

# Family Legacy: Depicting Diversity-Elevation Relationships of Tropical Tree Communities

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## Research Article

**Keywords:** Atlantic Forest, Beta diversity, ecological processes, elevational gradient, phylogenetic diversity, species conservation.

**Posted Date:** January 14th, 2022

**DOI:** <https://doi.org/10.21203/rs.3.rs-1236838/v1>

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# Abstract

Unveiling the ecological processes driving diversity and its relationship to the environment remains a central goal in ecological studies. Here, we investigated the elevation effect on plant diversity patterns of tropical rainforests, using beta-, phylogenetic and alpha diversities. To do so, we compiled a forest dataset with 22,236 trees (DBH  $\geq$  4.8 cm) from 17 plots of 1 ha each along an elevational gradient (0 – 1,200 m a.s.l) in the Atlantic Forest of Southeastern Brazil. We found high phylogenetic and species rates of turnover – beta-diversity - along the elevational gradient. Alpha phylodiversity showed a monotonic decrease with increasing elevation, including or not fern species (a distantly related clade usually ignored in tropical ecology studies), while the phylogenetic structure was highly affected by the inclusion of fern trees. Species diversity showed a unimodal pattern for the whole community, and different patterns for the richest families. The diversity pattern of the whole community emerges from differences among species distribution of the richest families, while phylogenetic diversity seems to be gradually filtered by elevation. At intermediate elevations, higher species diversification within families might have led to different strategies and cooccurrence in tropical rainforests. We also showed that intricate effects of elevation in species assemblages can be better assessed using both ecological and evolutionary approaches, stressing the importance of species selection in diversity analyzes. Finally, we demonstrate that elevation has different effects on the species distributions of the richest families and warn that these differences should be considered in conservation planning.

## 1. Introduction

Changes in species assemblages are associated with bounded abiotic conditions (Soberón 2007; Scheele et al. 2017), in which resource constraints should drive species' distribution (Huston 1994; Wang et al. 2020). Elevational gradients are among the most prominent abiotic gradients affecting species diversity and mirror latitudinal patterns (Rahbek 2005). Alongside elevation, other environmental factors change, such as temperature, atmospheric pressure, UV-B radiation, precipitation, wind speed and seasonality (Körner, 2007). Among these abiotic factors, temperature and humidity are expected to be the most important factors related to plant distributions (Gentry 1988; McCain and Grytnes 2010; Wang et al. 2020).

Elevational gradients are natural 'laboratories' for studying processes that cause variation in species distribution patterns (Lomolino 2001; Körner 2007) and thus to understand spatial variation in species composition, or Beta-diversity (Fitzpatrick et al. 2013). Beta-diversity is mainly caused by species turnover, and it should increase with environmental variations, revealing effects of filtering and dispersal limitation (Qian et al. 2009; Fontana et al. 2020). Plant Beta-diversity is expected to be hump-shaped along the elevational gradient (but see Moradi et al. 2020), however, its responses might be positive or negative, considering singular groups or shorter elevational ranges (Fontana et al. 2020). Beta-diversity was depicted into phylogenetic and species beta-diversities, to reveal the role of turnover at different phylogenetic levels. Species turnover should be higher with greater elevational variation, and a stronger effect should be observed to species, than to phylogenetic beta-diversity.

At the community level, environmental changes among different habitats (Levine and HilleRisLambers 2009) are expected to drive the patterns of diversity (Valencia et al. 2004; Laiolo et al. 2018). Four main spatial patterns were used to describe species diversity variation along elevational gradients: (i) monotonic decrease in diversity with elevation, (ii) unimodal pattern with peak at intermediate elevations, (iii) plateau of diversity at low elevations, then decreasing upwards, and (iv) no changes related to elevation (Rahbek 2005; McCain and Grytnes 2010). Species diversity patterns are not consistent among different geographic areas (Hsu et al. 2014; Khine et al. 2019), species groups (Peters et al. 2016) or diversity indices used (Chao et al. 2014; Tucker et al. 2017). For example, diversity patterns can differ between single-taxa, families and the whole community (see Descombes et al. 2017, Kamimura et al. 2017). By assessing how elevation leads to different diversity patterns for species groups (e.g. Vetaas and Grytnes 2002; Kamimura et al. 2017), allows us to elucidate ecological drivers conducting species assemblages (Kreft and Jetz 2007; Peters et al. 2016). However, ecological processes explaining species co-occurrence and distribution in high diversity areas remain controversial (Mittelbach et al. 2007; Condamine et al. 2019).

