

How environmental factors condition natural regeneration in the altitudinal gradient of a montane rainforest

Victor Braga Rodrigues Duarte

Federal University of Espírito Santo

Vítor Souza Abreu

Federal University of Lavras

Henrique Machado Dias (✉ henridias@yahoo.com.br)

Federal University of Espírito Santo

Sustanis Horn Kunz

Federal University of Espírito Santo

Eduardo van den Berg

Federal University of Lavras

Research Article

Keywords: environmental variation, species distribution, vegetation-environment relationship, elevation, rainforest, understory

Posted Date: November 21st, 2022

DOI: <https://doi.org/10.21203/rs.3.rs-2281878/v1>

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Abstract

The variation of abiotic factors, and the plant species response to it, influence the regeneration capacity and, consequently, the structure of the forest community. The aim of this study is to describe the structure of the regenerating stratum and investigate its relationship with environmental and spatial variables along an altitudinal gradient. This study was carried out in the Santa Marta valley, state of Espírito Santo, Brazil. Data on height and diameter at soil height of regenerating individuals and environmental variables were collected in seven altitudinal quotas; and spatial variables (Moran's Eigenvector Maps) were created based on geographic coordinates. Phytosociological parameters were calculated by species and the floristic similarity between the altitudinal quota were determined, as well as the species that characterize each group. Redundancy Analysis (RDA) was performed, and generalized linear models were adjusted to verify the influence of environmental and spatial factors on regenerating vegetation. The specie *Palicourea sessilis* presented the highest Importance Value. The formation of two floristic groups was verified, with 11 species indicative of the higher quota group (1,420 to 1,550 m) and only one of the second group (1,112 to 1,391 m). The first two axes of the RDA explained 51.02% of the variation in the floristic composition. The natural regeneration demonstrated environmental preferences, being influenced by luminosity, abundance in adult components, contents of calcium and sodium, plant litter accumulation, altitude, and spatial structure of the environment. The altitude did not seem to influence a pattern in abundance or richness of regenerating species.

Introduction

The forest is a dynamic system in constant change. The reconstitution of forest coverage is a natural and continuous process that occurs with the growth of young individuals, present in the understory, until they reach the upper stratum, gradually replacing the senescent trees in the canopy (Franco et al. 2014). This process is part of the forest maintenance cycle, which ranges from the initial stages of development to its recruitment and establishment (Boukili and Chazdon 2017).

The regeneration capacity and species composition in a plant community, in addition to being profoundly affected by the presence of progenitors, is directly associated with local environmental factors, such as light radiation, atmospheric temperature, rainfall, and soil characteristics (Dupuy and Chazdon 2008; Boukili and Chazdon 2017). These environmental factors can change intensely with altitude variation (McCain and Grytnes 2010; Oda et al. 2016). This environmental heterogeneity linked to altitude can generate distinct patterns of species distribution for each location (Souza et al. 2013).

Moreover, geographic distance can act as a limiting factor for the dispersion of some species, affecting the composition of regeneration. Thus, the spatial component can be crucial in understanding vegetation patterns in elevation gradients (Eisenlohr et al. 2013). Studies involving natural regeneration help to predict the behavior and future development of the forest (Santiago et al. 2014). The importance of this is even more evident when one considers that the dynamics of the processes that take place in the

regenerating stratum determines the characteristics of the adult vegetation, reflecting in the maintenance of forest biodiversity (Aguiar et al. 2017; Soboleski et al. 2017; Marcuzzo et al. 2020).

Thus, the objective of this study is to understand how the structure of natural regeneration of a Dense Ombrophilous Forest is affected by environmental and spatial factors along an altitudinal gradient.

Materials And Methods

Study area

This study was carried out in a Dense Ombrophilous Forest in the Santa Marta valley, municipality of Ibitirama, in the state of Espírito Santo, Brazil. The valley is located in the southern portion of the Caparaó National Park (*Parque Nacional do Caparaó*, PNC), an area with 31,853 hectares of protected Atlantic Forest, situated on the limits between the states of Espírito Santo and Minas Gerais, Brazil (20°37' and 20°19'S; 41°43' and 41°45'W) (Figs. 1a and 1b). Seven zones were distributed at different elevations along two valley slopes (Fig. 1c), which were steep and facing various directions of exposure (Table 1). Four plots of 2 × 20 m were arranged in each zone, totalling 28 plots.

Table 1
Altitudinal quotas distribution, average declivity, and direction of terrain exposure along the Santa Marta valley, Caparaó National Park, in the state of Espírito Santo, Brazil.

Elevation (m)	Average declivity (%)	Direction of terrain exposure
E1–1,112	69.55	East/Northeast
E2–1,219	58.29	East/Southeast
E3–1,302	75.00	Northeast
E4–1,319	75.00	East
E5–1,391	48.24	North
E6–1,420	73.39	South/Southeast
E7–1,550	58.00	Northeast

According to Köppen climate classification for Brazil, the predominant climate in the region is subtropical highland (Cwb) (Alvares et al. 2013), with average temperatures between 19 and 22°C, relative humidity usually above 70%, and average annual precipitation around 1,400 mm (MMA 2015).

The Santa Marta valley, with altitude varying between 800 and 2,300 m above sea level, is occupied by ombrophilous forests with two partially distinct physiognomies: Dense Ombrophilous Montane Forest (altitude between 500 and 1500 m) and Upper Montane Forest (altitude above 1500 m) (IBGE 2012). The

soils in the valley are classified as Dystrophic Yellow Latosol, Dystrophic Red-Yellow Latosol, Dystrophic Humic Cambisol, and Folic Organosol (Castro 2018).

Data collection

For each sample unit, data was recorded regarding height and diameter at ground height (DGH) for all individuals with a minimum height of 50 cm and diameter at breast height (DBH) lower than 2.5 cm. For identification, the seedlings' samples were compared with specimens stored in herbaria from the studied region, such as the Herbário Capixaba (CAP) and virtual herbaria, with aid from the literature and specialists in taxonomic groups. Taxonomic classification followed the Angiosperm Phylogeny Group (APG IV 2016), and species nomenclature followed *Flora do Brasil 2020* (<http://floradobrasil.jbrj.gov.br>).

To characterize the canopy opening, hemispherical digital photographs captured by a smartphone with a hemispherical lens attached were used (Tichý 2016). The device was positioned 1.30 m above ground level, with the upper part aligned with magnetic north and the lens pointed towards the sky at times of day when there was no direct penetration of light inside the canopy. We obtained the pictures under cloudy or mist conditions, in order to increase the contrast between sky and foliage and guarantee the accuracy of the classification of the elements in the image.

We used the soil chemical composition and plant litter accumulation data obtained for the study area by Araújo (2016) and Castro (2014), respectively. For the chemical composition, Araújo (2016) collected subsamples of soil in each of the altimetric quotas of this study at a depth of 0-20cm. In order to quantify plant litter accumulation, Castro (2014) carried out monthly collections between November 2012 and October 2013. In each collection, 12 plant litter samples were obtained from the forest floor at each altitude.

Data analysis

Phytosociological parameters such as density, dominance and frequency, Margalef richness index, Shannon diversity index, and Pielou evenness were estimated. Since the data for absolute density and species richness did not meet the assumptions of parametric statistics, the differences among the elevations were tested using the non-parametric Kruskal-Wallis test ($p < 0.05$).

The Bray-Curtis index was used to assess floristic similarities among elevations (Magurran 2013). This analysis was conducted considering only the morphotypes identified at least at the family level, excluding morphotypes that remained undetermined. From this index, and based on species abundances, a clustering analysis was performed using the UPGMA. To assess the consistency of the groups, bootstrap resampling was performed with 999 repetitions (Efron and Tibishirani 1993). The fit between the graphic representation of similarity and the original abundance matrix was assessed by estimating their cophenetic correlation coefficient.

