ORIGINAL PAPER

Disturbances, elevation, topography and spatial proximity drive vegetation patterns along an altitudinal gradient of a top biodiversity hotspot

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Abstract The correlation between vegetation patterns (species distribution and richness) and altitudinal variation has been widely reported for tropical forests, thereby providing theoretical basis for biodiversity conservation. However, this relationship may have been oversimplified, as many other factors may influence vegetation patterns, such as disturbances, topography and geographic distance. Considering these other factors, our primary question was: is there a vegetation pattern associated with substantial altitudinal variation (10–1,093 m a.s.l.) in the Atlantic Rainforest—a top hotspot for biodiversity conservation—and, if so, what are the main factors driving this pattern? We addressed this question by sampling 11 1-ha plots, applying multivariate methods, correlations and variance partitioning. The *Restinga* (forest on sandbanks along the coastal plains of Brazil) and a lowland area that was selectively logged 40 years ago were floristically isolated from the other plots. The maximum species richness (>200 spp. per hectare) occurred at

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approximately 350 m a.s.l. (submontane forest). Gaps, multiple stemmed trees, average elevation and the standard deviation of the slope significantly affected the vegetation pattern. Spatial proximity also influenced the vegetation pattern as a structuring environmental variable or via dispersal constraints. Our results clarify, for the first time, the key variables that drive species distribution and richness across a large altitudinal range within the Atlantic Rainforest.

Keywords Atlantic Rainforest · Conservation hotspot · Multivariate analysis · Species distribution · Species richness

Introduction

The investigation of vegetation patterns has been recognized as a crucial step in providing theoretical basis for biodiversity conservation (e.g., Ivanauskas et al. 2006; Marques et al. 2011). One of the most widely reported type of vegetation patterns for tropical forests is the variation in species distribution and richness along elevational gradients (Austin and Greig-Smith 1968; Beals 1969; Gentry 1988; Rodrigues and Shepherd 1992; Auerbach and Shmida 1993; Rahbek 1995; Lieberman et al. 1996; Vázquez and Givnish 1998; Oliveira-Filho and Fontes 2000; Zhao et al. 2005; Sanchez et al. 2013). However, it is unlikely that studies on this subject have found a realistic model because species distributions and richness can be influenced by other factors, such as the geographic distance between locations (e.g., Hubbell 2001; Diniz-Filho et al. 2012), disturbances of human or natural origin (e.g., Connell 1978; Vázquez and Givnish 1998; Laurance 2001; Pereira et al. 2007) and topography (e.g., Bourgeron 1983; O'Brien et al. 2000; Bohlman et al. 2008). When investigating ecological patterns, controlling or accounting for a set of factors that are potentially important for determining these patterns is essential to obtaining reliable results (Simberloff 1983; Rey Benayas and Scheiner 2002).

The Brazilian Atlantic Rainforest, a top hotspot for biological conservation (Myers et al. 2000; Laurance 2009; Ribeiro et al. 2011), lacks realistic, comprehensive models for understanding local floristic patterns. Despite this problem, several studies have addressed important questions concerning vegetation patterns along elevation gradients. Oliveira-Filho and Fontes (2000) reported that altitude is one of the principal factors influencing floristic differentiation in the Atlantic Forest sensu lato of southeastern Brazil. In an

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analysis of the floristic similarity between rainforest and semi-deciduous forest sites in São Paulo State, Ivanauskas et al. (2000) detected the establishment of certain groups relative to the elevation. Scudeller et al. (2001) found that the distinctions between the provincial and coastal Atlantic plateaus are linked to altitude, precipitation and temperature. Sanchez et al. (2013) found that the Serra do Mar rainforests along the seashore, mountain slopes and highlands differed dramatically in their floras, physiognomies and origins. At the local scale, Rodrigues and Shepherd (1992) and Moreno et al. (2003) also found consistent floristic links relative to altitude. Thus, well-supported relationships between altitude and floristic variations have been reported to the Atlantic Forest.

Our objective was to enhance the existing theoretical support for conservation initiatives for protecting lands in moist tropical forests, considering the existing need for more comprehensive approaches that include a set of potentially relevant predictors for vegetation patterns along altitudinal gradients. Strong particularities and novelties of this study are the thorough documentation of: (1) a broad and standardised sampling effort (11 ha of vegetation in equally sampled plots); (2) sampling conducted along a single conservation unit (Serra do Mar State Park) while minimising environmental factors that might interfere with the investigation; (3) the measurement of variable sets for the few factors that might interfere with the investigation, such as the topography and disturbance history, allowing for a consistent analysis of the vegetation patterns throughout the elevational range.