Both deterministic, such as environmental filtering, and random processes, such as stochastic recruitments, have been found to explain the spatial variation of species diversity in relation to elevational gradients (Rahbek 2005; Swenson 2013; Peters et al. 2016). To understand multiple ecological processes modulating diversity in elevational gradients (see Graham et al. 2014, Laiolo et al. 2018), we assessed diversity-environment relationships using evolutionary and ecological complementary approaches (Pavoine et al. 2011; Graham et al. 2014). Measures of phylogenetic diversity are appropriated to unravel the processes that build species assemblages (Pavoine and Ricotta 2019). Since including basal groups should strongly influence the results of phylogenetic analyzes (Feng et al. 2014; Qian et al. 2019), we disentangled phylogenetic diversity analysis considering the role of one basal and distantly related clade, usually excluded in high-diversity tropical forests studies, the tree ferns (Worthy et al. 2019).

Species-resource relationships and spatial constraints should affect species ranges for the whole community, and also within the richest families (Colwell et al. 2016; Kamimura et al. 2017). Thus, we used a taxonomic complementary approach and analyzed the species diversity-elevation relationships to the five richest botanical families in the community, to shed light on the ecological processes driving local diversity to each family (Chao et al. 2014; Kubota et al. 2018). Conservation priorities can be better planned by mapping biodiversity patterns (Socolar et al. 2016), understanding the processes underlying the variations patterns of beta- and alpha-diversity (Tucker et al. 2017), and assessing the species distributions of high diversity families (Murray-Smith et al. 2009). As species elevational ranges change in response to climate change (Zu et al. 2021), expanding the comprehension of diversity-elevation relationships is critical to guide efforts of biodiversity conservation.

Here, we used a large plot-dataset of preserved communities distributed along an elevational gradient in the Atlantic Forest, through an integrated phylogenetic-taxonomic approach of beta- and alpha-diversity metrics at different species scenarios. We addressed three questions: (i) does beta-diversity change along the elevational gradient? Are phylogenetic and species beta-diversities similar in their response to

elevation? (ii) How does phylogenetic diversity and structure change along the elevation gradient? Is this pattern different considering basal group in the analysis? (iii) How does alpha-diversity change along the elevational gradient? Is this pattern similar for the whole community and for the five richest families in the community? We hypothesized that the beta-diversity would show high turnover for both phylogenetic and species beta-diversity, which should be highly correlated to elevational changes (Condit et al. 2002; Elliott and Davies 2019). We expected to find a close covariation between species and phylogenetic diversity (Sandel 2018), and an increase of phylogenetic clustering at higher elevations, due to stronger environmental filtering (Körner 2007; Zhang et al. 2016; Qian et al. 2020). Finally, alpha-diversity should vary unimodally along the elevational gradient for the whole community (Rahbek 2005; Eisenlohr et al. 2013), emerging from patterns of the richest families (see Kamimura et al. 2017, Massante and Gerhold 2020).

## 2. Materials And Methods

### 2.1 Study area

The study was based on sampling plots of the tree community along the elevational range in a tropical montane system in the Serra do Mar State Park (SMSP, 23° 22' S and 45° 05'W), southeastern Brazil. The permanent plots are in three Nuclei of the SMSP (Cunha, Picinguaba and Santa Virgínia). The climate ranges from, Cfa to Cfb (Köppen's classification), annual average temperature goes from 20.8 °C to 16.7°C and average annual rainfall ranges from above 2,200 mm to 1,780 mm, respectively from the lowlands to the highlands. Rainfall is well distributed throughout the year (Alvares et al. 2013).

