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Local environmental controls of Atlantic Forest tree community assembly on a coastal continental island in southeastern Brazil

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ABSTRACT

Tropical forests with high species diversity are commonly found in rugged montane areas. We investigated causes of local tropical forest tree community assembly on a continental island with heterogeneous terrain. We recorded tree community (absolute species abundance), topography, soil, litter and location in 40 sampling units on two opposite sides of the island with similar heterogeneous terrain. We used transformation based Redundancy Analyses and variation partitioning to determine the contribution of environment (topography, soil and litter), spatial structure (geographic location and Moran Eigenvector Maps) and the shared effects of these to explain community assembly. The environment made a significant contribution to explain tree community patterns (species composition and abundance) across all models. Conversely, spatial structure showed minor impact. Contribution of strictly environmental effects and spatially structured environmental effects varied when evaluating each site independently as well as when evaluating the combined data. Evidence suggests that local tropical tree community assembly on heterogeneous terrain may be located much closer to the niche end of the hypothetic niche-neutral continuum. Findings indicate additionally that heterogeneity of environmental factors present in dissected mountainous terrain can affect the way tropical community assembly processes are perceived.

Keywords: community composition, community structure, floristics, neutral, niche, soil, spatial structure, topography, tropical forest

Introduction

Understanding the ecological processes that control species distributions and natural community assembly is a fundamental goal of community ecology deeply rooted in the theoretical foundations of this discipline (Tilman 2004). Niche-assembly and dispersal-assembly theories represent two contrasting perspectives in this regard (Chave 2008). While the former is based on interspecific competition (Tilman 1982) and environmental filtering (Grimme 1977) as the main structuring processes (Chase & Leibold 2003), a prevalent example of the latter (e.g. the Unified Neutral Theory of Biodiversity and Biogeography; Hubbell 2001) proposes that natural communities arise as a consequence mainly of stochastic demography, speciation and dispersal (Etienne & Alonso 2007; Leigh 2007). A long lasting debate over which perspective (niche or neutral) is more suitable to explain community assembly leads to a focus on

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disentangling the relative contribution of environmental filters (henceforth environmental conditions) and stochastic processes (e.g. dispersal-limitation) that originate spatially structured species distributions (Chave 2008; Clark 2012; Dray *et al*. 2012; Rosindell *et al*. 2012). This understanding is represented by hypotheses such as the niche-neutrality continuum, which suggests communities are located somewhere on a hypothetical axis according to the inputs that niche and neutral processes provide to their assembly (Tilman 2004; Gravel *et al*. 2006; Leibold & Mcpeek 2006). Determining where communities lie within this continuum is a key question in ecology to advance comprehension of the mechanisms behind species distribution and community assembly.

One pattern that has puzzled ecologists for decades is the high number of species in plant communities of tropical forests, in particular those covering the dissected landscape of mountain chains (Morley 2000; Richter 2008). The heterogeneous terrain of such areas displays abrupt land surface changes that affect a variety of environmental conditions (*e.g.* topography, soil, litter, climate) commonly associated with patterns of richness, distribution, and coexistence of plant species (Chase & Leibold 2003; Richter 2008; Jones *et al*. 2011; Hofer *et al*. 2008; Baldeck *et al*. 2012; Eisenlohr *et al*. 2013). Still, few studies have focused on disentangling the contribution of niche-related predictors (*e.g.* environmental conditions) and neutral-related predictors (*e.g.* spatial structure) to explain tropical tree community assembly at local-scale (< 20 km^2) heterogeneous terrain (Svenning *et al*. 2004; Baldeck *et al*. 2012; Cielo-Filho & Martins 2015). Most addressed this issue at large-scale (> 100 km^2) or by focusing on ferns and lycophytes instead of trees (Jones *et al*. 2011; 2013; Bergamin *et al*. 2012; Eisenlohr *et al*. 2013; Rezende *et al*. 2015; Saiter *et al*. 2015; Arellano *et al*. 2016; Nettesheim *et al*. 2018). Studies of tropical tree community assembly at smaller local-scale are necessary to build comprehensive knowledge of niche- and neutral-related effects across different scales.

Brazilian Atlantic Forest remnants can yield important insights for this discussion because they are commonly located on mountain chains with highly heterogeneous terrain (SOS Mata Atlântica 2015). Studies showing the contribution of environmental conditions and spatial structure to explain plant community assembly in this forest have begun to appear recently (Bergamin *et al*. 2012; Eisenlohr *et al*. 2013; Cielo-Filho & Martins 2015; Oliveira-Filho *et al*. 2015; Rezende *et al*. 2015; Saiter *et al*. 2015; Nettesheim *et al*. 2018). Most of these studies indicate a greater role of niche-related environmental effects when compared to neutral-related spatial structure effects to explain vegetation changes. However, an opposite trend was found in the only study carried out within a local-scale in this forest (Cielo-Filho & Martins 2015); this study did not sample soil data (instead using topography as a surrogate) on a scale where soil particularly is expected to be relevant to community assembly (John *et al*. 2007; Baldeck *et al*. 2012; Chang *et al*. 2013). There is mounting evidence indicating that Atlantic Forest tree community assembly benefits from environmental conditions associated with abrupt terrain changes across the heterogeneous mountainous landscape where it occurs. This suggests that even small terrain variation such as a slight surface change in slope orientation is sufficient to determine different environmental conditions (*e.g.* distinct amounts of sunlight incidence; see Nettesheim *et al*. 2015) which increase the array of habitats for the tree community. Understanding how heterogeneous terrain is related to the behavior of local-scale community assembly may provide valuable insight into the mechanisms behind the high number of species and high levels of endemism reported for the Atlantic Forest.