We addressed the following questions: (1) is there a pattern in the floristic composition associated with the altitudinal variation that we analysed (10–1,093 m) for trees in the Atlantic Rainforest; i.e., do areas having a similar altitude exhibit higher species similarity than those areas that are more distant with respect to altitude? (2) Does the species richness differ from areas of lower altitude to areas of higher altitude? (3) What are the principal factors driving the variation in tree species composition and richness?

Methods

Study area

We studied the Atlantic Rainforest in the Picinguaba and Santa Virginia Research Station of the Serra do Mar State Park, near Ubatuba and São Luis do Paraitinga municipalities in São Paulo State, southeastern (SE) Brazil (Fig. 1), which covers an elevation range of 1,083 m (10–1,093 m a.s.l.). The coordinates and other data on the areas studied are presented in Table 1; additional data can be found in Alves et al. (2010) and Joly et al. (2012). The climate is tropical (Af according to the Köeppen system), with higher rainfall in summer (Morellato et al. 2000) and without significant rainfall variations along the slope. The topography of the region includes the coastal plain, isolated hills and mountains of the elongated "Morraria" Coast and the inner slopes of the "Serrania" Coast (Ponçano et al. 1981).

The soils are generally low in nutrients, with low fertility and high levels of aluminium. In area "A" (*Restinga* forest), the soil type is classified as Quartzipsamment, whereas in the other areas the soils are Inceptisols (Table 1). Shallow and well-drained soils predominate along the slope, with the exception of the *Restinga* forest. Soils become more aged with elevation, according to "Kr" and "Ki" weathering indices—at the top, there is predominance of oxides (high levels of Al_2O_3). Soil carbon and nitrogen contents increase significantly with altitude. On the other hand, pH does not strongly vary along the elevational gradient (in general <4). The litter production has been higher at lower elevations (8–10 Mg ha^{-1} at plots lower than 100 m a.s.l. and 7 Mg ha^{-1} above 400 m a.s.l.). Those
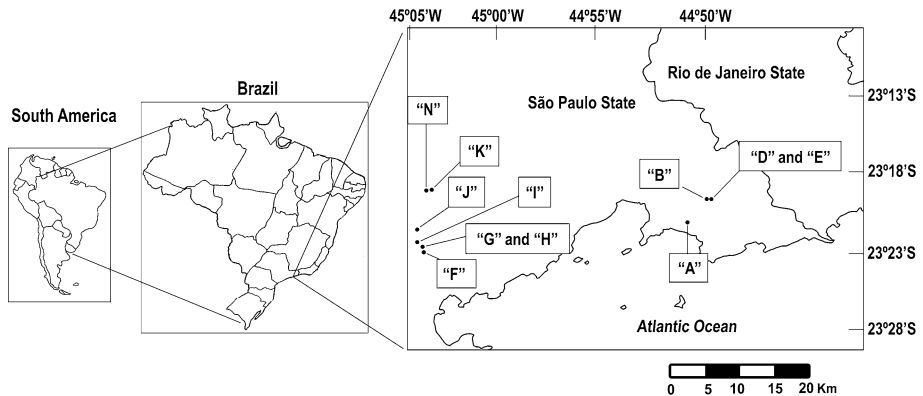
Fig. 1 Locations of the 11 study areas along an altitudinal gradient in the Atlantic Rainforest (SE Brazil). The codes for the localities are presented in Table 1

data were provided by SC Martins (unpublished data), Sousa Neto et al. (2011), Vieira et al. (2011) and Sanchez et al. (2013).

The codes for the localities where the sampling was completed are listed in Table 1 in alphabetical order according to their positions in the landscape. These codes follow those of the "BIOTA Functional Gradient" Project (Joly et al. 2012). It should be noted that the altitudinal belts (Table 1) do not follow the Brazilian classification system for vegetation (IBGE 2012), but rather used an alternative classification based on the field observations of the research team. The relative locations of the 11 1-ha areas are shown in Fig. 1. Area "A" (*Restinga* or Sandy Forest, at approximately sea level) is located where the major local rivers flow into the region. In this area, the soil is exposed to the seasonal water table (César and Monteiro 1995). Areas "B", "D", "E", "F", "G", "H", "I" and "J" are located at increasing altitudes along the slope of the Serra do Mar, whereas areas "K" and "N" are located at the summit (Table 1). According to long-time residents, area "F" was selectively logged ~40 years ago for the tree *Hieronyma alchorneoides* (Phyllanthaceae). A more detailed description of the study area was provided by Joly et al. (2012).