The study site is in the biogeographic province of the Atlantic Forest (Morrone 2017) which is represented by the dense ombrophilous forest (IBGE 2012; Joly et al. 2012), with five forest types along edaphic and topographical gradients, within the studied latitude (22° to 24° S IBGE 2012): (1) between 0 and 10 m of altitude, there is the seasonally flooded coastal forest (*Restinga*); (2) between 5 and 50 m, the lowland dense ombrophilous forest (LDOF); (3) between 50 and 500 m, the sub-montane dense ombrophilous forest (SMDOF); (4) between 500 and 1500 m, the montane dense ombrophilous forest (MDOF). Furthermore, (5) in the high lands (at 1200 m a.s.l.) there are some forests patches conditioned by flooding and organic soils, characterizing a high montane dense ombrophilous forest (HMDOF). Plots were distributed along the elevational gradient from 0 to 1200 m a.s.l (Table A.1).

### 2.2. Sampling design and data compilation

We compiled and revised the forest plot dataset, with 17 plots of 10,000 m<sup>2</sup> (1 ha) each, used as local communities. All tree individuals with diameter at breast height (DBH)  $\geq$  4.8 cm, including palm trees and tree ferns, were measured by their heights and DBH. Forest inventory dataset was obtained in published papers and academic thesis (Assis et al. 2011; Campos et al. 2011; Padgurschi et al. 2011; Prata et al. 2011; Ramos et al. 2011; Rochelle et al. 2011; Joly et al. 2012; Eisenlohr et al. 2013; Grillo 2016; Morais 2016; Kamimura et al. 2018; Souza et al. 2018). Fertile material was deposited in the herbarium UEC, IAC and HRCB (acronyms according to Index Herbariorum 2020). Revisions of specimen of the richest

families were done by consulting specialists or are available in the literature (Silva et al. 2016; Kamimura et al. 2017). The species classification among families followed the system of the Angiosperm Phylogeny Group (APG IV; Chase et al. 2016) and Pteridophyte Phylogeny Group (PPG I; Cole et al. 2016). In the analysis, we only included individuals identified to the species level (c.a. 86% of the total abundance), excluding dead individuals, morphotypes (not revised by specialists) and *conferatum* (*cf.*) or *affinis* (*aff.*) taxa.

## 2.3. Data analysis

We assessed the beta diversity by means of phylogenetic and species diversity similarities decay. Phylogenetic beta diversity was the fraction of branch-length shared between communities, using *phylosor* in the *picante* library (Kembel et al. 2010). Species beta-diversity was calculated using the Sørensen index of similarity, with *beta.pair* in the *betapart* package (Baselga et al. 2018), partitioned into the turnover and nestedness-resultant components. We then assessed correlations among elevational divergence with phylogenetic and species beta diversities through Mantel Partial tests (Legendre et al. 2005), to account for spatial autocorrelation, using *mantel.partial* in the *vegan* package (Oksanen et al. 2019). Finally, we measured the goodness-of-fit of models through multiples regression on distance matrices, based on permutation tests, using *MRM* in the *ecodist* package (Goslee and Urban 2007).

Phylogenetic diversity and structure were analyzed under two scenarios, including or not the tree ferns, the most distantly related clade (Cyatheaceae, in our case). We built two phylogenetic trees, considering the whole community and excluding Cyatheaceae species (ferns), from a consensus tree for seed plants, GBOTB (Smith and Brown 2018), using the function *phylo.maker* (Jin and Qian 2019). Branch lengths were estimated with the BLADJ algorithm (Webb et al. 2008), and unresolved genders were placed as basal polytomies within their families.

We then computed the phylogenetic diversity for each community. The phylogenetic diversity was expected to be correlated to species diversity (Sandel 2018), thus, we used a phylogenetic diversity index (PDI), which standardizes the phylogenetic diversity (Faith 1992) according to species richness (Sandel 2018). Finally, we assessed the phylogenetic structure, by means of the net relatedness index (NRI) (Webb 2000; Swenson et al. 2012). NRI was calculated using the standardized effect size (SES) of mean phylogenetic distance (MPD), with 999 probability times of the SES for MPD giving the NRI (Webb 2000; Kembel and Hubbell 2006). Negative values of NRI indicate an over-dispersed phylogenetic structure, while positive values of NRI show clustering (Webb 2000; Kraft and Ackerly 2010). We performed phylogenetic analyses using *PhyloMeasures* (Tsirogiannis and Sandel 2016) and *picante* (Kembel et al. 2010) packages.