Diverse Atlantic Forest along the coast of southeastern Brazil is commonly found on dissected heterogeneous mountain ranges. In fact, a mountain range in this region has been named a plant diversity hotspot of particular interest within the Atlantic Forest (Murray-Smith *et al*. 2009). Perhaps such high levels of plant diversity and endemism are due to a wide array of environmental conditions provided by the rough terrain of the mountain range. In this study, we address the causes of tree community assembly at the local-scale by evaluating a tropical continental island that displays the typically heterogeneous terrain of a mountain range covered by Atlantic Forest in southeastern Brazil. We determined if the role of niche-related environmental conditions (topography, soil and litter predictors) and neutral-related stochastic processes (spatial structure predictors) to explain tree community patterns (species composition and abundance) is comparable between sites with similar heterogeneous terrain but facing opposite geographic orientation. We also wanted to determine if assessing the combined data from both sites (greater local-scale evaluation) would yield comparable roles to the ones detected for each site independently (smaller local-scale evaluation). We hypothesized that the role of niche-related processes are altogether more important than the role of neutral-related processes for local tropical tree community assembly in areas with heterogeneous terrain; however, the scale of observation can affect our perception of these roles**.** Therefore, we expected that environmental conditions would be more important than the spatial structure regardless of the evaluated data (each site or combining the sites) and that the contribution of niche- and neutral-related processes would be similar for each site independently but not when sites are combined.

Materials and methods

Study area

We conducted investigations on the continental island of Marambaia (henceforth, Marambaia) in Rio de Janeiro

State, Brazil (Fig. 1, 23°4'26"S 43°58'25"W). This island is covered by Atlantic Forest and located within the Serra do Mar mountain range region known for its high levels of plant diversity and endemism (Murray-Smith *et al.* 2009). The Atlantic Forest covers about 22 km^2 of this continental island and is classified as dense sub-montane ombrophilous forest (IBGE 2012). Mean annual precipitation is 1240 mm and the average temperature over the year varies from 20.9 °C to 26.9 °C (Menezes *et al.* 2005). The origin of Marambaia is associated with geological evolution of the Serra do Mar mountain range; soils here cover the same crystalline gneiss parent material that underlies the Atlantic Forest across this mountain range (Almeida & Carneiro 1998; Menezes *et al.* 2005). Although Marambaia ranges over less altitude (0 to 641 m) than continental sections of Serra do Mar, it is marked by the typical heterogeneous terrain displayed by this mountain range (Nettesheim *et al.* 2015). The heterogeneous topography of Marambaia is characterized by a main ridge stretching across its mountainous terrain (Fig. 1).

Data collection

We recorded tree community data from January 2004 to December 2005 at two distinct sites (faces) of the mountainous Marambaia terrain (Fig. 1). These two sites have similar environmental conditions; Site A does not face the open sea and is mainly oriented in a northwest direction (henceforth, dataset A), while site B faces the open sea and is mainly oriented in a southeast direction (henceforth, dataset B). We further combined dataset A and dataset B into a single dataset (henceforth, dataset A-B) which therefore represents greater local-scale evaluation than either dataset alone and encompassed a wider range of environmental conditions.

We used 50 m × 2 m sample plots. We established 20 (100 m^2) plots at site A (0.2 ha) and 20 plots at site B (0.2 ha), for a total of 40 plots (4000 m^2 or 0.4 ha) representing the island (Fig. 1). The plots were established during randomized walks based on accessibility and representation of vegetation and topographic variation on each side of the main ridge. After reaching a location for a given plot we tossed a six-sided die to determine the direction of establishment of the longest side of the plot (in a circle – number obtained in dice multiplied by 60 degrees). We used a GPSMAP Garmin® 76CSx (Garmin International Inc., Kansas City, USA) to keep plot centers at least 50 m apart from each other. Inside the plots we recorded data on the identity and number of all tree species with trunk diameter of at least 5 cm at breast height (diameter at breast height – dbh ≥ 5 cm), along with topography, soil, litter and spatial structure (geographic location) predictors.

We recorded elevation above sea level (Elev), terrain slope angle (Slp) and annual amount of direct solar radiation (SoR) as topography (environmental) predictors. We used GPS to obtain Elev and a Geographic Information System (GIS) technique relying on a 1 arc second (~30 m resolution) raster image (South American Datum 1969 / UTM – 23S – coordinates) of the area (Valeriano & Rossetti 2011) to obtain Slp and SoR values for each plot (based on geographic location). We sampled and determined a total of 18 soil and litter (environmental) predictors (Tab. 1) within each plot (see detailed description of methodology in Nettesheim *et al.* 2015).

We first approached the spatial structure of the data based on each plot center coordinate (Longitude - X and Latitude – Y; Legendre & Legendre 2012). However, this is a rougher type of spatial structure mostly appropriate to detect linear spatial trends (henceforth linear spatial

Table 1. Soil and litter predictors measured in each plot. The table shows the method used to quantify each soil and litter predictors. Acronyms used to identify each of the recorded predictors in the analyses are also shown (for linear and quadratic forms).