Data collection and preparation of matrices

We measured all individual trees with a diameter equal to or greater than 4.8 cm at 1.30 m above the ground (DBH) in each 1-ha area (100 m × 100 m, a widely used sampling design in tropical forests, thus allowing comparisons with other studies) (Table 1). The sampling protocol was described in detail by Alves et al. (2010) and Joly et al. (2012).

To investigate the patterns of species distribution and variation in species richness, we first constructed three matrices, each of which included the 11 study areas. The first matrix contained data on the numbers of individuals of each species. The second matrix was composed of the following environmental variables (Table 1): topographic variables—aspect, slope and standard deviation of the slope (SD slope is reported in the tables and figures), 3D surface area (SurfArea), average elevation (Elevation) and elevational range (ElevRange); disturbance variables—gaps.area^{-1} (Gaps), basal area of standing dead stems (BAdead) and number of trees with two or more stems (MultStem); and two synthetic climatic variables—annual precipitation (AnnuPrec) and annual mean temperature (AnnMTemp). The units used for each variable are provided in Table 1.

Table 1 Codes and other environmental information for the 11 sampled areas along an altitudinal gradient in the Atlantic Rainforest, SE Brazil

Areas	Forest type	Geographic coordinates (lat, long)	Average elevation (m a.s.l.)	Elevational range (m a.s.l.)	Aspect	Slope (%) ±SD	Multiple stemmed trees	Total gaps. area^{-1} (m^2)	Basal area of standing dead stems (m^2)	Annual rainfall (mm)	Annual mean temperature (°C)
"A"	*Restinga*	23°21′21″S, 44°51′04″W	10	1	−0.956	1.10 ± 0.7	117	2,662	0.40	2,406	22.60
"B"	Lowland Forest	23°20′14″S, 44°50′06″W	46	23	−1.000	14.7 ± 5.8	69	2,700	0.44	2,406	22.60
"D"	Lowland Forest	23°20′08″S, 44°50′00″W	57	26	−0.807	12.6 ± 5.5	65	3,526	0.89	2,324	22.25
"E"	Lowland Forest	23°20′04″S, 44°49′57″W	73	25	−0.876	11.1 ± 4.8	75	2,774	1.03	2,324	22.25
"F"	Lowland Forest	23°22′53″S, 45°04′46″W	105	28	−0.956	11.9 ± 6.8	184	4,770	1.12	2,582	21.90
"G"	Submontane Forest	23°22′26″S, 45°04′51″W	188	22	−0.987	12.2 ± 4.6	46	1,970	1.95	1,975	18.31
"H"	Submontane Forest	23°22′25″S, 45°04′55″W	208	16	−0.988	9.20 ± 3.5	56	3,245	1.73	1,975	18.31
"I"	Submontane Forest	23°22′01″S, 45°05′01″W	350	48	−0.852	27.3 ± 6.3	48	1,627	0.83	1,865	17.46
"J"	Submontane Forest	23°21′58″S, 45°05′03″W	375	46	−1.000	25.5 ± 8.0	31	1,749	2.11	1,865	17.46
"K"	Montane Forest	23°19′32″S, 45°04′05″W	1,066	47	0.850	25.5 ± 8.3	44	2,314	3.16	1,724	16.28
"N"	Montane Forest	23°19′36″S, 45°04′32″W	1,025	34	0.787	15.8 ± 5.4	64	3,860	3.14	1,724	16.28

Other data are reported by Alves et al. (2010) and Joly et al. (2012). Altitudinal belts (see :"Forest type" column) do not follow the Brazilian classification system for vegetation (IBGE 2012), but rather used an alternative classification based on the field observations of the BIOTA research team

SD standard deviation

To acquire data on the topographic variables, we first used the elevation information from each 10×10 m corner point determined in the field using high-precision equipment (a total station) to create a digital elevation model (DEM) at a 1-ha scale. The DEM was created using the "topo-to-raster" tool, an interpolation method implemented in ArcGIS to generate DEMs (Hutchinson 1989). This procedure allowed us to store topographic information in a raster format with a high spatial resolution. The new elevation data from the DEM was fitted to probability density functions to extract the expected value (e.g., the mean for a Gaussian distribution) and deviation for each plot. The 3D surface variable was also estimated from the DEM. We estimated gaps.area^{-1} as the surface area directly under a canopy opening, extending to the base of the forest edge, according to the extended gap definition of Runkle (1982). Gaps are relatively small-sized in our Atlantic forest site. The mean gap area varies between 60.4 and 115.2 m^2, and the maximum total gap area per plot was 2,598.9 m^2, corresponding to less than 30 % of the plot area. The climatic variables were extracted from WORLDCLIM (Hijmans et al. 2005). Although some authors do not recommend using WORLDCLIM for climatic interpolation in mountainous areas (Sklenář et al. 2008), to our knowledge, there is no disadvantage in the Atlantic Forests.

