52	Litterfall height	-0.17	0.07
Canopy opening 2017	0.03	0.05	0.64	Canopy opening 2017	-0.08	0.07
Canopy opening 2008	0.02	0.04	0.65	Canopy opening 2008	0.03	0.05

Table 3. Akaike's information criterion values for four competing hypothesis explaining spatial relationships at distance $r = 1-50$ m between small and large trees, and between medium and large trees of conspecifics of three *Myrcia* species sampled in a 1-ha plot of *restinga* forest, southeastern Brazil. Bold indicates the best fitted model. Bold face indicates the most parsimonious model(s).

Conspecifics interactions	Independence	Association due to dispersal limitation	Association due to habitat filtering	A
Intensity function	$\lambda_1(x,y)$	$\lambda_d(x,y)$	$\lambda_h(x,y)$	
<i>M. brasiliensis</i>				
Large x Small trees	-158.58	-152.78	-144.56	-1
Large x Medium trees	-119.88	-85.48	-107.06	-8
<i>M. multiflora</i>				
Large x Small trees	-121.28	-179.66	-144.78	-1
Large x Medium trees	-106.12	-150.42	-159.78	-1
<i>M. racemosa</i>				
Large x Small trees	-159.58	95.52	-159.74	-1
Large x Medium trees	-171.90	-130.62	-163.84	-1

Figure 1. Geographical distribution of *Myrcia brasiliensis*, *M. multiflora* and *M. racemosa* in Brazil. Data obtained from the speciesLink platform (2019). The green crosses are the coordinates reported by biological collections; the delimited regions represent the different phytogeographical domains of Brazil.

Figure 2. Spatial relationship, as measured by the bivariate pair correlation function $g_{12}(r)$, between medium trees of *Myrcia multiflora* and *M. racemosa* (pairwise) sampled in a 1-ha plot of *restinga* forest, southeastern Brazil. The spatial relationship was compared to a null model representing large-scale habitat association. The observed $g_{12}(r)$ is represented by closed circles, the mean $g_{12}(r)$ of 199 simulations by grey solid lines, and the global simulation envelope at $\alpha = 5\%$ by dotted lines. The black horizontal line at $g_{12}(r) = 1$ is the expectation for spatial independence between congeners.

Figure 3. Mean stem diameter at soil height (DSH), as measured by the bivariate r -mark correlation function $\kappa_{\mu 1}(r)$, between medium trees of *Myrcia racemosa* in relation to *M. brasiliensis* and *M. multiflora* (pairwise) sampled in a 1-ha plot of *restinga* forest, southeastern Brazil. The mean DSH was compared to the independent marking null model (A and B) and to the local random marking null model with $R = 25$ m (C and D). The observed $\kappa_{\mu 1}(r)$ is represented by closed circles, the mean $\kappa_{\mu 1}(r)$ of 199 simulations by grey solid lines, and the global simulation envelope at $\alpha = 5\%$ by dotted lines. The horizontal line at $\kappa_{\mu 1}(r) = 1$ is the expectation for independence between DSH and distance between congeners.

Data accessibility

Data available from Knowledge Network for Biocomplexity (KNB) <https://knb.ecoinformatics.org/view/urn:uuid:ede260ba-124a-4174-8e3e-107fcf6c5e27>

Authors contributions

K.F.O.R., V.F.M. and F.A.M.S conceived the ideas and designed the study; K.F.O.R collected the data. All authors contributed to analysing the data, interpreting the results and writing the manuscript, and approved the final version.

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Appendix S1.

We sampled environmental variables that are likely related to different species requirements in a *restinga* forest. We quantified soil moisture, canopy opening, elevation, terrain slope, flooding height, and litterfall height in a 1-ha, permanent plot of *restinga* forest in southeastern Brazil. The plot was divided into 100 subplots of 10 m 10 m (Joly *et al.*, 2012). Soil moisture was determined as the volumetric soil water content measured at the centre of each subplot at 12-cm depth with a HS2 Hydrosense II sensor (Campbell Scientific, Logan, Utah, USA).