Soil and litter factors	Method of quantification / extraction	Linear factors acronyms	Quadratic factors acronyms
pH	1 : 2.5 soil : H_2O suspension	pH_{soil}	pH_{soil}^2
Organic Carbon	walkley and black method	C_{soil}	C_{soil}^2
Nitrogen	semi-micro kjedahl method	N_{soil}	N_{soil}^2
Phophorus	solution: H_2SO_4 0.0125 mol L^{-1} + HCl 0.05ml L^{-1}	P_{soil}	P_{soil}^2
Potassium	solution: H_2SO_4 0.0125 mol L^{-1} + HCl 0.05ml L^{-1}	K_{soil}	K_{soil}^2
Sodium	solution: H_2SO_4 0.0125 mol L^{-1} + HCl 0.05ml L^{-1}	Na_{soil}	Na_{soil}^2
Extractable acidity	solution: 0.5 mol L^{-1} calcium acetate at pH of 7	$H+Al_{soil}$	$H+Al_{soil}^2$
Calcium (Ca^{2+})	solution: 1 mol L^{-1} KCl	Ca_{soil}	Ca_{soil}^2
Magnesium (Mg^{2+})	solution: 1 mol L^{-1} KCl	Mg_{soil}	Mg_{soil}^2
Aluminum (Al^{3+})	solution: 1 mol L^{-1} KCl	Al_{soil}	Al_{soil}^2
Sand (%)	pipette method	$sand_{soil}$	$sand_{soil}^2$
Clay (%)	pipette method	$clay_{soil}$	$clay_{soil}^2$
Silt (%)	pipette method	$silt_{soil}$	$silt_{soil}^2$
Nitrogen in litter	sulfuric digestion, semi-micro kjeldahl method	N_{litter}	N_{litter}^2
Potassium in litter	sulfuric digestion, flame photometry	K_{litter}	K_{litter}^2
Calcium in litter	sulfuric digestion, atomic absorption spectrometry	Ca_{litter}	Ca_{litter}^2
Phosphorus in litter	sulfuric digestion, colorimetric method	P_{litter}	P_{litter}^2
Magnesium in litter	sulfuric digestion, atomic absorption spectrometry	Mg_{litter}	Mg_{litter}^2

structure). It does not allow modeling more refined patterns that can arise due to stochastic effects (*e.g.* patchy spatial structures). Thus, we centered the linear spatial structure (X and Y) and synthesized a set of refined (distance-based Moran Eigenvector Map; henceforth, dbMEM) spatial structure predictors (Legendre & Legendre 2012). We synthesized dbMEMs independently for dataset A, dataset B and dataset A-B and only kept dbMEMs with positive Moran´s *I* (Moran´s *I* greater than expected Moran´s *I*).

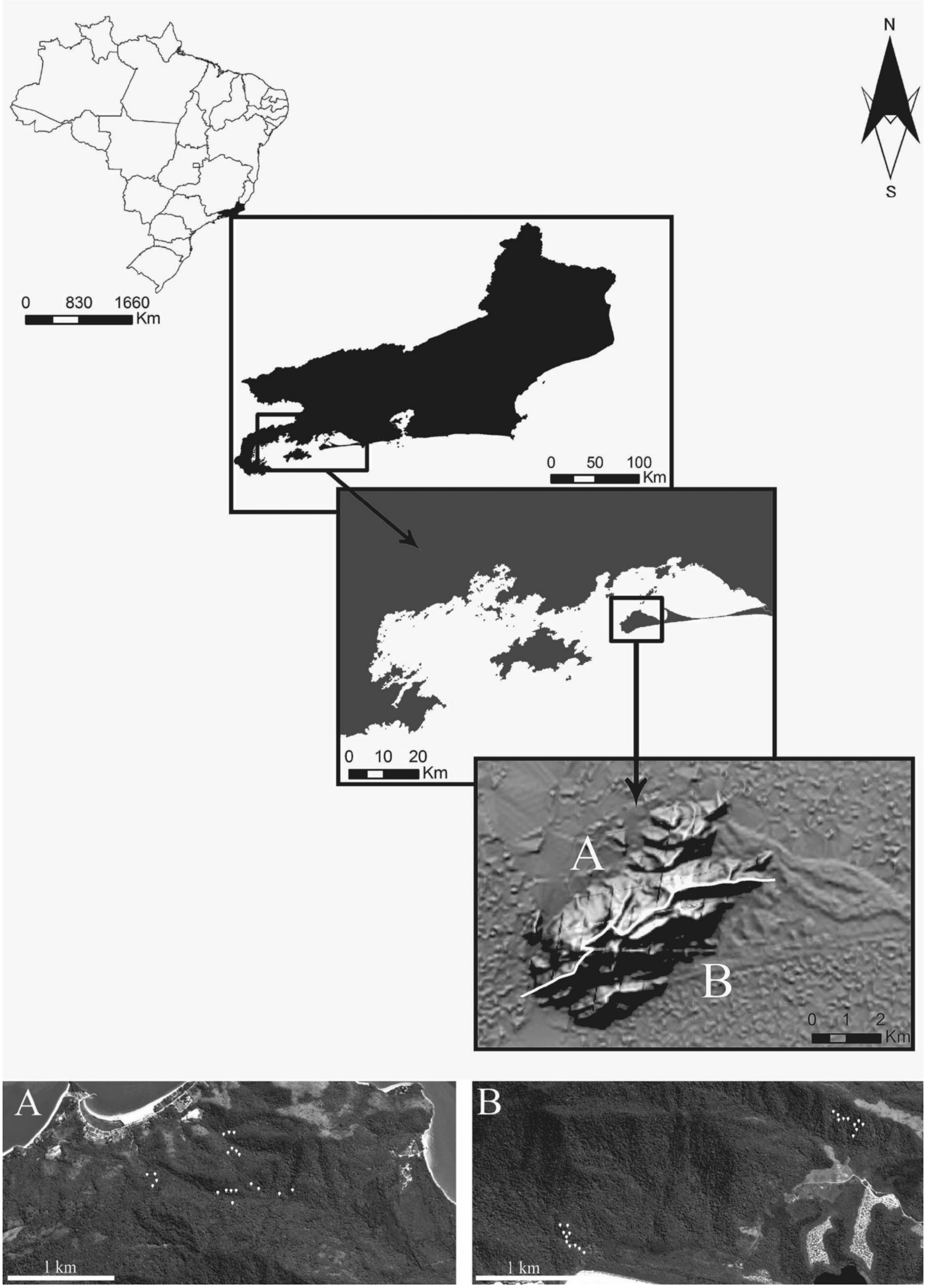

Figure 1. The study area (continental island of Marambaia – 23°4'26"S 43°58'25"W) is located in Brazil. Detailed maps show the location of the island in the state of Rio de Janeiro. The refined terrain image shows the heterogeneous terrain at the island and sites A and B (separated by a white line). The lower images show the location of the plots at sites A and B.