Finally, we constructed a coordinate matrix, containing the latitude and longitude of each area, for the purpose of assessing and controlling spatial autocorrelation and performing variance partitioning (below).

Variations in floristic patterns and correlations with predictor variables

To ordinate the 11 areas without interference from any environmental variable, we performed a DCA (Detrended Correspondence Analysis) using PC-ORD 6.0 (McCune and Mefford 2011). We discarded the NMS (Non-Metric Multidimensional Scaling), a widely recommended method (McCune and Grace 2002), following the same reasons that Santos et al. (2012). We removed the 243 singletons because the Chi squared distance used in DCA is sensitive to rare species (McCune and Grace 2002). The DCA was performed using the options "down-weight rare species" and "rescale axes".

We used OLS multiple linear regressions (Quinn and Keough 2002) to analyse the predictability of the environmental variables on the floristic variation summarised by the two principal axes of the DCA. We initially discarded variables with very weak correlations ($r < 0.3$) with the DCA axis and removed colinearities, keeping only the most important variable ($>r$ with the respective DCA axis) in each group of collinear variables. After this procedure, no variables remaining with a variance inflation factor >10 (Quinn and Keough 2002), and we then chose the best model (lowest AICc—Corrected Akaike Information Criterion; Burnham and Anderson 2002). However, we detected a strong outlier in the linear trend of the OLS models, the *Restinga* plot (area "A"). We then opted to present both DCAs (DCA1, with *Restinga*, and DCA2, without *Restinga*), illustrating the overall floristic patterns, while discarding the linear model that included *Restinga*. Further information on the OLS procedure can be found in the Common procedures for all OLS models section below.

Variations in species richness and correlations with predictor variables

To avoid a dependent relationship between the numbers of individuals and species, we estimated the species richness by running an individual-based rarefaction analysis (Gotelli and Colwell 2001) using ECOSIM, version 7.71 (Gotelli and Entsminger 2004). We compared the estimated species richness among sites using the same sampling effort

(numbers of individuals) with 95 % confidence intervals. This level of sampling corresponds to the number of individuals in area "B" (1,082 trees) because this site had the lowest value among the studied areas. The obtained species richness was hereafter treated as the estimated species richness.

Finally, we performed a multiple linear regression analysis (OLS) to investigate whether changes in species richness could be explained by our environmental predictors. The colinearities were removed, as described above, with one exception: although altitude was less correlated with species richness than was basal area of standing dead stems, the effect of removing the multicolinearity was more powerful when we discarded the last variable; therefore, we decided on the altitude. We used the same methods described in the floristic variation section above to select the best model (see also the Common procedures for all OLS models section below).

Common procedures for all OLS models

We followed the general format of the procedures proposed by Eisenlohr (2013) for the aforementioned OLS multiple linear regression models and heeded the caveats identified by this same author. We used correlograms to apply Moran's I coefficient as an indicator of spatial autocorrelation (SAC) using SAM 4.0 (Rangel et al. 2010) to check for possible violations of the assumption of spatial independence in the residuals of both the full and selected OLS models (Diniz-Filho et al. 2003; Diniz-Filho et al. 2008). The number and size of distance classes used the defaults for SAM. The significance of SAC was detected by sequential Bonferroni criteria (Fortin and Dale 2005). When significant SAC in the residuals of the OLS models was detected, we used spatial filters (Moran's Eigenvector Maps—MEMs; Dray et al. 2006), obtained using the "spacemakeR" package in the R environment (The R Foundation for Statistical Computing 2012), as additional predictors. We selected MEMs until we found randomness (non-significant SAC) in the residuals. When we found SAC in the full model (i.e. prior to AICc selection), we used MEMs as fixed variables in the selection (Diniz-Filho et al. 2008).

We confirmed the assumptions of homoscedasticity and linearity by creating graphical displays of the residuals analysis (X: predicted values; Y: residuals), demonstrating an even distribution of the points above and below the zero-residual horizontal line (Quinn and Keough 2002). The normality of the residuals was confirmed by using the Shapiro–Wilk test.

The significance of the linear model was assessed using the F test. The relative influence of each environmental variable on the floristic data was assessed based on partial regression coefficients and t tests. In all of the tests, we used 5 % as the significance level.

Variance partitioning

We also performed variance partitioning using a partial regression analysis to obtain the components that explain the variation in each response variable (ordination axes and species richness) (Legendre and Legendre 2012). The environmental variables were the same as in the respective OLS models, and the spatial variables (MEMs) were forward-selected using the "packfor" package for the R environment. The forward procedure is justified by our requirement to obtain only MEMs that provide significant contributions to the response variables (Bellier et al. 2007). Note that the MEMs selected for variance partitioning were not necessarily the same MEMs chosen for the removal of spatial autocorrelation from the OLS residuals because the objectives were distinctly different.