To obtain the species that characterized the floristic clusters formed by the UPGMA analysis, an Indicator Species Analysis (ISA) was carried out combining the values of abundance and relative frequency of the

species, calculated independently for each species (Dufrêne and Legendre 1997). The significance of the results was verified by the Monte Carlo test (Cassey and King 2001).

A Redundancy Analysis – RDA was performed to evaluate the interaction between the regenerating community and the environmental and spatial elements along the Santa Marta valley. For this, two data matrices were created. The primary one contained the values of abundance of the species, and the secondary, the environmental and spatial variables.

For the elaboration of the abundance matrix, species with less than 10 individuals in the total sample were disregarded since rare species generate enormous statistical noise and add little to the ecological interpretation of the data. Next, the Hellinger transformation method was used on the abundance data (Legendre and Legendre 2012), with the aim of reducing the influence of highly abundant groups.

The environmental variables were standardized for scales with zero mean and standard deviation equal to 1 (Borcard et al. 2011). Through correlation matrices and principal component analysis (PCA), the identified collinear environmental variables were removed from the set and the ecologically important predictors for this study were maintained (Eisenlohr 2014), such as the potential soil acidity (H + Al), magnesium in the soil (Mg), plant litter accumulation (LA), and abundance of adult individuals in the plot (ABa). The collinearity of the variables selected from the Variance Inflation Factor (VIF < 10) were verified and were, subsequently, applied the global test to assess the significance of environmental covariates (Blanchet et al. 2008).

As proposed by Borcard and Legendre (2002), geographic coordinates (latitude and longitude) were used to create spatial variables (MEMs – *Moran's Eigenvector Maps*) and understand the influence of space on the distribution of species in the community. A total of 9 MEMs were created, among which the most significant (MEM 1) was chosen for the model by the forward selection method (Blanchet et al. 2008). These procedures were performed with the “vegan” and “spacemakeR” package in R environment (R Core Team 2017).

The final matrix of species (38 species) with transformed abundance values (Hellinger transformation) and the matrix formed by the environmental (selected after correlation tests and PCA) and spatial (MEM 1 - selected by *forward selection*) variables were used in the elaboration of the RDA. The significance of the main axes of the RDA was evaluated by the Monte Carlo permutation test with 999 repetitions.

Based on the results of the RDA and the possession of the selected environmental and spatial variables, the variance was partitioned to verify how much the variation in the composition of the regenerating community is being explained only by the environmental variables (a), by the interaction between the environment and space (b), only by spatial variables (c), and by indeterminate variables (d). The significance of fractions (a), (b), and (c) was tested by permutation test.

We adjusted the generalized linear models (GLM) to analyze how the number of individuals, species richness, and diversity of the regenerating per plot are influenced by environmental variables. The

correlated environmental variables were removed in order to ensure the parsimony of the models. All combinations between independent variables were compared using the “glmulti” package in R environment and the best models were obtained by the lowest Akaike information criterion (AICc) values. Due to the observed overdispersion, the negative binomial family was adopted to adjust the models of number of individuals and richness of species and Gaussian family for diversity of regenerators. The normality conditions of the residues were verified by the Shapiro-Wilk and QQ-Plots tests.

Results

We found a total of 2,055 individuals ($18,348 \text{ ind ha}^{-1}$), distributed in 136 species and 46 families, in addition to the morphotypes that remained unidentified and/or with taxonomic uncertainties (Supplementary file 1). The Shannon diversity index (H') – considering all morphotypes identified at the species level – was $3.98 \text{ nats ind}^{-1}$, and the Pielou equability index (J') was 0.81. The highest values for H' were observed in the E4 ($3.41 \text{ nats ind}^{-1}$) and E5 ($3.55 \text{ nats ind}^{-1}$) quotas; and the lowest, in the E7 ($2.70 \text{ nats ind}^{-1}$). The J' index was higher in the E3 and E5 quotas, with 0.90 and 0.92, respectively, and lower in the E7 (0.81).

The group of shade-tolerant species were predominant (60%), followed by intermediate shade-tolerant trees (27%) and shade-intolerant (13%). The absolute density of individuals was higher in the E1, E2, E4, and E6 quotas (Table 2). The altitudinal quotas differed significantly in terms of species richness, forming small groups similar to each other. However, the Margalef Richness Index did not show a pattern of change regarding the elevation of altitudinal quotas.

Table 2

Absolute density and richness index of Margalef in the different altimetric quotas, along the Santa Marta valley, Caparaó National Park, in the state of Espírito Santo. The means followed by the same letter in the columns do not differ from each other, according to the Kruskal-Wallis nonparametric test ($p < 0.05$).

Altitudinal quotas	Elevation (m)	Density (ind ha^{-1})	Margalef Richness (D_{Mg})
E1	1,112	20,187.50 a	6.19 a
E2	1,219	25,187.50 a	5.90 ab
E3	1,302	9,250.00 b	2.43 d
E4	1,319	26,875.00 a	6.03 a
E5	1,391	12,937.50 b	4.33 bc
E6	1,420	20,625.00 a	5.15 ab
E7	1,550	13,375.00 b	3.57 c

The ten species that showed the highest Importance Value (IV) in the regenerating stratum of the community studied were *Palicourea sessilis* (5.00%), *Guapira opposita* (3.68%), *Leandra melastomoides*

(2.54%), *Psychotria* sp. 5 (2.14%), *Bathysa australis* (1.19%), *Miconia latecrenata* (1.70%), *Cabralea canjerana* (1.67%), *Cupania racemosa* (1.53%), *Ocotea sulcata* (1.32%), and *Myrcia splendens* (1.24%), reaching 23.00% of the total IV to community.

Cluster analysis revealed the formation of two groups with greater similarity of species (Fig. 2): group 1, formed by the highest quotas (1,420 to 1,550 m); and group 2, composed of the lowest elevations (1,112 to 1,391 m). We observed the formation of subgroups within group 2, with quotas E4 and E5 having greater similarity between them than with E1, E2, and E3, which formed a second subgroup. Group 1 formation (E6 and E7) showed a bootstrap support of 72%; whereas in group 2, subdivision E4 and E5 had a bootstrap of 91%, and the subgroup formed by E1, E2, and E3, of 64%. The dendrogram generated presented a cophenetic correlation coefficient of 0.7963, demonstrating that the grouping of individuals by the UPGMA method did not present data distortions.

According to the Indicator Species Analysis (ISA), 12 species had a significantly differentiated distribution ($p < 0.05$). *Cordia* cf. *myrciifolia*, *Inga schinifolia*, *Maytenus* sp. 2, *Miconia* cf. *ibaguensis*, *Miconia* sp. 7, *Myrcia subcordata*, *Piper* sp. 1, Primulaceae sp. 1, and *Weinmannia pinnata* are perfect indicators (Indicator Value [IV] = 100%) of group 1 of the cluster analysis. In addition to these, *Miconia* cf. *longicuspis* and *Begonia angularis* also had significantly differentiated distribution in this group. As for group 2, only *Sorocea bonplandii* was a perfect indicator. In this group, other species presented high IV, but did not obtain statistical significance (Table 3).

Table 3

Indicator Species (IV > 70) of the floristic groups of the Santa Marta valley, Caparaó National Park, in the state of Espírito Santo, Brazil, from cluster analysis (UPGMA).