Data analysis

We began analysis by calculating the quadratic form of each recorded environmental predictor to allow modeling unimodal associations. We did this because all the recorded raw topography, soil and litter predictors are appropriate to model linear associations with the response data, but they are poor in deducing unimodal trends (Jones *et al*. 2008). We used orthogonal second order polynomials to expand all raw linear environmental predictors into their quadratic forms. Final set of quadratic soil and litter predictors can be seen in Table 1; these also include $Elev^2$, Slp^2, SoR^2 (not shown in Tab. 1).

We then organized the tree community, topography, soil and litter data into the following data matrices (independently for dataset A, dataset B and dataset A-B): community response matrix (species abundance – absolute number of marked individuals – in each plot); environmental (E) explanatory matrix (raw – linear – and quadratic topography, soil and litter predictors in each plot); linear spatial structure (S_L) explanatory matrix (X and Y geographic coordinates of each plot); and refined spatial structure (S_R) explanatory matrix (positive dbMEM predictors for each plot). We excluded all species that occurred in less than five plots from the community response matrices; all subsequent analyses rely on parametric regressions that should, ideally, be estimated with at least five data points for each response variable – species. A lower cut threshold could lead to biased results due to a greater chance of skewed data points. Additionally, the adopted cut ensures greater focus on the main dominant species and trends of the community and their association with the environment (see Wagner 2003 and Garbin *et al*. 2012 for similar procedures in this regard). We used the Hellinger transformation for all community response matrices (Legendre & Legendre 2012).

Before running independent transformation based Redundancy Analysis (tbRDA) and variation partitioning for datasets A, B and A-B, we performed a variable selection of environmental and spatial structure (linear and refined) predictors independently for each dataset. The selection of environmental factors initially consisted of detecting high collinearity ($r > 0.7$) among all chosen environmental factors (multicollinearity should be avoided before performing automated variable selection procedures; Legendre & Legendre 2012; Dormann *et al*. 2013). We discarded highly correlated predictors (one at a time) based on relevance to explain tree variation in the study area; and continued dropping environmental predictors until there were no more correlations (r) > 0.7 and the Variation Inflation Factor of remaining predictors was smaller than 5. We finished the selection routine of environmental predictors by running a forward selection procedure using the remaining set of predictors and relying on the two stopping rules suggested by Blanchet *et al.* (2008). Variable selection of linear and refined spatial structure factors for datasets A, B and A-B relied only on forward selection because spatial factors are orthogonal to each other.

Finally, we ran complete and partial tbRDAs (Legendre & Legendre 2012) which allowed us to perform variation partitioning to quantify the effects of pure, combined, and shared contributions of environment (E), linear (S_L) and refined (S_R) spatial structures to explain tree community patterns for each dataset (see Økland 2003 and Legendre & Legendre 2012 for detailed descriptions of variation partitioning for multivariate data). Reported fractions of explained variance represent adjusted fractions of variation (Peres-Neto *et al*. 2006). We tested the significance of the models with randomization procedures based on 9999 iterations (Legendre & Legendre 2012); we interpreted contribution of model fractions if the complete model was significant. We carried out all analyses in the R 3.2.1 environment (R Foundation for Statistical Computing, Vienna, AT) with functions from the packages vegan, packfor and spacemakeR.

Results

The final factors in the tbRDA to explain tree community patterns for dataset A were N_{soil}, $H+Al_{soil}$, Mg_{litter}, Ca^2_{soil}, $pH2_{soil}$, Slp^2, Y and dbMEM1_A; for dataset B were N_{soil}, Al_{soil}, C^2_{soil}, Mg^2_{soil}, X and dbMEM1_B; and for dataset A-B were $H+Al_{soil}$, SoR, C_{soil}, Elev, N_{litter}, Ca^2_{soil}, Y, X, dbMEM2 and dbMEM1_AB (see Tab. 1 for acronyms). All three models yielded statistically significant relationships and achieved adjusted coefficients of variation between 0.189 and 0.309 (Tab. 2).

Table 2. Results of the variation partitioning routine relying on transformation based Redundancy Analyses to explain tree community patterns. Fractions are shown for each examined dataset (dataset A, dataset B, and dataset A-B). TVE: total variation explained; E: contribution of environmental predictors; SL: contribution of linear spatial structure predictors; SR: contribution of refined spatial structure predictors; ∩: shared contribution; UV: unexplained variation; R^2_a: corrected proportions of explained variation; %TVE: percentage of contribution from fractions relative to the total variation explained by the model. Negative fractions are interpreted as zeroes. Significance was determined for each of the three complete models by obtaining the probability that an equal or better model would be encountered at random: $P \leq 0.05^*$, $P \leq 0.01^{**}$, $P \leq 0.001^{***}$.