Axis 1 of the DCA2 did not have any significant spatial variables, and thus, we did not perform a variance partitioning in this case.

Results

Considering the overall sampling from 11 ha of the Atlantic Rainforest in southeastern Brazil, we registered a total of 16,796 trees, 563 species, 195 genera and 68 families (including 'singletons'). A summary of the vegetation data from each area is presented in Table 2, and other details are provided by Joly et al. (2012).

Variations in floristic patterns and correlations with predictor variables

The first axis of DCA1 showed contrast between areas "A" (*Restinga*), "K"+"N" (montane forests) and the other areas (Fig. 2a). Topography (slope and SD slope) and elevational range were the most highly correlated with this axis (Table 3). Considering the strong differences between soils of *Restinga* and other areas, we might infer that the edaphic component was also important in such floristic differentiation. For the second axis, areas "F" (lowland forest, selectively logged) and "I"+"J" (submontane forest) were dissociated from each other and from other areas (Fig. 2a). The disturbance variables (mainly multiple stems) appeared to be the most relevant in this case (Table 3).

The first axis of DCA2 showed dissociation between areas "F", "K"+"N" and the other areas (Fig. 2b). Disturbance (total gap area and basal area of standing dead stems) and elevation variables once again assumed great importance (Fig. 2b; Table 3). The linear model indicated gaps and average elevation as being significant variables (Table 4). The second axis suggested a significant role for the basal area of standing dead stems and the annual mean temperature (Fig. 2b); however, only the spatial filter (MEM) added to account for the spatial autocorrelation was significant (Table 4). Thereafter, climatic variables did not present a primary role in the floristic patterns. Since there is predominance of oxides at the top and soil carbon and nitrogen contents increase along the slope, soil could also be important to explain the floristic dissociation between "K"+"N" and the

Table 2 Number of trees and the species, genus and family richness for 11 sites sampled along an altitudinal gradient in the Atlantic Rainforest (SE Brazil)

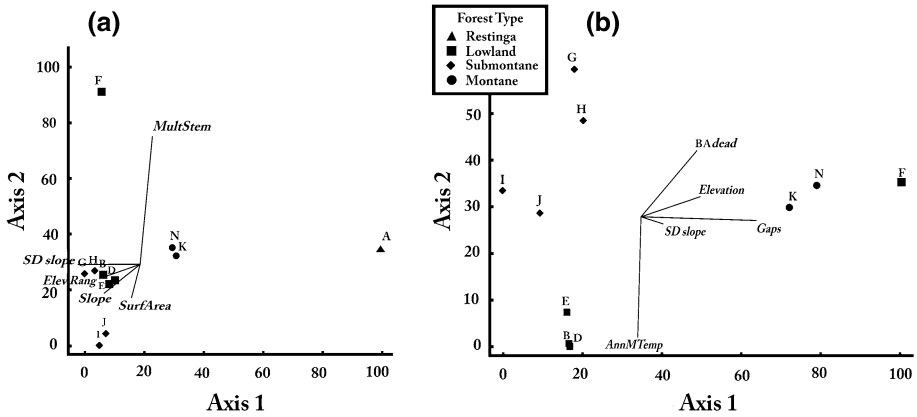| Site (area)	Number of trees	Species richness	Genus richness	Family richness
"A"	1,671	85	61	32
"B"	1,082	136	87	39
"D"	1,286	156	94	42
"E"	1,240	141	93	41
"F"	1,381	106	72	38
"G"	1,496	151	101	41
"H"	1,528	152	98	41
"I"	1,993	203	111	50
"J"	1,832	211	117	49
"K"	1,851	178	83	44
"N"	1,436	148	73	39
All	16,796	563	195	68

Fig. 2 DCA ordinations from species abundance data along an altitudinal gradient in the Atlantic Rainforest (SE Brazil). *Arrows* indicate a posteriori Pearson correlations with environmental variables. **a** Ordination with *Restinga* and **b** without *Restinga*. The abbreviations are defined in the Methods section. Weak ($r < 0.3$) and redundant variables were not represented

Table 3 DCA ordination results for species distribution patterns along an altitudinal gradient in the Atlantic Rainforest (SE Brazil) and a posteriori Pearson correlations for environmental variables