Group 1 (Elevation – 1,420 to 1,550 m)			Group 2 (Elevation – 1,112 to 1,391 m)		
Indicator Species	IV	p-value	Indicator Species	IV	p-value
<i>Cordia</i> cf. <i>myrciifolia</i>	100.00	0.048*	<i>Sorocea bonplandii</i>	100.00	0.048*
<i>Inga schinifolia</i>	100.00	0.048*	<i>Leandra melastomoides</i>	80.00	0.230
<i>Maytenus</i> sp. 2	100.00	0.048*	<i>Meliosma itatiaiae</i>	80.00	0.294
<i>Miconia</i> cf. <i>ibaguensis</i>	100.00	0.048*	<i>Meriania tetrâmera</i>	80.00	0.280
<i>Miconia</i> sp. 7	100.00	0.048*	<i>Mollinedia schottiana</i>	80.00	0.186
<i>Myrcia subcordata</i>	100.00	0.048*	<i>Ocotea aciphylla</i>	80.00	0.233
<i>Piper</i> sp. 1	100.00	0.048*	<i>Psychotria leiocarpa</i>	80.00	0.142
Primulaceae sp. 1	100.00	0.048*	<i>Miconia tristes</i>	77.60	0.414
<i>Weinmannia pinnata</i>	100.00	0.048*	<i>Cupania racemosa</i>	70.90	0.428
<i>Miconia</i> cf. <i>longicuspis</i>	98.90	0.048*			
<i>Begonia angularis</i>	97.60	0.048*			
<i>Miconia</i> cf. <i>elegans</i>	89.30	0.094			
<i>Daphnopsis fasciculata</i>	81.80	0.095			
<i>Myrcia eugenioides</i>	76.90	0.144			
<i>Miconia latecrenata</i>	74.70	0.193			
<i>Miconia setosociliata</i>	71.40	0.245			
<i>Guapira opposita</i>	70.40	0.390			
IV: importance value (%); p-value: significance degree.					

The eigenvalues of the first two axes of the RDA explained 51.02% of the variation of the species (Table 4). The axes indicated strong positive correlations between species and covariates (values > 0.80); only the first axis, however, indicated a significant correlation according to the Monte Carlo test ($p < 0.05$). Strong correlations between covariates and axes were observed (Table 5).

Table 4
Statistical summary of the canonical axes of redundancy analysis (RDA) for the relationship between regenerating vegetation and environment, in the Santa Marta valley, Caparaó National Park, in the state of Espírito Santo.

	Axis 1	Axis 2
Eigenvalue	17.10	9.71
Variation of species data explained by axis (%)	32.54	18.48
Cumulative percentage of variation	32.54	51.02
Pearson's correlation (species – covariates)	0.999	0.993
F	3.04	1.73
Monte Carlo test (<i>p-value</i>)	0.022	0.335

Table 5
Correlations between the canonical axes of Redundancy Analysis (RDA) and predictor variables, in the Santa Marta valley, Caparaó National Park, in the state of Espírito Santo.

Components	Correlation	
	Axis 1	Axis 2
H + Al	0.961	-0.168
Mg	0.319	-0.186
LA	-0.485	0.461
ABa	0.317	0.837
MEM 1	0.917	-0.082
In bold, correlations with values > 0.8. H + Al: potential acidity of the soil; Mg: magnesium; LA: plant litter accumulation; ABa: abundance of adult individuals; MEM 1: spatial filter (Moran's Eigenvector Maps).		

In the diagram of altitudinal quotas sequencing (Fig. 3), axis 1 reinforced the existence of the altitudinal gradient observed in the similarity dendrogram. The E6 and E7 quotas are clearly differentiated from E1, E2, and E3, which are negatively related to the variables H + Al, Mg, ABa, and MEM 1, with E4 and E5 in an intermediate position. This sequencing revealed an environmental gradient directed by the increase in potential acidity (H + Al), magnesium, and spatial filter MEM 1 for the highest quotas (E6 and E7), by the increase in the number of adult individuals in the intermediate quotas (E4 and E5), and by the higher plant litter accumulation values at the lowest quotas (E1, E2, and E3).

The pattern of distribution of species as a function of environmental and spatial variables demonstrates that the first group of species is associated with the lowest and intermediate altitudinal quotas (1,112 to

1,391 m), and this environment is characterized by higher values of plant litter accumulation and more basic soils. (Fig. 4). We highlight the occurrence of the *S. bonplandii* species in this group (represented by *Sobon* in the diagram), considered an indicator of this environment. On the other hand, some species were more strongly associated with higher altitudes (1,420 to 1,550 m), where there are soils with higher potential acidity, magnesium content, and higher spatial filter (MEM 1). In this group, we observed the occurrence of many species of the family Melastomataceae, mainly of the genus *Miconia*, considering that *M. cf. ibaguensis* (Miiba) and *M. cf. longicuspis* (Milon) had significantly differentiated distribution in this environment, according to the Indicator Species Analysis.

The partitioning of variance indicated that the environmental (fraction “a + c”, $p = 0.028$) and spatial (fraction “b + c”, $p = 0.012$) variations significantly explained 19% and 8% of the variation in the floristic composition of the valley, respectively (Fig. 5). The interaction between environmental and spatial variables (fraction “c”) indicated that the spatially structured environment explains 7% of the variation in the valley, however, the isolated variables (fractions “a” and “b”) do not significantly explain this variation. The high percentage of the fraction “d” (66%) denotes that much of the variation is explained by other important predictors, which were not considered in this study, and stochastic events.

The better adjustment of the GLM to understand the variations in the number of regenerating individuals in the valley was due to the variables calcium, sodium, and abundance of adult individuals ($AICc = 142.46$, $R^2 = 0.81$, $p < 0.05$). The prediction of species richness occurred as a function of the abundance of adult individuals and altitude ($AICc = 86.86$, $R^2 = 0.63$, $p < 0.05$). The model for regenerating diversity per plot was adjusted according to the abundance of adult individuals and potassium ($AICc = 24.95$, $R^2 = 0.52$), however, the independent variables were not significant ($p > 0.05$).

Discussion

The Pielou’s equitability index (0.81) and diversity ($3.98 \text{ nats ind}^{-1}$) indicate low species dominance and high diversity in the regenerating stratum when compared to other studies in ombrophilous forests, in which the values varied between 1.5 and $3.5 \text{ nats ind}^{-1}$ (Dias et al. 2000; Lima et al. 2012; Oliveira et al. 2013). The indexes did not show a clear pattern of change along the gradient; the plots with greater diversity, however, were associated with the adult component and plant litter accumulation in the RDA, indicating that the tolerance to shading, given the predominance of a late-successional ecological group, and the gentler slope, represented by the greater accumulation of plant litter, contribute to the high richness of species at intermediate altitudes. Less abundant species were determinant in the high diversity found (Magurran 2013).

The species *Palicourea sessilis* presented the highest Importance Value (IV) in the regenerating stratum of the vegetation. This species was represented by a large number of individuals (126), well distributed among the sample units, along the environmental gradient. *Palicourea sessilis* has wide distribution throughout the Atlantic Forest (Taylor et al. 2015). This species tends to form a bank of seedlings and young plants rather than extensive seed banks in the area (Abreu 2017). Moreover, in the adult

component, where the species presented the second highest IV in the community, most individuals were found under the forest canopy, with an average height of 5.5 m, typical behavior of shade tolerant species (van den Berg et al. 2012; Araújo 2016).

The luminosity in the valley varies according to the orientation of the slope of the terrain, influencing the local microclimate, patterns of deposition and germination of propagules, and on the establishment and growth of certain species (Quadros et al. 2013; Morel et al. 2015). In the valley, the luminous incidence on the North and Northeast slopes, especially in winter, is more perpendicular and constant, implying a greater amount of energy in these areas (Facco et al. 2009). In these slopes, with the exception of quota E1, the lowest absolute density values were recorded, indicating that the highest luminosity may be affecting the establishment of species belonging to the mature stages of succession, predominant in the valley (Bovolenta et al. 2021).