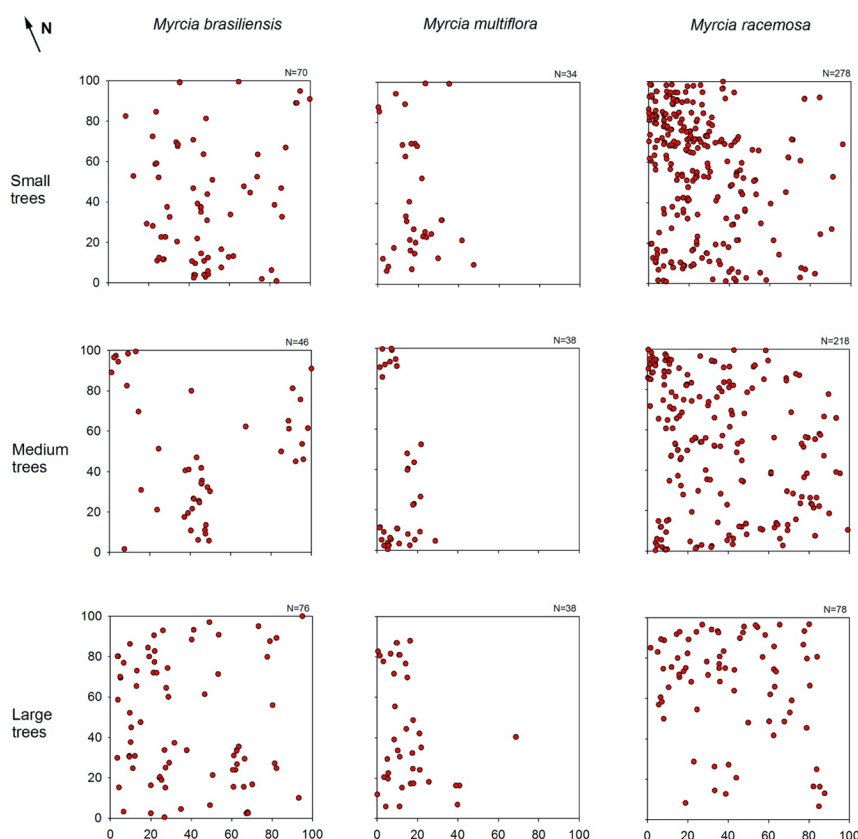
We obtained the percentage of canopy opening from hemispheric photographs taken at the centre of each subplot at two different moments, 2008 and 2017, as recent light environment should influence smaller plants and past light environment likely influenced large trees as they were growing (Poorter, 2007). In 2008, two digital cameras with similar settings were used, a Nikon Coolpix 950 and a Nikon Coolpix 5000, both with a fisheye lens Nikon FC E8 (Eisenlohr *et al.*, 2013). In 2017, we took the photographs using a Nikon D7200 digital camera with Sigma fisheye lens 4.5 mm f/2.8 EX DC and similar settings from 2008. At the two moments, the cameras were positioned on a tripod with the lens facing upwards at 1.3 m from the soil surface and parallel to it, with the magnetic north at the top of the photographs (Eisenlohr *et al.*, 2013).

The photographs were taken when the sky was uniform and showed high contrast with the canopy, between 8 h - 10 h and 15 h - 17 h (Rich, 1990). All photographs were processed with the software Gap Light Analyzer (Frazer *et al.*, 1999) in order to obtain the relative proportion of black and white (representing canopy opening) pixels.

We calculated the elevation of each subplot as the mean elevation of the four corners delimiting the subplots (data from the Functional Gradient Project Biota/FAPESP 03/12595-7 – available upon request). Terrain slope was calculated as the difference between the maximum and the minimum elevation of the four corners of each subplot (Rodrigues *et al.*, 2007). We considered flooding height as the height of the water column during the rainy season (January 2017). We measured water column and litterfall height at four diagonal points 3.5 m from each corner of the subplots using a graduated stake (Souza and Martins, 2005). Therefore, flooding height and litterfall height were measured at a 5 m 5 m scale, while soil moisture, canopy opening, elevation, and terrain slope were obtained at a 10 m 10 m scale. The values of the variables measured are presented in Figure A1.