Fraction	dataset A		dataset B		dataset A-B	
	R^2_a	% TVE	R^2_a	% TVE	R^2_a	% TVE
TVE	0.189**	100	0.309**	100	0.218**	100
pure E	0.113	59.8	0.227	73.5	0.059	27.1
pure SL	- 0.016	- 8.5	0.012	3.9	- 0.006	- 2.7
pure SR	0.002	1.1	0.002	0.6	- 0.003	- 1.4
SL ∩ E	0.029	15.3	- 0.028	-9.1	0.056	25.7
SL ∩ SR	0.037	19.6	0.005	1.6	0.028	12.8
E ∩ SR	0.015	7.9	- 0.024	-7.8	0.018	8.3
E ∩ SL ∩ SR	0.009	4.8	0.115	37.2	0.066	30.3
UV	0.857	–	0.691	–	0.782	–

Pure environment was responsible for the greater proportion of explained variation relative to pure linear and pure refined spatial structures in all three models. We did not detect contributions from pure linear and pure refined spatial structures for datasets A and A-B, but they were present (albeit low) for dataset B. The contribution of spatially structured environmental fractions (shared contribution between environment and spatial structure) was present in all three models. The pure environmental fraction was more important than the spatially structured environmental fractions in datasets A and B, but not in dataset A-B. The contribution of shared effects between linear and refined spatial structures ($S_L \cap S_R$) was much higher than from the pure spatial structure fractions in datasets A and A-B; in dataset B it was quite small. These results are detailed in Table 2.

A comparison of overall patterns based on the percentage of variation explained by fractions relative to the total variation explained in each model (Tab. 2) allowed detecting consistent trends in the contribution of niche-related environmental effects and neutral-related spatial structure effects for the three datasets (Tab. 3). The contribution of pure environmental fraction in dataset A-B was, at most, half that was found in dataset A or dataset B (first entry of Tab. 3). Conversely, when all spatially structured environmental fractions are considered together, the contribution of environment-related effects was at least two times greater in dataset A-B than in datasets A or B (second entry of Tab. 3). Following this line of reasoning, if we combine spatially structured environmental fractions with the pure environmental fraction (assuming both represent niche-related effects), niche-related effects remain rather constant among all three models (third entry of Tab. 3). Contribution of neutral-related spatial structure effects also remained constant among the datasets when considering only the pure spatial structure fractions or all the spatial structures together (respectively fourth and sixth entries of Tab. 3). Finally, all ratios between the contribution of niche-related environmental effects and neutral-related spatial structure effects showed that the former are more important than the latter regardless of how the fractions are combined (last three entries of Tab. 3).

Discussion

In this study we corroborate that niche-related environmental conditions (topography, soil and litter) play an overall greater role than neutral-related spatial structure to explain local-scale tropical tree community patterns at two sites with opposite geographic orientation. We also show evidence that the contribution from pure environmental and spatially structured environmental fractions to explain that these tree community patterns can change according to the range of environmental heterogeneity encompassed in the scale of an established sampling design. It should be noted that although our models captured a relatively small amount of response data variation (large residuals), this is normal when modelling tropical vegetation data and does not weaken or diminish the importance of the detected relationships (Braak 1988; Oliveira-Filho & Fontes 2000; Jones *et al.* 2011; Bergamin *et al.* 2012; Legendre & Legendre 2012; Rezende *et al.* 2015; Saiter *et al.* 2015; Arellano *et al.* 2016). Additionally, while some studies interpret the residuals (unexplained variation) of their variation partitioning models as a result of stochastic processes (see Liu *et al.* 2013; Punchi-Manage *et al.* 2014), we chose to focus solely on that part of the variation explained by the models. Thus, we treated the residuals of our models simply as random variation, sampling error, etc., and avoided providing them with an ecological interpretation (Legendre & Legendre 2012).

Our findings of a greater role for niche- relative to neutral-related predictors are similar to those of other studies carried out at several other Atlantic and Amazonian forest sites (Svenning *et al.* 2004; Jones *et al.* 2011; Bergamin *et al.* 2012; Eisenlohr *et al.* 2013; Pansonato *et al.* 2013;

Table 3. Contribution of different sources of variation to explain tree community patterns for dataset A, dataset B and dataset A-B. Sources of variation are based on pooling together contribution of fractions determined with the variation partitioning routine (Tab. 2). Values represent the percentage of variation explained relative to the total variation explained by the complete model (Tab. 2) of each dataset. Negative values are interpreted as zeros.

Source of variation	Fractions pooled together	dataset A	dataset B	dataset A-B
Pure Environment	“pure E”	59.8	73.5	27.1
Spatially Structured Environment	“$E \cap S_L$” + “$E \cap S_R$” + “$E \cap S_L \cap S_R$”	28	20.3	64.3
All environmental fractions	“pure E” + “$E \cap S_L$” + “$E \cap S_R$” + “$E \cap S_L \cap S_R$”	87.8	93.8	91.4
Pure Spatial Structures (Linear and Refined)	“pure S_L” + “pure S_R”	-7.4	4.5	- 4.1
Shared spatial fractions (Linear and Refined)	“$S_R \cap S_L$”	19.6	1.6	12.8
All Spatial Structures	“pure S_L”+ “pure S_R” + “$S_R \cap S_L$”	12.2	6.1	8.7
Ratio Pure Environment : Pure Spatial Structures (Linear and Refined)	“pure E” : “pure S_L” + “pure S_R”	59.8:0	16.3:1	27.1:0
Ratio Pure Environment : Spatial Structure (pure and shared fractions)	“pure E” : “pure S_L” + “pure S_R” + “$S_R \cap S_L$”	4.9:1	12:1	3.1:1
Ratio Environment (pure and shared fractions) : Spatial Structure (pure and shared fractions)	“E” + “$E \cap S_L$” + “$E \cap S_R$” + “$E \cap S_L \cap S_R$” : “S_L” + “S_R” + “$S_R \cap S_L$”	7.2:1	15.4:1	10.5:1