The number of regenerating individuals was also influenced by the abundance of adult individuals and sodium and calcium contents, which varied in conjunction with the regenerating individuals in different altitudinal quotas and slopes of the valley. In relation to species richness, the tendency is to remain high due to intermediate altitudes and greater abundance of the adult component and to decline with the reduction in the number of adult individuals and increased elevation (Santana et al. 2021; McCain and Grytnes 2010). Notably, places higher in the mountain tend to have lower species richness, although there is a tendency to have a higher proportion of endemic individuals, precisely because of ecological limitations, such as frosts (Santana et al. 2021).

The altitude clearly influenced the formation of floristic groups in cluster analysis. In this analysis there is the floristic distinction between the quotas of highest altitude, E6 (1,420 m) and E7 (1,550 m), and the altitudinal quotas from 1,112 (E1) to 1,391 m (E5), forming a second group. Even with the noticeable formation of these groups, we noticed that the similarity values were low, which may indicate that the valley has high beta diversity (β) (Magurran 2013). Considering that the similarity indices represent the inverse of beta diversity, the low similarity between altitudinal quotas suggests the occurrence of biotic alterations with substitution of species along the valley, proving its high floristic heterogeneity (Carvalho and Felfili 2011).

The results of the RDA showed that the distribution of the species in the regenerating community has a significant relationship with environmental and spatial characteristics, demonstrating to be influenced by the amount of plant litter accumulated on the forest floor, potential soil acidity ($H + Al$), magnesium content, abundance of adult individuals, and the spatial variable MEM 1. In addition to these characteristics, the reduction of air temperature with increasing altitude plays an important role on the structure and composition of the plant community along the gradient (Joly et al. 2012; Pinto-Junior et al. 2020).

The higher plant litter accumulation observed in quotas E1, E3, and E5 is probably due to a system of high productivity resulting from the higher luminous incidence in the plots, while the lower accumulations in plots E6 and E7 may be related to the lower abundance and size of adult individuals and to the steep

slope, which causes the litter to be dragged by the surface runoff of rainwater (Castro 2014). Plant litter seems to affect the germination and seedling development of some species, influencing the structure and dynamics of the community (Facelli and Pickett 1991; Santos and Válio 2002).

Variations in altitudinal elevation provide changes in the chemical and physical characteristics of the soil, which can influence the structure of the vegetation. In fact, the analysis of soil chemical attributes revealed an increase in organic matter (OM) and magnesium in line with the increase in altitude. Environments richer in OM tend to present higher levels of H + Al, as observed in this study (Camargos et al. 2008). This behavior, associated with other edaphic and environmental factors, influenced the occurrence of species exclusive to the highest altitudinal quotas (1,420 to 1,550 m).

The space, generally not evaluated in research of this nature, ecologically influences the patterns of distribution of species in environmental gradients (Eisenlohr et al. 2013; Oliveira Filho et al. 2013). In this study, it was clear that the “pure” environment did not significantly explain the variation observed. However, spatially structured environmental variables (joint action of environment and space) revealed a significant fraction of total variance, indicating that biotic factors, such as dispersion and competition, may also be influencing species composition (Lewis et al. 2014).

The association of abiotic factors with biotic interactions is commonly recommended as a predictor of species distribution (Boulangeat et al. 2012). The seed dispersal process, for example, can determine differentiated spatial patterns of floristic composition, especially in the regenerating stratum, since plant species have varied dispersal mechanisms. Additionally, the density of individuals of the species also influences the spatial distribution (Maçaneiro et al. 2016).

Fluctuations in the number of regenerating species between the slopes orientations were associated with the abundance of the adult component, especially in the intermediate quotas that presented, in both strata, the smallest (E3) and larger (E4) numbers of individuals. Soil conditions and geomorphological characteristics, such as elevation, slope, and slope orientation, may have affected both the regenerating and the superior stratum (Collins and Carson 2004). Along the gradient, the richness of regenerating was also associated with the adult component, which acts directly in the regenerating stratum, as a source of propagules, and indirectly by the formation of microclimates, greater plant litter deposition, and alteration of edaphic conditions (Ádám et al. 2013; Kovács et al. 2017).

The high percentage of unexplained variation (66%) is a common result in studies evaluating the predictor power only of environmental and spatial variables on the floristic heterogeneity of an area (Gasper et al. 2015; Araújo 2016; Maçaneiro et al. 2016), considering the environmental heterogeneity and stochasticity of various processes (Nettesheim et al. 2018). Baldeck et al. (2013) suggested, for example, that environmental variables related to soil luminosity and moisture may be important to explain patterns of species distribution in tropical forests. The results of this study highlight that the predictors not investigated in this research probably contribute substantially to the variation of the composition of regenerating species.

Conclusion

Natural regeneration demonstrated environmental preferences along the Santa Marta Valley, being influenced by luminosity, mainly due to the orientation of the slopes, abundance in adult components, contents of calcium and sodium, plant litter accumulation, altitude, and spatial structure of the environment. The elevation of altitude, however, did not seem to influence a pattern of increase or reduction in abundance or richness of regenerating species.

Nevertheless, the largest fraction of this variation along the valley was not explained by factors contemplated in this study. We suggest for future studies to test the influence of other predictor variables, such as dispersion, competition, soil moisture, among others.

Declarations

Funding

This study was supported in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) - Finance Code 001, Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq through the Universal Public Call 14/2011 (475471/2011-3), Fundação de Amparo à Pesquisa e Inovação do Espírito Santo (FAPES) Universal Public Call no. 03/2017 (T.O.169 - SIAFEM: 80709605/18), and PDPG/FAPES-CAPES (T.O.131 - Process 2021-FDGS5)

Competing Interests

The authors have no relevant financial or non-financial interests to disclose

Author Contributions

All authors designed the study. Victor Braga Rodrigues Duarte and Vítor de Souza Abreu collected and analyzed the field data with support from Henrique Machado Dias. Victor Braga Rodrigues Duarte and Vítor de Souza Abreu wrote the manuscript. Henrique Machado Dias, Sustanis Horn Kunz, and Eduardo van den Berg discussed the results and revised manuscript versions. All authors read and approved the final manuscript.

References

1. Abreu VS (2017) Regeneração natural e banco de sementes do solo em um gradiente altitudinal de Floresta Ombrófila Densa. Thesis, Federal University of Espírito Santo.
2. APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot J Linn Soc, London 181:1-20.
<https://doi.org/10.1111/boj.12385>