We also computed alpha species diversity for (i) whole community (all species) and (ii) for the five richest families in the study area (which comprised more than 50% of the total species richness). For each plot and for the selected families, we estimated species diversity in the matter of Hill numbers (Chao et al. 2014), reporting the Shannon's diversity index ( $q=1$ ).

To detect the effects of elevation on phylogenetic diversity and structure, and on species diversity, we performed linear mixed-effects models (LMM) using the 'lme4' package (Bates et al. 2015). For each scenario analyzed (see above), we compared the results of the null model (diversity~1) and models with elevation or quadratic function elevation as fixed effects. Forest types were used as a random factor to account for the different numbers of plots across forest types. The best models were chosen based on the Akaike information criterion (AIC). We tested the significance of each explanatory variable using the *Anova* function in the *car* package (Firth et al. 2009).

To account for spatial autocorrelation, we applied spatial autoregressive models (SAR; Bivand et al. 2013). Moran's I was calculated at 5-m interval distances between 0 and 50 m. Moran's I was significant at 5–10 m ( $P \leq 0.001$ ). Thus, we constructed the spatial weights matrix, in which the distance 10 km was defined for the response variable (diversity) reached its maximum. We then added the spatial structure to the models and evaluated the goodness of fit of the regression models by means of Nagelkerke R-Square ( $R^2$ ) (Nagelkerke 1991). Spatial autoregressive modeling was conducted by using the *spautolm* function implemented in the in library *spatialreg* (Bivand and Piras, 2015). All analyses were performed using R (R Core Team 2021), adopting  $\alpha \leq 0.05$ , and permutational tests were based on 999 randomized datasets obtained from Monte Carlo randomizations.

### 3. Results

We evaluated 22,236 tree individuals belonging to 626 species, distributed in 75 botanical families. Myrtaceae was the richest family (20.9% of the total number of species), followed by Lauraceae (11.7%), Rubiaceae (7.82%), Fabaceae (7.18%) and Melastomataceae (4.15%). Most species (455, 72.6%) presented one or two individuals. Two species occurred in all plots analyzed (*Euterpe edulis* Mart. Arecaceae, and *Guapira opposita* (Vell.) Reitz, Nyctaginaceae), while 244 species were present in only one plot.

#### 3.1 Beta-diversity along the elevation gradient

Both phylogenetic and species dissimilarities increased with increasing elevational divergence (Figure 1), and beta-diversity was mainly due to species turnover. Species turnover means were 0.86 for the phylogenetic and 0.91 for species approach. For both phylogenetic and species beta diversities, models presented similar coefficient of determination ( $R^2 = 0.53$  for PD and  $R^2 = 0.45$  for SD) and Mantel-r values (Figure 1). Species dissimilarities were higher than phylogenetic dissimilarities following differences in the elevation of the plots, ranging from 0.5 to 0.75 to PD, compared to 0.25 to 0.5 of SD (Figure 1).

#### 3.2 Elevational patterns of phylogenetic diversity and structure

Correlation between species diversity and phylogenetic diversity was strongly affected by the choice of species scenarios in analyses (Figure 2a). For both species' scenarios, including or not the tree ferns,

phylogenetic diversity monotonically decreased with elevation (Figure 2b). The inclusion of Cyatheaceae in the analyses also affected the results of the phylogenetic structure (Figure 2c).

In scenario 1, elevation affected the phylogenetic structure, driving a monotonic increase of NRI values along the gradient. The random phylogenetic structure was predominant among the plots (73% of the total), but in the *Restinga* forest, phylogenetic structure was clustered, while in the plots above 1,000 m a.s.l. presented overdispersed phylogenetic structures. In scenario 2, elevation slightly affected the phylogenetic structure, driving an inverted hump-shaped model of NRI variation along the gradient. The random phylogenetic structure was again predominant (94% of the total). A strong clustered phylogenetic structure was found in *Restinga* forest, while only one plot above 1,000 m a.s.l. presented overdispersed structure (Figure 2c).