Oliveira-Filho *et al*. 2015; Rezende *et al*. 2015; Saiter *et al*. 2015; Nettesheim *et al*. 2018). These studies confirm the notion that changes in environmental conditions determine habitat filters, which lead important roles in allowing a high number of species to (apparently) thrive in tropical forests (Jones *et al.* 2011; Baldeck *et al.* 2012; Arellano *et al.* 2016). In agreement, our results showed that areas with heterogeneous terrain seem to maximize the influence of environmental conditions (filters) on tropical tree communities. Such areas may exhibit higher levels of heterogeneous environmental conditions that can be decisive in providing habitats relevant to tree species establishment and development. Detection of quadratic environmental effects in all three studied datasets further suggest that heterogeneous terrain exhibits conditions where species response can be better modelled when non-linear relationships are taken into account. This also indicates that at least part of tropical tree community assembly in areas with rough terrain is affected by optimal resource availability. Therefore, it seems reasonable to expect a greater role of niche-related processes (environmental filtering) over topical community assembly as the terrain of areas become increasingly heterogeneous (*e.g.* higher elevations; see Nettesheim *et al*. 2018).

Contribution of fractions varied between the datasets to explain tree community patterns. Studies in the Amazon region showed that the extent of environmental gradients can play a central role in determining which factors are important in explaining tree community assembly (Costa *et al.* 2009; Pansonato *et al.* 2013). However, our evaluation revealed an interesting trend in the pattern of fraction contributions that can further elucidate our understanding of how environmental gradients affect community assembly. When we pooled together fractions that represent pure environment and spatially structured environment the contribution of environmental-related fractions was high and similar in all three datasets (Tab. 3). However, when these fractions are considered apart (Tab. 3) one may observe an exchange in the overall pattern of contribution between pure environment and spatially structured environment when comparing either dataset A or dataset B with dataset A-B. There is an obvious decrease in the contribution of pure environment with a simultaneous increase in the contribution of spatially structured environment between datasets A or B and dataset A-B. This is likely because dataset A-B encompasses all the heterogeneous environmental conditions existing within the rough terrain of the study area, while dataset A (as well as dataset B) represents only part of this terrain and its heterogeneous environmental conditions. Consequently, the greater influence of spatially structured environmental conditions that ultimately affect tree community patterns could only be detected when evaluating the whole terrain of the study area (dataset A-B). Thus, researchers should be aware that the amount of environmental heterogeneity captured when establishing a sampling design in a given study area (especially on rough heterogeneous terrain) can affect the way processes behind community assembly are perceived.

Our findings also shed light on how to interpret the spatially structured environmental fractions of models from areas with heterogeneous terrain. Shared fractions of explained variation between environment and spatial structure are problematic in variation partitioning because they can either represent niche-related effects mediated by environmental conditions that are spatially structured or neutral-related stochastic effects confounded with environmental gradients (Legendre & Legendre 2012; Arellano *et al.* 2016). However, the fact that only the pure environmental and spatially structured environmental fractions varied interchangeably while the pure and shared spatially structured fractions remained low and constant strikes as evidence that the spatially structured environmental fraction for the study area can be interpreted as niche-related effects. This is not to say that all shared fractions of explanation between environment and space in variation partitioning models should be inferred as niche-related effects. However, given the conspicuous terrain changes within small distances typically associated with mountainous areas it seems fairly reasonable that studies in tropical areas with heterogeneous terrain assume the relevance of spatially structured environmental fractions as effects of niche-based processes over community assembly.

The absence or weak signal from pure spatial structure fractions within all three models suggest that neutral-related processes such as dispersal seem to play a negligible role over tree community patterns at the study area. However, studies in tropical forests commonly show that pure spatial structure fractions can be important to explain plant community assembly (Svenning *et al.* 2004; Eisenlohr *et al.* 2013; Punchi-Manage *et al.* 2014). The unusual reduced contribution of pure spatial structure effects detected here is explained by the fact that signs of neutral-related effects were mostly represented in the shared fraction between linear and refined spatial structures. Although these spatial structure effects may arguably represent environmental conditions not considered in the models (Gilbert & Bennet 2010; Diniz-Filho *et al.* 2012; Legendre & Legendre 2012), their small contributions and the extensive set of (linear and quadratic) environmental predictors used here, provides reasonable assurance to interpret them as a signal of neutral-related processes. This shared fraction between linear and refined spatial structure indicates that (at least) some tree species in the area seem to form linearly distributed patches independent from the environment, likely due to stochastic effects (*e.g.* dispersal limitation). Moreover, the detection of small neutral-related effects may also be a consequence of sampling design. Other studies that relied on plots randomly distributed within their study area also detected smaller contributions from pure spatial structure fractions and higher participation from environmental fractions (Bergamin *et al.* 2012; Eisenlohr *et al.* 2013; Arellano *et al.* 2016). On the other hand, studies that used systematic sampling design (*e.g.* regular grid) found results in the opposite direction; *e.g.* higher proportions of spatial structure fractions (Jones *et al.* 2011; Baldeck *et al.* 2012; Punchi-Manage *et al.* 2014). This indicates a potential bias in the results of variation partitioning that can be attributed to the sampling design. Although the (small; particularly the shared) spatial structure fractions support that neutral-related effects hold (at least) a discrete role in local community assembly across heterogeneous terrain, this issue requires further evaluation using regular sampling designs.

The increased relevance of environmental conditions regardless of the evaluated dataset corroborates that topography, soil and litter represent important resources for the plant community in areas with heterogeneous terrain. This is in general agreement with the reported relevance of topography and soil predictors in explaining plant community assembly and in distribution models of tree species in tropical forests (Tuomisto *et al.* 2003; John *et al.* 2007; Baldeck *et al.* 2012; Eisenlohr *et al.* 2013). On the other hand, this result calls attention to the role that litter chemistry can play in community assembly; representing information which is seldom used in community ecology but proved important for two out of the three current final models. Perhaps, litter predictors are left aside because most nutrients found in this ecosystem component are expected to be lost before being used by plants (Huggett 2007). Nevertheless, findings here suggest that the litter may hold relevant environmental information, which is not usually considered, and can be confounded with the pure spatial fractions. The extent to which litter has similar or greater relevance than soil and topography as explanatory variable for community assembly remains to be determined. These findings support that tropical forests on dissected mountainous landscapes can encompass a broad range of small local-scale niches associated with a heterogeneous terrain that affects independent soil and litter habitat compartments (Baldeck *et al.* 2012).