3. Araújo EA (2016) Estrutura, composição florística e relação vegetação-ambiente em Floresta Ombrófila Densa no Parque Nacional do Caparaó, Espírito Santo. Thesis, Federal University of Espírito Santo.
4. Castro KC (2014) Serapilheira e estoque de carbono ao longo de um gradiente altitudinal na Floresta Ombrófila Densa, no Parque Nacional do Caparaó, ES. Thesis, Federal University of Espírito Santo.
5. Castro KC (2018) Ciclagem de nutrientes em diferentes condições edafoclimáticas em trecho de floresta ombrófila densa. Dissertation, Federal University of Espírito Santo.
6. Eisenlohr PV (2014) Persisting challenges in multiple models: a note on commonly unnoticed issues regarding collinearity and spatial structure of ecological data. *Braz J Bot* 37:365–371. <https://doi.org/10.1007/s40415-014-0064-3>
7. Instituto Brasileiro de Geografia e Estatística – IBGE (2012) Manual técnico da vegetação brasileira. 2. ed. Rio de Janeiro.
8. Magurran AE (2013) Medindo a diversidade biológica. EdUFPR, Curitiba.
9. Ministério do Meio Ambiente – MMA (2015) Plano de Manejo do Parque Nacional do Caparaó. Brasília.
10. R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Áustria.
11. Tichý L (2016) Field test of canopy cover estimation by hemispherical photographs taken with a smartphone. *J Veg Sci* 27:427-435. <https://doi.org/10.1111/jvs.12350>
12. Borcard D, Legendre P (2002) All-scale spatial analysis of ecological data by means of principal coordinates of neighbor matrices. *Ecological Modelling* 153:51-68. [https://doi.org/10.1016/S0304-3800\(01\)00501-4](https://doi.org/10.1016/S0304-3800(01)00501-4)
13. Boukili VK, Chazdon RL (2017) Environmental filtering, local site factors and landscape context drive changes in functional trait composition during tropical forest succession. *Perspect Plant Ecol Evol Syst* 24:37–47. <https://doi.org/10.1016/j.ppees.2016.11.003>
14. Carvalho FA, Felfili JM (2011) Aplicação da diversidade alfa e beta para definição de áreas prioritárias para conservação: uma análise das florestas decíduais sobre afloramentos calcários no vale do Paranã, Goiás. *Biosci J* 27:830-838.
15. Cassey P, King RAR (2001) The problem of testing the goodness-of-fit of stochastic resource apportionment models. *Environmetrics* 12:691-698. <https://doi.org/10.1002/env.493>
16. Collins RJ, Carson WP (2004) The effects of environment and life stage on *Quercus* abundance in the eastern deciduous forest, USA: are sapling densities most responsive to environmental gradients?. *For Ecol Manag* 201:241-258. <https://doi.org/10.1016/j.foreco.2004.06.023>
17. Dufrêne M, Legendre P (1997) Species assemblages and Indicator Species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67:345-366. [https://doi.org/10.1890/0012-9615\(1997\)067\[0345:SAAIST\]2.0.CO;2](https://doi.org/10.1890/0012-9615(1997)067[0345:SAAIST]2.0.CO;2)

18. Dupuy JM, Chazdon RL (2013) Interacting effects of canopy gap, understory vegetation and leaf litter on tree seedling recruitment and composition in tropical secondary forests. *For Ecol Manag* 255:3716–3725. <https://doi.org/10.1016/j.foreco.2008.03.021>
19. Efron B, Tibshirani RJ (1993) An introduction to the bootstrap. Chapman & Hall, New York.
20. Facelli JM, Pickett STA (1991) Plant litter: Its dynamics and effects on plant community structure. *Bot Rev* 57:1-32. <https://doi.org/10.1007/BF02858763>
21. Legendre P, Legendre L (2012) Numerical ecology. Elsevier, Amsterdam.
22. McCain CN, Grytnes JA (2010) Elevational gradients in species richness. In: *Encyclopedia of Life Sciences*. John Wiley & Sons, Ltd: Chichester.
23. Santos SL, Válio IFM (2002) Litter accumulation and its effect on seedling recruitment in a Southeast Brazilian Tropical Forest. *Braz J Bot* 25:89-92. <https://doi.org/10.1590/S0100-84042002000100011>
24. Ádám R, Ódor P, Bölöni J (2013) The effects of stand characteristics on the understory vegetation in *Quercus petraea* and *Q. cerris* dominated forests. *Community Ecology* 14:101-109. <https://doi.org/10.1556/ComEc.14.2013.1.11>
25. Aguiar MD, Silva AC, Higuchi P, Negrini M, Schollemberg AL (2017) Similaridade entre adultos e regenerantes do componente arbóreo em floresta com Araucária. *Floresta Ambient* 24:e00083214. <https://doi.org/10.1590/2179-8087.083214>
26. Alvares CA, Stape JL, Sentelhas PC, Gonçalves JDM, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorol Z* 22:711-728. <https://doi.org/10.1127/0941-2948/2013/0507>
27. Baldeck CA, Harms KE, Yavitt JB, John R, Turner BL, Valencia R, Navarrete H, Davies SJ, Chuyong GB, Kenfack D, Thomas DW, Madawala S, Gunatilleke N, Gunatilleke S, Bunyavejchewin S, Kiratiprayoon S, Yaacob A, Supardi MNN, Dalling JW (2013) Soil resources and topography shape local tree community structure in tropical forests. *Proc R Soc B* 280:20122532. <https://doi.org/10.1098/rspb.2012.2532>
28. Blanchet FG, Legendre P, Borcard D (2008) Forward selection of explanatory variables. *Ecol* 89:2623–2632. <https://doi.org/10.1890/07-0986.1>
29. Borcard D, Gillet F, Legendre P (2011) Numerical Ecology with R. Springer, New York.
30. Boulangeat I, Gravel D, Thuiller W (2012) Accounting for dispersal and biotic interactions to disentangle the drivers of species distributions and their abundances. *Ecology Letters* 15:584-593. <https://doi.org/10.1111/j.1461-0248.2012.01772.x>
31. Bovolenta YR, Rodrigues DR, Bianchini E, Pimenta JA (2021) Population structure of understory, canopy/emergent tree species in Brazilian Atlantic Forest remnants with different Conservation status. *Research, Society and Development*, 10:e487101119897. <http://dx.doi.org/10.33448/rsd-v10i11.19897>
32. Camargos VL, Silva AF, Meira Neto JAA, Martins SV (2008) Influência de fatores edáficos sobre variações florísticas na Floresta Estacional Semidecídua no entorno da Lagoa Carioca, Parque

- Estadual do Rio Doce, MG, Brasil. Acta Bot Bras 22:75-84. <https://doi.org/10.1590/S0102-33062008000100010>
33. Dias AC, Custodio Filho A, Franco GADC (2000) Diversidade do componente arbóreo, em floresta pluvial Atlântica secundária, São Paulo, Brasil. Revista do Instituto Florestal de São Paulo 12:127-153.
 34. 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. Biodivers Conserv 22:2767-2783. <https://doi.org/10.1007/s10531-013-0553-x>
 35. Facco AG, Ribeiro A, Sediya GC, Leite FP, Barros NFD (2009) Saldo de radiação em plantios de eucalipto em áreas de relevo ondulado. Rev Árvore 33:471-480. <https://doi.org/10.1590/S0100-67622009000300009>
 36. Franco BKS, Martins SV, Faria OCL, Ribeiro GA, Miranda Neto A (2014) Estrato de regeneração natural de um trecho de Floresta Estacional Semidecidual, Viçosa, MG. Rev Árvore 38:31-40. <https://doi.org/10.1590/S0100-67622014000100003>
 37. Gasper AL, Eisenlohr PV, Salino A (2015) Climate-related variables and geographic distance affect fern species composition across a vegetation gradient in a shrinking hotspot. Plant Ecol Divers 8:25-35. <https://doi.org/10.1080/17550874.2013.843604>
 38. Joly CA, Assis MA, Bernacci LC et al (2012) Florística e fitossociologia em parcelas permanentes da Mata Atlântica do sudeste do Brasil ao longo de um gradiente altitudinal. Biota Neotrop 12:125-145. <https://doi.org/10.1590/S1676-06032012000100012>
 39. Kovács B, Tinya F, Ódor P (2017) Stand structural drivers of microclimate in mature temperate mixed forests. Agric For Meteorol 234:11-21. <https://doi.org/10.1016/j.agrformet.2016.11.268>
 40. Lewis RJ, Pakeman RJ, Mars RH (2014) Identifying the multi-scale spatial structure of plant community determinants of an important national resource. J Veg Sci 25:184-197. <https://doi.org/10.1111/jvs.12071>
 41. Lima AS, Feliciano AL, Marangon LC, Oliveira LS, Mayara MDL (2012) Regeneração natural de um fragmento de Floresta Ombrófila Densa na Bacia Hidrográfica do Rio Capibaribe, PE. Rev Bras Ciênc Agrár 8:273-278. <http://dx.doi.org/10.5039/agraria.v8i2a2369>
 42. Maçaneiro JPD, Oliveira LZ, Seubert RC, Eisenlohr PV, Schorn LA (2016) More than environmental control at local scales: do spatial processes play an important role in floristic variation in subtropical forests? Acta Bot Bras 30:183–192. <https://doi.org/10.1590/0102-33062015abb0294>
 43. Marcuzzo SB, Vieira M, Salin M (2020) Regeneration under the canopies of native species in a restoration area. Floresta Ambient 27:e20170521. <https://doi.org/10.1590/2179-8087.052117>
 44. Morel H, Mangenet T, Beauchêne J, Ruelle J, Nicolini E, Heuret P, Thibaut B (2015) Seasonal variations in phenological traits: leaf shedding and cambial activity in *Parkia nitida* Miq. and *Parkia velutina* Benoist (Fabaceae) in tropical rainforest. Trees 29:973-984. <https://doi.org/10.1007/s00468-015-1177-4>