The abbreviations are defined in the "Methods" section

	DCA1 (with *Restinga*)		DCA2 (without *Restinga*)	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.610	0.4193	0.4200	0.1864
Gradient length	3.419	3.111	2.539	1.513
Gaps	0.003	0.823	0.701	−0.113
MultStem	0.271	0.881	0.639	−0.052
BAdead	−0.116	−0.007	0.485	0.492
Slope	−0.450	−0.420	−0.102	0.026
SD slope	−0.596	−0.024	0.308	−0.156
SurfArea	−0.225	−0.458	−0.159	−0.039
Elevation	0.054	−0.064	0.502	0.269
ElevRang	−0.476	−0.293	0.076	0.015
AnnMTemp	0.182	0.318	−0.131	−0.665
AnnuPrec	0.124	0.503	0.037	−0.524

other areas. Both models exhibited high coefficients of determination (Axis 1: $R^2_{\text{Adj}} = 0.7380$; Axis 2: $R^2_{\text{Adj}} = 0.7175$).

The floristic gradients were at least moderate for all the axes (except for Axis 2 from DCA2), which was evidenced by the eigenvalues and the gradient length (Table 3). These results indicated an intermediate to high level of species turnover for the main trends of floristic variation along this altitudinal variation.

Variations in species richness and correlations with predictor variables

Areas "I" and "J" (submontane forest) were the richest in species among the 11 areas investigated (Fig. 3). The poorest locality in species richness was area "A" (*Restinga* forest), followed by area "F" (lowland forest, selectively logged) (Fig. 3).
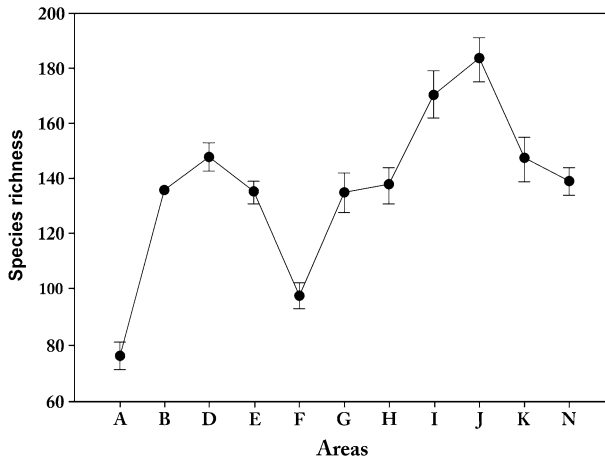
Fig. 3 Comparison of species richness among the 11 areas along an altitudinal gradient in the Atlantic Rainforest (SE Brazil) at the point of equal numbers of individuals (individual-based rarefaction algorithm). Narrow bars indicate 95 % confidence intervals

Multiple stems negatively predicted the variation in estimated species richness and the standard deviation of the slope positively predicted that variation (Table 4). This model also demonstrates a high predictive power ($R^2_{\text{Adj}} = 0.8362$).

Variance partitioning

We detected the primary role of the spatially structured environmental factors (fraction [b]) on the floristic patterns emerged from Axis 2 of the DCA2 (Fig. 4a); 22 % of the species distribution remained undetermined (fraction [d]; Fig. 4a). The variations in species richness also indicated a high level of explanation for [b] and demonstrated a high level of explanation for the sum of components [a], [b] and [c], whereas component [d] represented only 3 % of the explanation (Fig. 4b). The isolated spatial fraction ([c]) was more relevant than the isolated environmental fraction ([a]) in both variance partitioning calculations.

Discussion

The ordination analysis indicated several floristic patterns: (i) the strong dissociation of *Restinga* ("A") relative to the other areas, most likely due to topographic and edaphic differences (the *Restinga* soil is classified as a Quartzipsamment and is subject to seasonal exposure to the water table); (ii) the strong dissociation of the lowland area ("F"), which appears to be influenced by past disturbance, reflected by an increase in the number of the multiple stemmed trees and total gaps.area^{-1} variables; (iii) the equivalence of blocks "I"+"J", most likely due to topographic factors; and (iv) "K"+"N", which might be influenced by gaps.area^{-1} and the elevation average. Explanations for these patterns are possible when considering the geomorphological processes, disturbances and/or elevation zonation.