### **3.3 Changes in alpha species diversity along the elevation gradient**

Overall, we found significant effects of the elevation on the species diversity patterns (Table 1). For the whole community, species diversity was unimodally distributed along the elevational gradient (Figure 3a, b).

Table 1

Linear Mixed Models results of diversity-elevation relationships for the whole community and for the five richest families along an elevational gradient in the Atlantic Forest, southeastern Brazil. Bold – models selected; AICc - Akaike information criterion;  $elevation^2$  -quadratic function of elevation; P – p-values; Phylo. Div. – phylogenetic diversity; Phylo. struc. – phylogenetic structure;  $R^2$  - Nagelkerke R-Square; Sc.1 – Scenario 1, including all species; Sc.2 – Scenario 2, excluding tree ferns.

Models	Diversity ~1	Diversity ~elevation	Diversity ~elevation <sup>2</sup>
Community			
Species diversity	AICc = 51.32	AICc = 55.08	<b>AICc= 49.35 / P = 0.01 / R<sup>2</sup> = 0.56</b>
Pyhlo. div. sc.1	AICc = 47.81	<b>AICc= 40.35 / P &lt; 0.01 / R<sup>2</sup> = 0.5</b>	AICc = 50.71
Pyhlo. div. sc.2	AICc = 48.81	<b>AICc= 40.01 / P &lt; 0.01 / R<sup>2</sup> = 0.52</b>	AICc = 51.96
Pyhlo. struc. sc.1	AICc = 45.02	<b>AICc= 33.71 / P &lt; 0.01 / R<sup>2</sup> = 0.69</b>	AICc = 46.78
Pyhlo. struc. sc.2	AICc = 40.84	AICc = 46.65	<b>AICc= 38.98 / P = 0.02 / R<sup>2</sup> = 0.25</b>
Families			
Fabaceae	AICc = 49.15	<b>AICc= 46.86 / P &lt; 0.01 / R<sup>2</sup> = 0.58</b>	AICc = 54.66
Lauraceae	AICc = 54.09	<b>AICc= 52.74 / P &lt; 0.01 / R<sup>2</sup> = 0.59</b>	AICc = 55.08
Melastomataceae	<b>AICc = 47.93</b>	AICc = 52.34	AICc = 49.85
Myrtaceae	AICc = 52.91	AICc = 54.61	<b>AICc= 48.45 / P &lt; 0.01 / R<sup>2</sup> = 0.67</b>
Rubiaceae	<b>AICc = 54.71</b>	AICc = 58.68	AICc = 55.81

Regarding the richest families, three different variation patterns were found: (i) unimodal variation pattern (Myrtaceae); (ii) monotonic decrease in species diversity with elevation (Fabaceae); (iii) monotonic increase in species diversity with elevation (Lauraceae), besides insignificant changes in species diversity for Melastomataceae and Rubiaceae (Table 1, Figure 3a, b).

## 4. Discussion

Evaluating diversity-environment relationships at different species scenarios is important to understand how tropical tree community patterns emerge from its different components. Phylogenetic and species turnover rates both increased with the elevational divergence between communities, and species

dissimilarities were more pronounced than phylogenetic dissimilarities. Random phylogenetic structure occurred at low and intermediate elevations, becoming clustered at higher elevations. Also, assessing phylogenetic and species-diversity shed light on the processes shaping spatial patterns of biodiversity. We showed that diversity patterns differ for the whole community and for the richest families. Last but not least, since the effects of elevation on species distribution of rich families were different, we highlight the importance of assessing diversity-elevation for different species assemblages of tropical tree communities, especially when climate changes have profound impacts on tropical biodiversity of mountain systems.

## 3.1 Beta-diversity along elevational gradients in tropical forests

Beta diversity was mainly explained by turnover with a very low fraction of nestedness, both in phylogenetic and species terms. It is expected that species dissimilarity between communities increases with the geographical distance between them (Soininen et al. 2007; König et al. 2017). In our case, although communities close in space presented high species dissimilarities, environmental filters associated to higher elevation act on species distribution, in which high species turnover rates were greatly related to the elevational divergence between communities (Dauby et al. 2014; Mariano et al. 2020). This supports that beta diversity of tropical tree communities is mainly influenced by geographic distance, limited by dispersion processes, affecting the species' responses to the current environment and/or geographical barriers (Weinstein et al. 2015; Du et al. 2021).