45. Nettesheim FC, Garbin ML, Pereira MG, Araujo DSD, Viveiros Grelle CE (2018) Local-scale elevation patterns of Atlantic Forest tree community variation and assembly drivers in a conservation hotspot in southeastern Brazil. *Flora* 248:61-69. <https://doi.org/10.1016/j.flora.2018.08.016>
46. Oda GAM, Braz MIG, Portela RCQ (2016) Does regenerative strategy vary between populations? A test using a narrowly distributed Atlantic Rainforest palm species. *Plant Ecol* 217:869-881. <https://doi.org/10.1007/s11258-016-0612-y>
47. Oliveira LS, Marangon LC, Feliciano AL, Cardoso MDO, Lima AS, Albuquerque MDJ (2013) Fitossociologia da regeneração natural de uma Floresta Ombrófila Densa em Moreno, Pernambuco, Brasil. *Rev Bras Ciênc Agrár* 8:119-124. <https://doi.org/10.5039/agraria.v8i1a2097>
48. Oliveira-Filho AT, Budke JC, Jarenkow JA, Eisenlohr PV, Neves DR (2013) Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. *J Plant Ecol* 8:242-260. <https://doi.org/10.1093/jpe/rtt058>
49. Pinto-Junior HV, Villa PM, Menezes LFT, Pereira MCA (2020) Effect of climate and altitude on plant community composition and richness in Brazilian inselbergs. *J Mt Sci* 17:1931-1941. <https://doi.org/10.1007/s11629-019-5801-4>
50. Quadros LCL, Carvalho JOPD, Gomes JM, Taffarel M, Silva JCF (2013) Sobrevivência e crescimento de mudas de regeneração natural de *Astronium gracile* Engl. em clareiras causadas por exploração florestal na Amazônia brasileira. *Ciênc Florest* 23:411-416. <https://doi.org/10.5902/1980509810552>
51. Santana LD, Prado-Junior JA, Ribeiro JHC, Ribeiro MAS, Pereira KMG, Antunes K, Carvalho FA, van den Berg E (2021) Edge effects in forest patches surrounded by native grassland are also dependent on patch size and shape. *For Ecol Manag* 482:118842. <https://doi.org/10.1016/j.foreco.2020.118842>
52. Santiago DS, Fonseca CR, Carvalho FA (2014) Fitossociologia da regeneração natural de um fragmento urbano de Floresta Estacional Semidecidual (Juiz de Fora, MG). *Rev Bras Ciênc Agrár* 9:117-123. <https://doi.org/10.5039/agraria.v9i1a3538>
53. Soboleski VF, Higuchi P, Silva ACD, Loebens R, Souza K, Buzzi Junior F, Lima CL, Cruz AP, Silva MAF, Dallabrida JP (2017) Variação de atributos funcionais do componente arbóreo em função de gradientes edáficos em uma floresta nebulosa no sul do Brasil. *Rodriguesia* 68:291-300. <https://doi.org/10.1590/2175-7860201768201>
54. Souza PB, Meira Neto JAA, Souza AL (2013) Diversidade florística e estrutura fitossociológica de um gradiente topográfico em Floresta Estacional Semidecidual Submontana, MG. *Cerne* 19:489-499. <https://doi.org/10.1590/S0104-77602013000300017>
55. van den Berg E, Chazdon R, Corrêa BS (2012) Tree growth and death in a tropical gallery forest in Brazil: understanding the relationships among size, growth, and survivorship for understory and canopy dominant species. *Plant Ecol* 213:1081-1092. <https://doi.org/10.1007/s11258-012-0067-8>

Figures

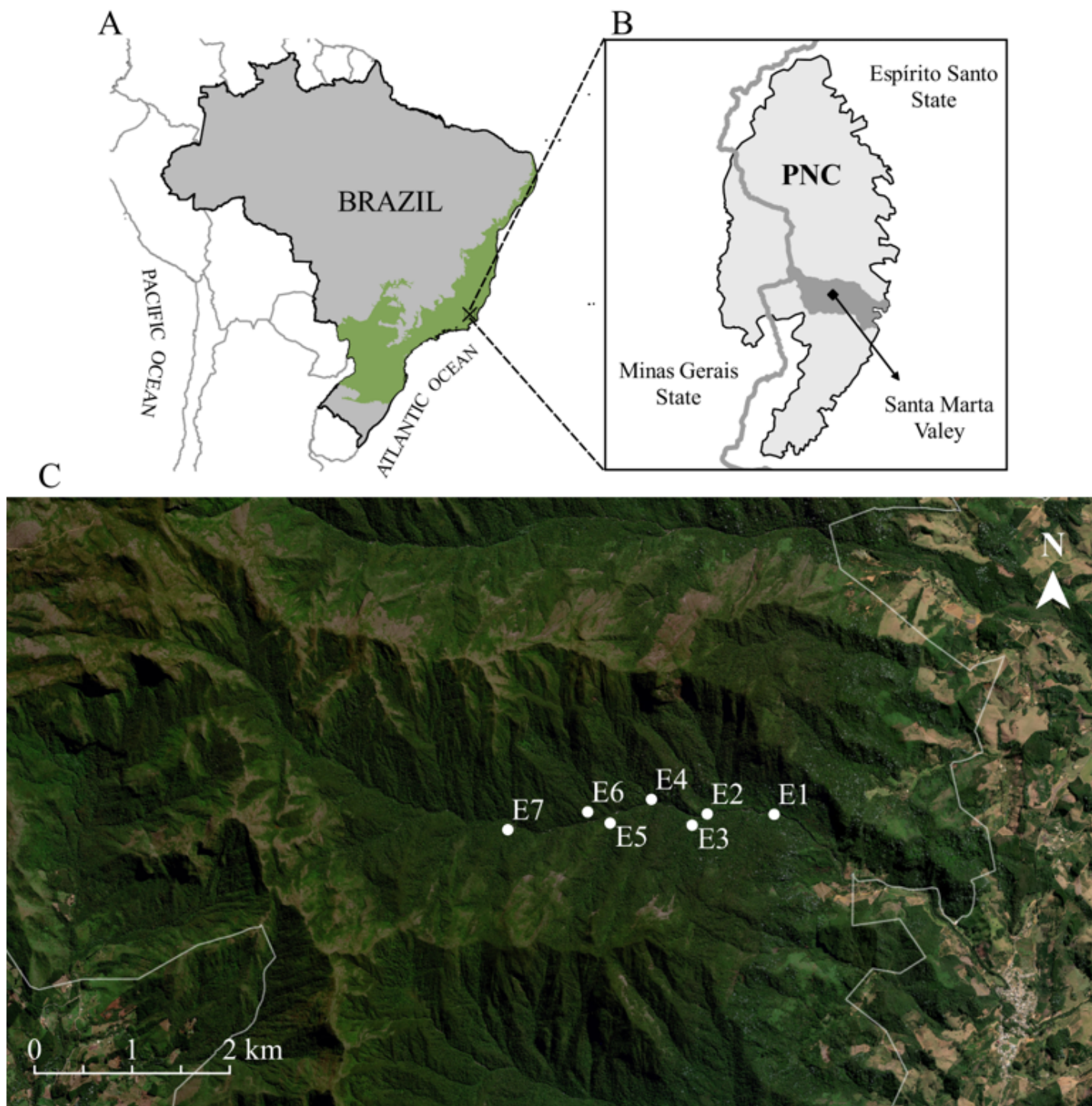


Figure 1

Zones location in the Santa Marta valley (c), Caparaó National Park, Brazil.