The geomorphological processes occurring in the *Restinga* forest area (Araújo and Lacerda 1987; Assis et al. 2011) are markedly different from those in the other studied areas, as described by Sanchez et al. (2013). The processes operating in *Restinga* lead to a

Table 4 Summary of the linear regression models prepared for DCA2 and estimated species richness along an altitudinal gradient in the Atlantic Rainforest (SE Brazil)

	Beta	Std. Err. of Beta	B	Std. Err. of B	p level
Axis 1					
Constant	–	–	−141.85	48.16	**0.02**
Gaps	0.74	0.17	0.07	0.02	**<0.01**
Elevation	0.55	0.17	0.13	0.04	**0.01**
Axis 2					
Constant	–	–	3.44	113.70	0.98
AnnMTemp	0.18	0.31	3.47	5.86	0.57
MEM 1	1.03	0.31	155.34	47.00	**0.01**
Species richness					
Constant	–	–	132.712	13.705	**<0.01**
SD slope	0.499	0.14	6.96	1.84	**<0.01**
MultStem	−0.68	0.14	−0.46	0.09	**<0.01**

The abbreviations are defined in the "Methods" section. Beta: standardised coefficients. B: unstandardised coefficients. Significance p level (≤ 0.05) in bold

Axis 1: $R^2_{Adj} = 0.7380$; $p < 0.01$. Axis 2: $R^2_{Adj} = 0.7175$; $p < 0.01$; Species richness: $R^2_{Adj} = 0.8362$; $p < 0.01$
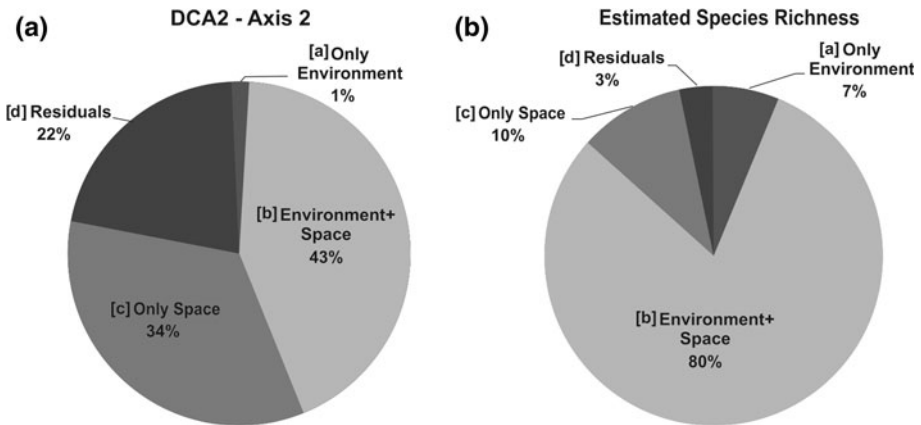
Fig. 4 Variance partitioning among the components that explain the variations in **a** DCA2 Axis 2 scores and **b** estimated species richness along an altitudinal gradient in the Atlantic Rainforest (SE Brazil). Axis 1 of the DCA2 did not have any significant spatial variables, and thus, we did not perform a variance partitioning in this case

restrictive environment (Assis et al. 2011) and, consequently, to species selectivity due to environmental filters (Ackerly 2003; Assis et al. 2011). Disturbances, in turn, can affect water conditions and temperature (Zhao et al. 2005), which are principal factors affecting the distribution of vegetation (Holdridge 1947; Gentry 1988). The logging of *Hyeronima alchorneoides* in area "F" appears to have been largely responsible for the local loss of certain species due to changes in the dynamics and succession (Villela et al. 2006), as the logged species was a large tree reaching a large volume of wood. Human disturbances have also appeared to influence species distributions in other studies (e.g., Vázquez and Givnish

1998), and it has been highlighted as a factor influencing biodiversity in the Atlantic Forest (Pereira et al. 2007; Tabarelli et al. 2010).

We also found evidence of the influence of gaps on floristic variation. The opening of gaps influences the germination and growth of forest species (Paz and Martínez-Ramos 2003). Gap area seems to be a key variable influencing species composition, since it determines the amount of light that reaches the area of the gap (Barton et al. 1989). Therefore, different species colonise gaps of different sizes (Whitmore 1996).

The dissociation between "I" + "J" and the other areas appears to be related to topographic variables, as described below. Regarding the floristic differences between higher ("K" + "N") and lower elevation areas, regional studies performed in the Brazilian Atlantic forest have indicated that altitude is important for detecting floristic affinities (e.g., Oliveira-Filho and Fontes 2000; Meireles et al. 2008; Sanchez et al. 2013). The relationship between vegetation patterns and altitude is well established (Rahbek 1995; Givnish 1999; Körner 2007), and several different patterns have been observed (He and Chen 1997). In the same conservation unit used for this study, Sanchez et al. (2013) addressed altitudinal limits for certain tree species, where most cases of restricted distribution (51 %) occurred at higher elevations. Thus, our results confirm that segregation patterns are driven by a set of factors related to altitude.