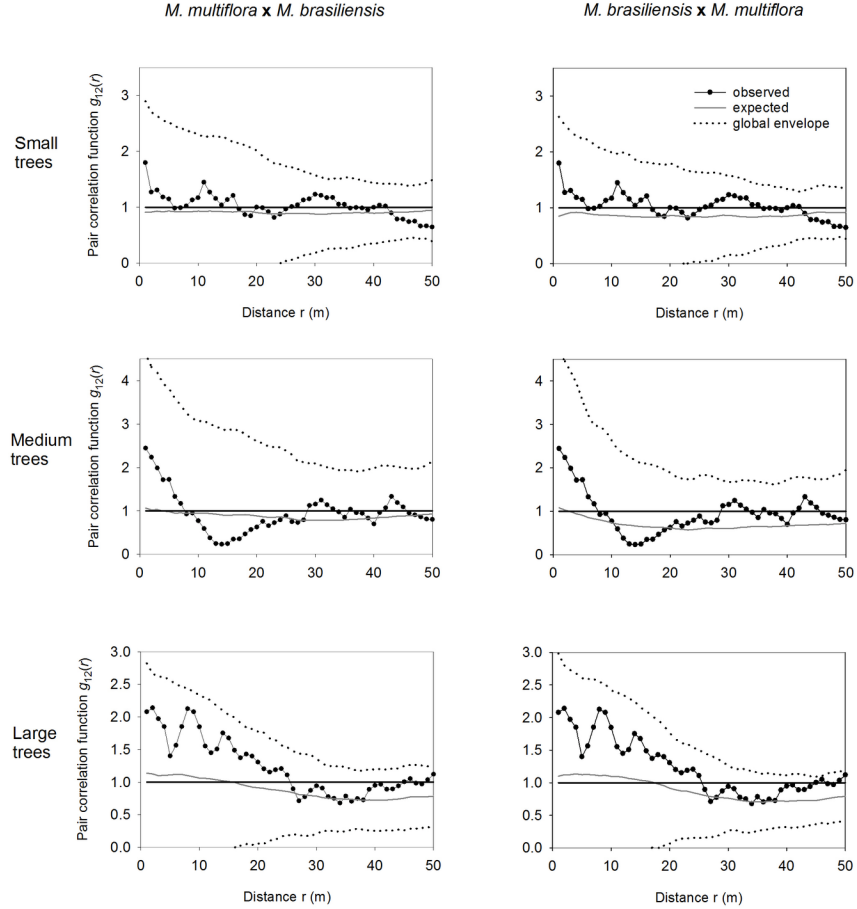
Appendix S2.

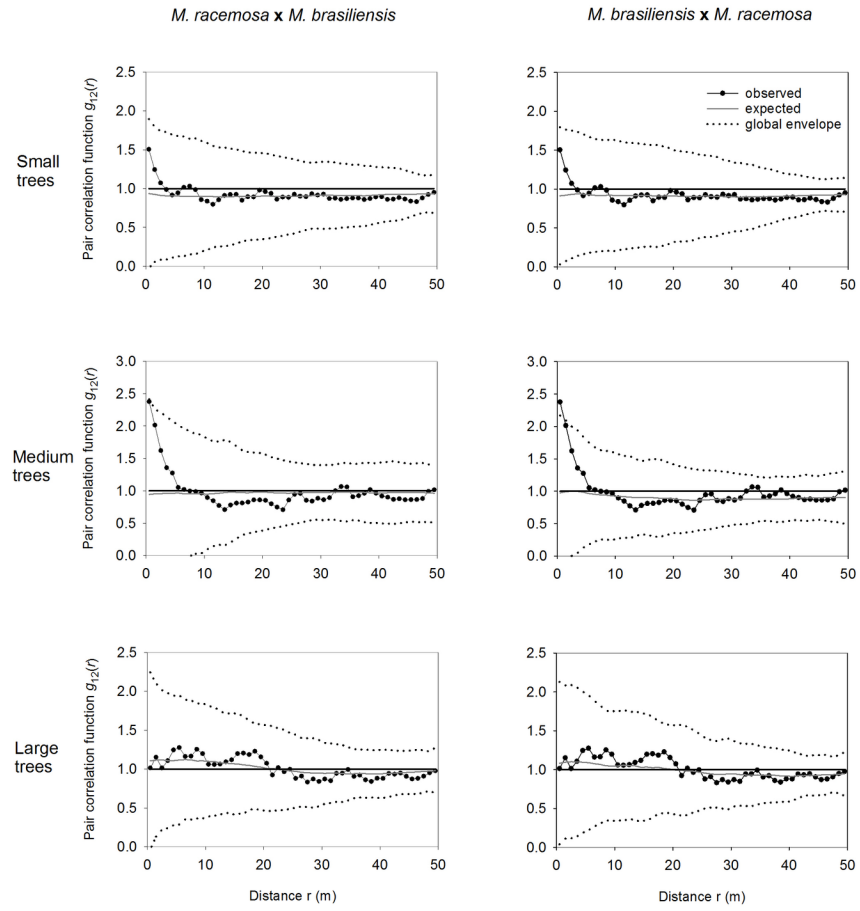
Distribution of individuals of different size classes of three *Myrcia* species in a 1-ha plot of *restinga* forest, southeastern Brazil. For size thresholds, please see the text.



Appendix S3.