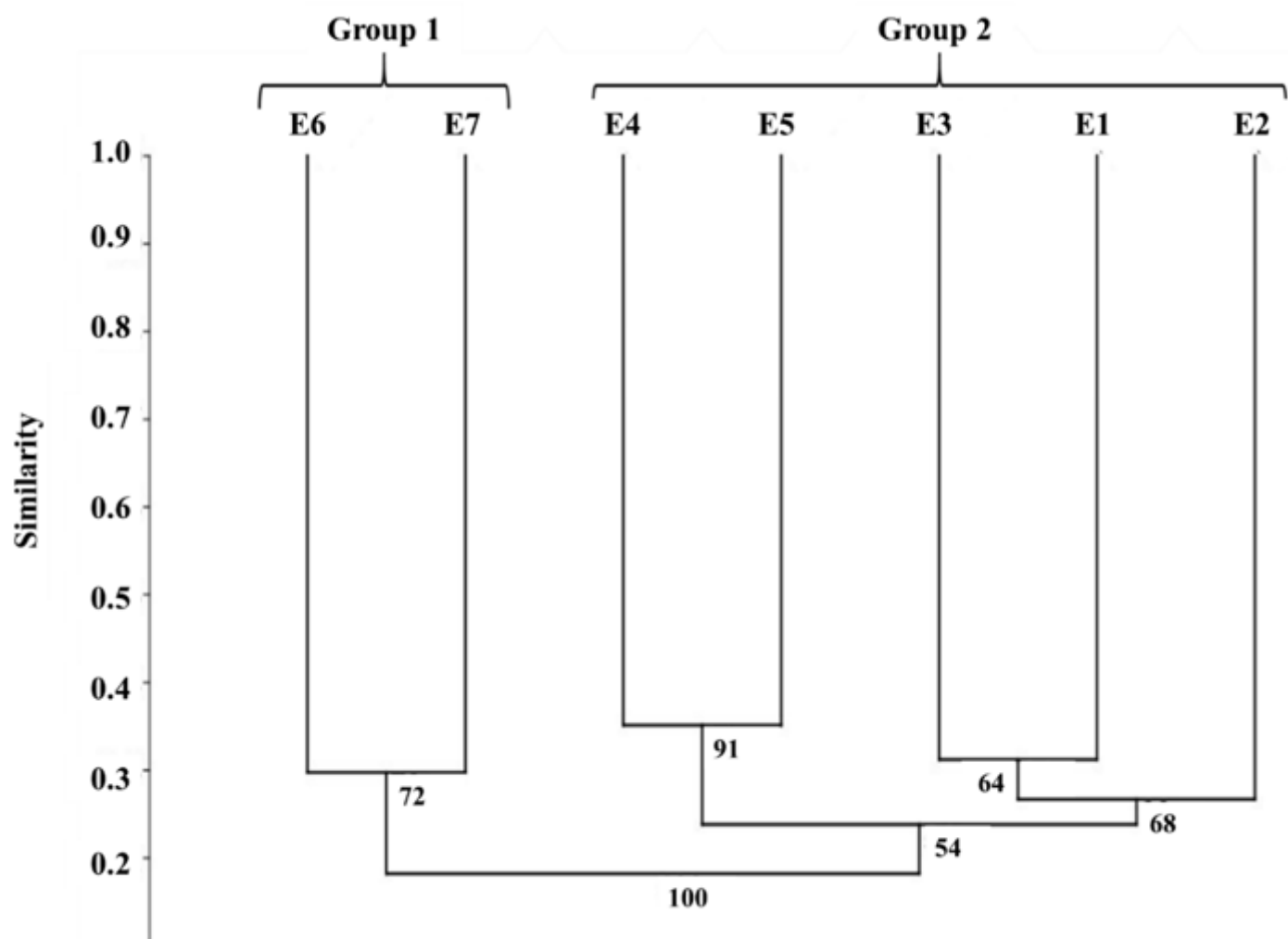


Figure 2

Floristic similarity dendrogram of the regenerating stratum among altimetric quotas of the Santa Marta valley, Caparaó National Park, in the state of Espírito Santo, according to the Bray-Curtis index and UPGMA clustering method.

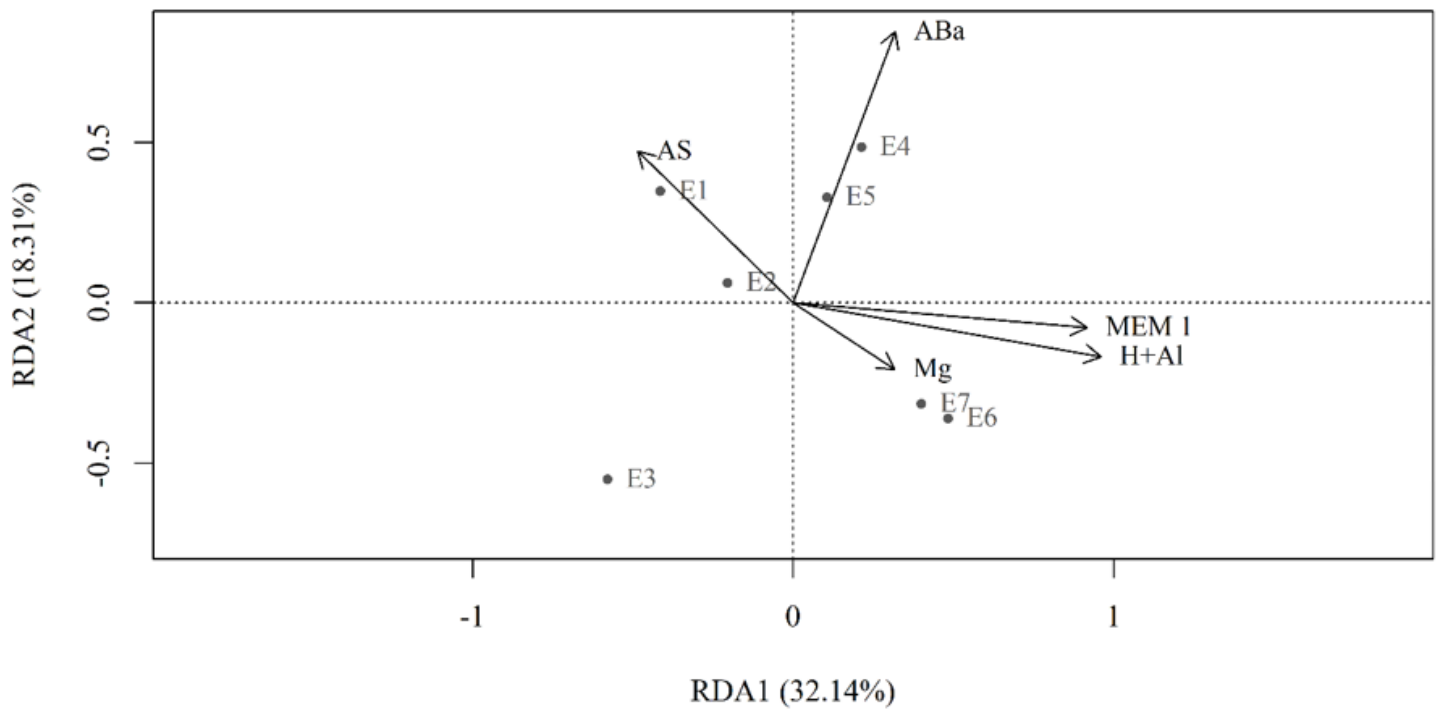


Figure 3

Redundancy Analysis (RDA) with the sequencing of altimetric quotas in the Valley of Santa Marta, Caparaó National Park, in the state of Espírito Santo, in the first two canonical axes, based on predictor variables.