In line with our first hypothesis, species and phylogenetic beta diversity were similar, whilst species turnover was higher than phylogenetic, across different elevations. On one hand, similar patterns of species and phylogenetic beta diversity found along environmental gradients can be associated with the conservatism of functional attributes (Du et al. 2021). On the other hand, species turnover was higher in relation to phylogenetic, indicating species diversification observed in species-level, rather than in genus or family levels. Temperature, resources and energy limitations along the elevational gradient, the harsh local conditions in stressful habitats, but not environmental threshold capacity or limited dispersed diaspores, have been described as determinants of species dissimilarities along elevational gradients (Qian 2009; Wang et al. 2020). Harsh local conditions may produce greater phylogenetic distance among regional abundant families in relation to less stressful habitats (Scarano 2002; Massante and Gerhold 2020), while an inverted pattern may be found for species diversity, where lower abiotic constraints and species competition should allow higher species cooccurrence (Levine and HilleRisLambers 2009; Mayfield and Levine 2010). Nevertheless, we found that elevation drives more species turnover than the phylogenetic turnover in tropical tree communities. This supports the hypothesis of the slow evolution of niches, in which species to remain in their origin area despite their dispersal capacity (Daru et al. 2017). Thus, analyses of different metrics of beta diversity (species or phylogenetic) help the understanding of the spatial structure and to elucidate the ecological processes conducting local species assemblages (Socolar et al. 2016).

## 3.2 Ecological processes driving local tree assemblages: species scenarios matter

Using a phylogenetic approach, we found trends that have not explicitly been described (Zhang et al. 2016; Chun and Lee 2018; Ramírez et al. 2019). In general, a monotonic decrease or unimodal pattern of phylogenetic diversity have been found for different plant groups along elevational gradients in different mountain systems (e.g. Chun and Lee 2018, Manish and Pandit 2018, Qian et al. 2019). Here, we found that random processes were dominant in community assemblages along the elevational gradient, however including or not tree ferns changed the results for the *Restinga* and Montane forest types. Thus, we combined phylogenetic diversity and structure analysis to obtain a better understanding of ecological processes driving the species assemblages (Mazel et al. 2016).

The sensitivity of including basal groups in phylogenetic structure analyzes has been reported in a few studies (but see Feng et al. 2014; Worthy et al. 2019). Analyzing the phylogenetic structure of the whole community, we found clustered phylogenetic structure, likely caused by extreme temperatures at higher elevations (Vieira et al. 2011). The exclusion of tree ferns from the analyzes revealed stronger prevalence of random phylogenetic structure and an outstanding phylogenetic overdispersion in the *Restinga* forest. As expected, by analyzing all species, our findings support the Tropical Niche Conservatism hypothesis (Wiens and Donoghue 2004), in which the changes in local conditions affect local assemblages, sorting species with similar environmental tolerances (Webb et al. 2002; Cardillo 2011).

Notwithstanding, excluding tree ferns from the analyses hidden the environmental filtering of elevation of local tree assemblages. This can be related to differences of phylogenetic dispersion sensitivity to harsh environments among families with different evolutionary histories (Qian et al. 2019). Specifically, phylogenetic clustering was found in higher elevations when including Cyatheaceae, reinforcing the niche convergence between tree ferns and Angiosperms (Feng et al. 2014; Worthy et al. 2019). Hence, we show how the decision about species scenarios approaches used into the phylogenetic analyzes deeply change the understanding of the patterns of phylogenetic diversity and structure and, consequently, the environmental filters effects on species assemblages (e.g. Feng et al. 2014; Qian and Chen 2016; Zhang et al. 2016). In a nutshell, assessing diversity-elevation relationships under different approaches is especially necessary (e.g. Manish and Pandit 2018, Qian et al. 2019), since the loss of phylogenetic diversity may have negative effects on ecosystem function and stability (Cadotte et al. 2012; Gerhold et al. 2015).