Altogether, our evidence corroborates that tropical tree communities distributed across areas with heterogeneous terrain can be expected to lay much closer to the niche end of the niche-neutral continuum. The assessed tree community responded more strongly to the variation of environmental conditions associated with the terrain than to spatial structures associated to stochastic processes. Even though the overall contribution of environmental conditions did not differ between the examined datasets as expected, the independent fractions of pure and spatially structured environment did, suggesting that the amount of environmental heterogeneity embedded in the terrain of a study area (and scale of evaluation) can affect the way we perceive processes governing community assembly. These findings highlight the fact that tropical forests thriving on heterogeneous mountainous terrain are unique research models which can increase our understanding of community assembly processes and species distributions. In this regard, future studies may yield interesting results by addressing how environmental and spatial structure predictors behave to explain plant community assembly across gradients of increasing terrain and environmental heterogeneity.

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References

Almeida FFM, Carneiro CR. 1998. Origem e evolução da Serra do Mar. Revista Brasileira de Geociências 282: 1-20.

Arellano G, Tello JS, Jorgensen PM, *et al.* 2016. Disentangling environmental and spatial processes of community assembly in tropical forests from local to regional scales. Oikos 125: 326-335.

Baldeck CA, Harms KE, Joseph B, *et al.* 2012. Soil resources and topography shape local tree community structure in tropical forests. Proceedings of the Royal Society of London B 280: 20122532. doi: 10.1098/rspb.2012.2532

Bergamin RS, Müller S, Mello RSP. 2012. Indicator species and floristic patterns in different forest formations in southern Atlantic rainforests of Brazil. Community Ecology 13: 162-170.

Blanchet FG, Legendre P, Borcard D. 2008. Forward selection of explanatory variables. Ecology 89: 2623-2632.

Braak CJF. 1988. CANOCO - A FORTRAN program for canonical community ordination by (partial) (detrended) (canonical) correspondence analysis, principal components analysis, and redundancy analysis, version 2.1. Technical report LWA-88-02. Wageningen, TNO-Institute of Applied Computer Science.

Chang LW, Zeleny D, Li CF, Chiu ST, Hsieh CF. 2013. Better environmental data may reverse conclusions about niche- and dispersal-based processes in community assembly. Ecology. 94: 2145-2151.

Chase JM, Leibold MA. 2003. Ecological niches: linking classical and contemporary approaches. 1st. edn. Chicago, The University of Chicago Press.

Chave J. 2008. Spatial variation in tree species composition across tropical florests: pattern and process. In: Carson WP, Schnitzer SA. (eds.) Tropical Forest Community Ecology. New Jersey, Wiley-Blackwell. p. 11-30.

Cielo-Filho R, Martins FR. 2015. Detection of fine scale niche assembly in a tropical forest through analysis of indirect environmental variables. Flora 215: 60-66.

Clark JS. 2012. The coherence problem with the Unified Theory of Biodiversity. Trends in Ecology and Evolution 27: 198-202.

Costa FRC, Guillaumet JL, Lima AP, Pereira OS. 2009. Gradients within gradients: the mesoscale distribution patterns of palms in a central Amazonian forest. Journal of Vegetation Science 20: 69-78.

Diniz-Filho JA, Siqueira T, Padial AA, Rangel TF, Landeiro VL, Bini LMB. 2012. Spatial autocorrelation analysis allows disentangling the balance between neutral and niche processes in metacommunities. Oikos 121: 201-210.

Dormann CF, Elith J, Bacher S, *et al*. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36: 027-046.

Dray S, Pélissier R, Couteron P, *et al*. 2012. Community ecology in the age of multivariate multiscale spatial analysis. Ecological Monographs 82: 257-275.

Eisenlohr PV, Alves LF, Bernacci LC, *et al*. 2013. Disturbances, elevation, topography and spatial proximity drive vegetation patterns along an altitudinal gradient of a top biodiversity hotspot. Biodiversity and Conservation 22: 2767-2783.

Etienne RS, Alonso D. 2007. Neutral community theory: how stochasticity and dispersal-limitation can explain species coexistence. Journal of Statistical Physics 128: 485-510.

Garbin ML, Carrijo TT, Sansevero JBB, Sánchez-Tapia A, Scarano FR. 2012. Subordinate, not dominant, woody species promote the diversity of climbing plants. Perspectives in Plant Ecology, Evolution and Systematics 14: 257-265.

Gilbert B, Bennett JR. 2010. Partitioning variation in ecological communities: do the numbers add up? Journal of Applied Ecology 47: 1071-1082.

Gravel D, Canham CD, Beaudet M, Messie RC. 2006. Reconciling niche and neutrality: the continuum hypothesis. Ecology Letters 9: 399-409.

Grimme JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. American Naturalist 111: 1169-1194.

Hofer G, Wagner HH, Herzog F, Edwards PJ. 2008. Effects of topographic variability on the scaling of plant species richness in gradient dominated landscapes. Ecography 31: 131-139.

Hubbell SP. 2001. The unified neutral theory of biodiversity and biogeography. 1st. edn. New Jersey, Princeton University Press.

Huggett RJ. 2007. Fundamentals of geomorphology. 2nd. edn. New York, Routledge.