Spatial relationship, as measured by the bivariate pair correlation function $g_{12}(r)$, between individuals in the same size class of three *Myrcia* species (pairwise) sampled in a 1-ha plot of *restinga* forest, southeastern Brazil. The observed $g_{12}(r)$ is represented by closed circles, the mean $g_{12}(r)$ of 199 pattern reconstruction simulations of the point pattern underlying the independence null model by grey solid lines, and the global simulation envelope at $\alpha = 5\%$ by dotted lines. The location of the first species was randomized while the location of the second species was kept fixed. The black horizontal line at $g_{12}(r) = 1$ is the expectation for spatial independence between congeners without large-scale habitat association.





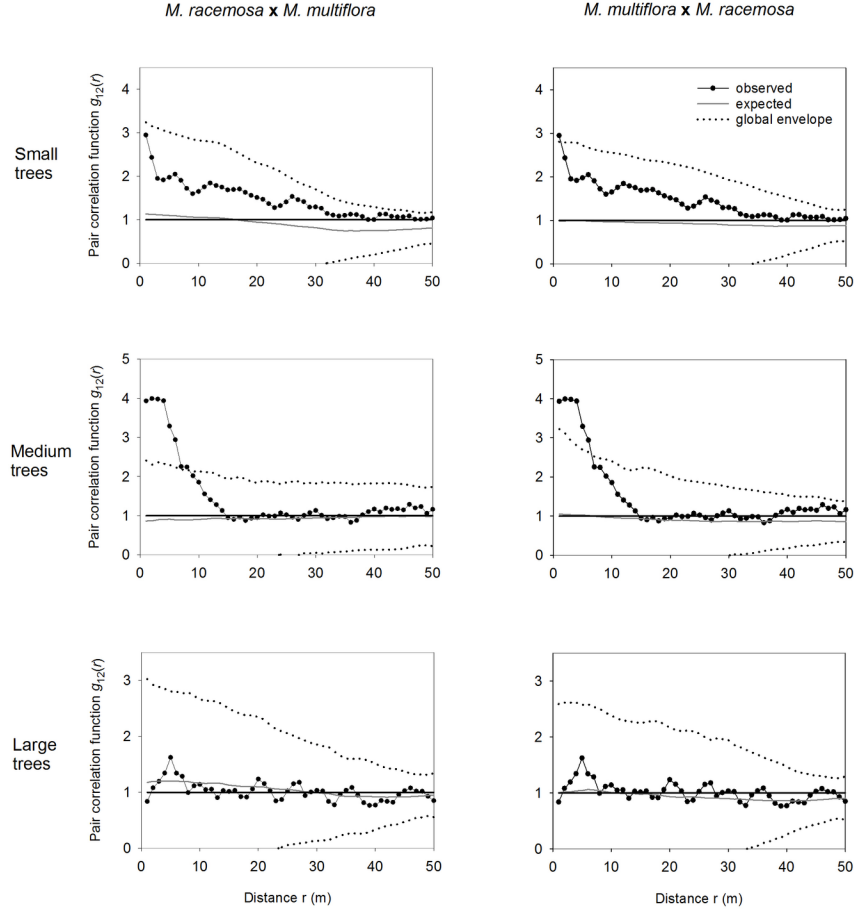


Figure 1. Geographical distribution of *Myrcia brasiliensis*, *M. multiflora* and *M. racemosa* in Brazil. Data obtained from the speciesLink platform (2019). The green crosses are the coordinates reported by biological collections; the delimited regions represent the different phytogeographical domains of Brazil.

Figure 2. Spatial relationship, as measured by the bivariate pair correlation function $g_{12}(r)$, between medium trees of *Myrcia multiflora* and *M. racemosa* (pairwise) sampled in a 1-ha plot of *restinga* forest, southeastern Brazil. The spatial relationship was compared to a null model representing large-scale habitat association. The observed $g_{12}(r)$ is represented by closed circles, the mean $g_{12}(r)$ of 199 simulations by grey solid lines, and the global simulation envelope at $\alpha = 5\%$ by dotted lines. The black horizontal line at $g_{12}(r) = 1$ is the expectation for spatial independence between congeners.

Figure 3. Mean stem diameter at soil height (DSH), as measured by the bivariate r -mark correlation function $\kappa_{\mu 1}(r)$, between medium trees of *Myrcia racemosa* in relation to *M. brasiliensis* and *M. multiflora* (pairwise) sampled in a 1-ha plot of *restinga* forest, southeastern Brazil. The mean DSH was compared to the independent marking null model (A and B) and to the local random marking null model with $R = 25$ m (C and D). The observed $\kappa_{\mu 1}(r)$ is represented by closed circles, the mean $\kappa_{\mu 1}(r)$ of 199 simulations by grey solid lines, and the global simulation envelope at $\alpha = 5\%$ by dotted lines. The horizontal line at $\kappa_{\mu 1}(r) = 1$ is the expectation for independence between DSH and distance between congeners.