At each level of a slope, the vegetation is a result of a confluence of the constituent species, climate, soils and disturbances (e.g., Zhao et al. 2005). The confluence of these factors, which have been occurring for thousands of years, might result in elevation zonation, reflecting differences in species diversity levels for different regions of the slope (Zhao et al. 2005). However, two observations did not support the pattern of decreases in diversity with increases in altitude: (i) there was no significant correlation between species richness and altitude, and (ii) the species richness in higher altitude areas ("K" and "N", >500 m, in montane rainforest) decreased relative to "I" and "J". This result would suggest a "mid-altitude bulge" pattern for this gradient (Lomolino 2001), thereby confirming the results provided by Zhao et al. (2005), among others. However, because we did not sample the vegetation along the complete altitudinal range due to logistic limitations (Joly et al. 2012), this potential pattern could not be confirmed. Further research on this question is needed.

It has been proposed that depending on the substrate, species diversity might display an increase or decrease along an elevation gradient (Wilson et al. 1990). Throughout the area investigated in this study, the soil carbon, nitrogen and total alkalinity levels were highest in "I" and "J" (the richest species areas), which can be explained by topographic factors influencing the microclimate (SC Martins, unpublished data). The slope and surface area could help us to understand the floristic segregation of areas "I" and "J", as we found a significant interference from variations in slope (SD Slope) on species richness. Accordingly, topography was important for some of the trends of variation in species distribution, in agreement with Guerra et al. (2013), for example, and topography mainly affected species richness, as reported by Wolf et al. (2012). Wolf et al. (2012) also noted that higher species richness is expected where local-scale variations in topography result in higher soil water availability. This result is expected because higher species richness is usually found in forests with low seasonal variation in climate (Gentry 1988; Pyke et al. 2001).

The number of multi-stemmed trees per hectare exhibited a significant negative correlation with species richness. Probably many adult trees were dying as a consequence of slope, thus opening new gaps in the forest. These gaps allowed the increased branching of the remaining trees, resulting in a greater number of multiple stems; thus, multiple stems would be associated with gap opening. This phenomenon is supported by the fact that the death of many adults could result in a decline in species richness (personal observations).

For example, a peak in multiple stems and gaps.area^{-1} was observed at one of the areas ("F") having the lowest species richness among all studied sites. Thus, we propose that despite the expected high species richness in areas with wider gaps (e.g., Terborgh 1992), in the investigated forests, a more complex pattern has occurred, perhaps due to the significant effects of logging in area "F".

The summit might experience more fog, with associated decline in species richness, and increase in floristic differentiation (e.g., Bertoncello et al. 2011). However, our field observations indicate that the presence of low-level cloud cover and fog formation is not frequent in the Montane Forest plots. Despite a clear decline in air and soil temperatures (Vieira et al. 2011), probably such climate condition is not a main driver on vegetation patterns (Alves et al. 2010). We believe that our Montane forest site is located in a transitional area exposed to varying degrees of cloud impaction, thus it might be considered as a lower montane forest under some influence of clouds. Additional studies on micrometeorology and forest hydrology are necessary to understand this topic.

The studied areas "I" and "J" had a unique level of richness, since it is unusual to observe an alpha diversity of more than 200 species for Atlantic Rainforest sites (Siqueira 1994; Tabarelli and Mantovani 1999; Scudeller et al. 2001). Our results surpass the species richness found in other studies developed in Neotropical forests (see Tabarelli and Mantovani 1999) and contrast with the argument given by these authors that Atlantic Rainforests has lower species richness when compared to other Neotropical forests.

The variance partitioning indicated a clear influence from the spatially structured environment and a secondary influence of the "pure" spatial component on variations in species composition and richness. The former comprises a well-known pattern in the Atlantic Forest (e.g., Oliveira-Filho and Fontes 2000; Scudeller et al. 2001) despite the lack of specific approaches to assessing this component of variation. The influence of the "pure" spatial component suggests limitations to biotic dispersal and indicates the importance of stochastic mechanisms (Hubbell 2001). Both components (the spatially structured environment and "pure" space) could be related to the well-known (Martins 1991; Scudeller et al. 2001; Caiafa and Martins 2010) geographically restricted distribution of tree species in the Atlantic Forest (see Diniz-Filho et al. 2012). Thus, spatial proximity is undoubtedly a crucial factor driving the vegetation patterns along the altitudinal range investigated in this study.

We found evidence for a floristic variation influenced by certain environmental variables, such as disturbances, topography and elevation related variables as well as spatial proximity, and a high regional richness (a total of 563 species in the investigated area) and extraordinarily high species richness (>200 spp.) in two montane areas. These results indicate that the hillside forest studied here is an important location for additional detailed studies to investigate the processes that generate and maintain its floristic composition and diversity and is worthy of increasing efforts to preserve its biological heritage.

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