IBGE – Instituto Brasileiro de Geografia e Estatística. 2012. Manual técnico da vegetação brasileira. 1st. edn. Rio de Janeiro, IBGE.

John R, Dalling JW, Harms KE, *et al*. 2007. Soil nutrients influence spatial distributions of tropical tree species. Proceedings of the National Academy of Sciences USA 104: 864-869.

Jones MM, Ferrier S, Condit R, Manion G, Aguillar S, Pérez R. 2013. Strong congruence in tree and fern community turnover in response to soils and climate in central Panama. Journal of Ecology 101: 506-516.

Jones MM, Szyska B, Kessler M. 2011. Microhabitat partitioning promotes plant diversity in a tropical montane forest. Global Ecology and Biogeography 20: 558-569.

Jones MM, Tuomisto H, Borcard D, Legendre P, Clark DB, Olivas PC. 2008. Explaining variation in tropical plant community composition: influence of environmental and spatial data quality. Oecologia 55: 593-604.

Legendre P, Legendre L. 2012. Numerical ecology. 3rd. edn. Amsterdam, Elsevier Science BV.

Leibold MA, Mcpeek MA. 2006. Coexistence of the niche and neutral perspectives in community ecology. Ecology 87: 1399-1410.

Leigh EG. 2007. Neutral theory: a historical perspective. Journal of Evolutionary Biology 20: 2075-2091.

Liu X, Swenson NG, Zhang J, Ma K. 2013. Environment and space, not phylogeny, determine trait dispersion in a subtropical forest. Functional Ecology 27: 264-272.

Menezes LFT, Peixoto AL, Araujo DSD. 2005. História natural da Marambaia. 1st. edn. Seropédica, Editora da Universidade Federal Rural do Rio de Janeiro.

Morley RJ. 2000. Origin and evolution of tropical rainforests. 1st. edn. Chichester, John Wiley and Sons.

Murray-Smith C, Brummitt NA, Oliveira-Filho AT, *et al*. 2009. Plant diversity hotspots in the Atlantic Coastal Forests of Brazil. Conservation Biology 23: 151-163.

Nettesheim FC, Conto T, Pereira MG, Machado DL. 2015. Contribution of topography and incidente solar radiation to variation of soil and plant litter at an area with heterogeneous terrain. Revista Brasileira de Ciência do Solo 39: 750-762.

Nettesheim, FC, Garbin ML, Rajão PHM, Araujo DSD, Grelle CEV. 2018. Environment is more relevant than spatial structure as a driver of regional variation in tropical tree community richness and composition. Plant Ecology and Diversity 11: 27-40.

Økland RH. 2003. Partitioning the variation in a plot-by-species data matrix that is related to n sets of explanatory variables. Jornal of Vegetation Science 14: 693-700.

Oliveira-Filho AT, Budke JC, Jarenkow JA, Eisenlohr PV, Neves DRM. 2015. Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. Journal of Plant Ecology 8: 242-260.

Oliveira-Filho AT, Fontes MAL. 2000. Patterns of floristic differentiation among Atlantic Forest in southeastern Brazil and the influence of climate. Biotropica 32: 793-810.

Pansonato MP, Costa FRC, Castilho CV, Zuquim G. 2013. Spatial scale or amplitude of predictors as determinants of the relative importance of environmental factors to plant community structure. Biotropica 45: 299-307.

Peres-Neto PR, Legendre P, Dray S, Borcard D. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87: 2614-2625.

Punchi-Manage R, Wiegand T, Wiegand K, Getzin G, Gunatilleke CVS, Gunatilleke IAUN. 2014. Effect of spatial processes and topography on structuring species assemblages in a Sri Lankan dipterocarp forest. Ecology 95: 376-386.

Rezende VL, Eisenlohr PV, Vibrans AC, Oliveira-Filho AT. 2015. Humidity, low temperature extremes, and space influence floristic variation across an insightful gradient in the Subtropical Atlantic Forest. Plant Ecology 216: 759-774.

Richter M. 2008. Tropical mountain forests – distribution and general features. In: Gradstein SR, Homeier J, Gansert D. (eds.) The Tropical Mountain Forest – patterns and processes in a biodiversity hotspot. Göttingen, Göttingen Centre for Biodiversity and Ecology. p. 7-24.

Rosindell J, Hubbell SP, He F, Harmon L, Etienne RS. 2012. The case for ecological neutral theory. Trends in Ecology and Evolution 27: 203-208.

Saiter FZ, Eisenlohr PV, Barbosa MRV, Thomas WW, Oliveira-Filho AT. 2015. From evergreen to deciduous tropical forests: how energy-water balance, temperature, and space influence the tree species composition in a high diversity region. Plant Ecology and Diversity 9: 45-54.

SOS Mata Atlântica. 2015. Atlas dos remanescentes florestais da Mata Atlântica; Período 2013-2014. São Paulo, Fundação SOS Mata Atlântica / Instituto Nacional de Pesquisas Espaciais.

Svenning JC, Kinner DA, Stallard RF, Engelbrecht BMJ, Wright SJ. 2004. Ecological determinism in plant community structure across a tropical forest landscape. Ecology 85: 2526-2538.

Tilman D. 1982. Resource competition and community structure. Princeton, Princeton University Press.

Tilman D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. Proceedings of the National Academy of Sciences USA 101: 10854-10861.

Tuomisto H, Poulsen AD, Ruokolainen K, *et al*. 2003. Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. Ecological Applications 13: 352-371.

Valeriano MM, Rossetti DF. 2011. Topodata: Brazilian full coverage refinement of SRTM data. Applied Geography 32: 300-309.

Wagner HH. 2003. Spatial covariance in plant communities: integrating ordination, geostatistics, and variance testing. Ecology 84: 1045-1057.