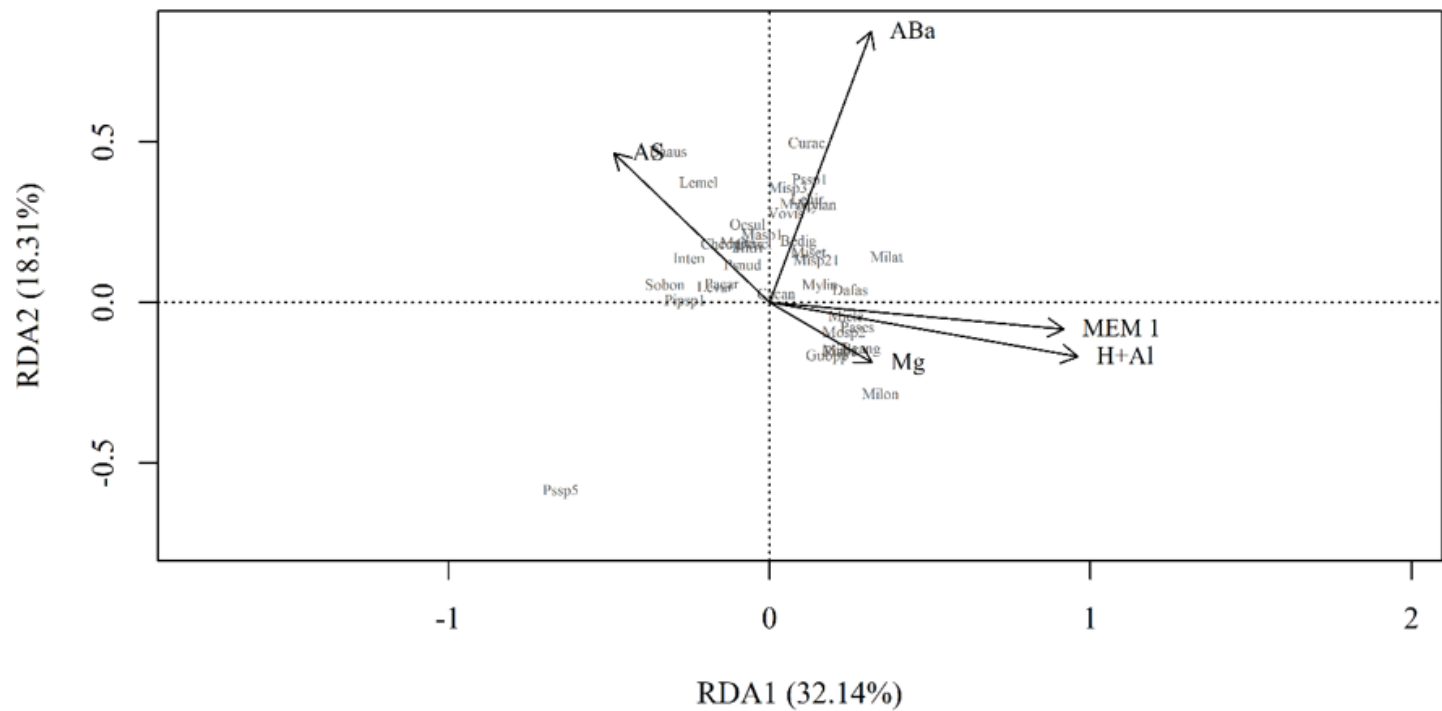


Figure 4

Redundancy Analysis (RDA) with the ordering of species of natural regeneration of the Santa Marta valley, Caparaó National Park, in the state of Espírito Santo, in the first two canonical axes, based on the abundance of the 38 species and their correlation with the predictor variables. The legend with all abbreviations of the names of the species is found in the Supplementary Material.

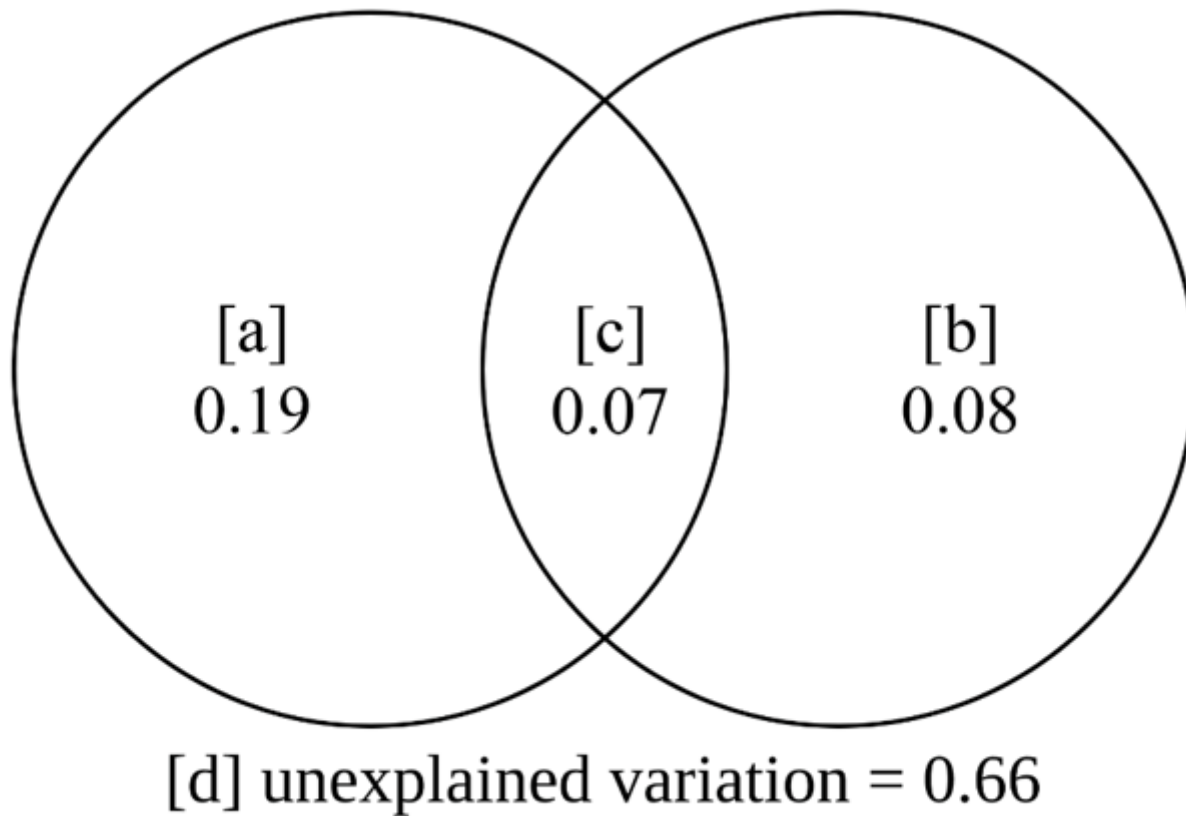


Figure 5

Partitioning of variance between fractions that explain the distribution patterns of species of natural regeneration of the Santa Marta valley, Caparaó National Park, in the state of Espírito Santo. (a): percentage of variation explained by the “pure” environment; (b): percentage of variation explained by the spatially structured environment; (c): percentage of variation explained by “pure” space.

Supplementary Files

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