## 3.3. Alpha-diversity-elevation relationships: the families legacy

Our results did not corroborate close covariation between phylogenetic and species diversity which is usually reported for tree communities in mega-diverse regions (e.g. Gómez-Hernández et al. 2016, Zhang et al. 2016). Phylogenetic diversity was negatively correlated with elevation, whilst higher species diversity at intermediate elevations did not lead to higher phylogenetic diversity, in either species

scenarios analyzed. These patterns might be associated with niche conservatism, in which most species tend to evolve *in situ* rather than shifting their habitats (Crisp et al. 2009; Souza-Neto et al. 2016), causing increases in species diversity, but not in phylogenetic diversity.

The whole community alpha diversity presented a unimodal pattern, with a peak at intermediate elevations. Along the elevational gradient in the Atlantic Forest, local heterogeneity of environmental conditions, mainly topographic and edaphic variations have been reported as the main predictors of tree diversity variation (Sanchez et al. 2013; Eisenlohr et al. 2013). The larger the environmental heterogeneity, the higher co-occurrence of species (Levine and HilleRisLambers 2009; McCain and Grytnes 2010), while harsher conditions at higher elevations are expected to decrease species diversity (Zhang et al. 2016; Martínez-Camilo et al. 2018). Here, we argue that an interplay of abiotic factors and constraints on species spatial distribution led to changes in species diversity along the elevational gradient. Thus, the species diversity peak at intermediate elevations can be related to the intermediate fertility and intrinsic topographic factors at middle elevations (Sanchez et al. 2013; Eisenlohr et al. 2013), together with species distribution overlap (Colwell and Lees, 2000) at those elevations.

Historically, the southern Atlantic Forest was considered unstable during the Quaternary climatic oscillations (Graham et al. 2014), however, recent studies have demonstrated that optimal forest conditions must have occurred (Aguiar-Melo et al. 2019). This implies that, even in a cold and dry period, rainfall must have been enough in this part of the Serra do Mar, allowing the maintenance of a forest refugium to host species diversity. In the lowlands at the windward and, in the highlands, the scattered montane (cloud) forests occurred in protected valleys surrounded by a matrix of grasslands (Behling and Safford 2010). In this way, the high diversity in low and intermediate elevations may have also been maintained during the climatic oscillations, and led to the strong differentiation of the high-altitude flora, exemplified by basal clades of typically cold environments (e.g. Cyatheaceae, Winteraceae), and also Lauraceae which exhibits high diversity in the montane forests (Gentry 1988; Kamimura et al. 2017). Furthermore, Myrtaceae has been reported to have diversified mainly in mountainous and colder places of the Atlantic Forest (e.g. Amorim et al. 2019), while Fabaceae follows the decreasing pattern along with the elevational increase (e.g. Silva et al. 2015), putatively as a consequence of its history with high diversification in lowland and rainy forests (e.g. Silva et al. 2012; Conceição Oliveira et al. 2021).

Three among five richest families alpha diversities were related to elevation, however with different patterns, indicating an interaction between environmental drivers and distributions constraints conducting the diversity patterns (Colwell et al. 2016). Those differences also reflect the biogeographic history of these families of tropical wet and hot climates, which can help to explain the current patterns of species distribution observed along the environmental gradients (Chanderbali et al. 2001; Bardon et al. 2013; Berger et al. 2016). Elevation can have different effects on the species diversity of richest families of tropical tree communities, highlighting the importance to assess the diversity-environment relationships for different species assemblages and not only for the whole community. This is special in a scenario of human impacts on biodiversity (Vačkář et al. 2012; Joly et al. 2014), in which the effects of

climate change can shift the elevational range of species from important families, deeply impacting on mountain biodiversity (Zu et al. 2021).

## 5. Conclusions

By analyzing beta diversity under species diversity and phylogenetic diversity approaches, we demonstrated that elevation and local harsh conditions lead to higher species turnover, stronger at species than at family level. We show that the inclusion of basal plant groups had significant effects on phylogenetic analyzes of diversity, which mainly decreased along the elevation gradient, indicating an effect of environmental filtering in driving species assemblages. Phylogenetic and alpha diversities patterns differed, helping to understand the processes driving community assemblages. By splitting the analyzes of alpha diversity into different species scenarios, we showed that diversity-elevation relationships can be different for the richest families, whilst analysis of the whole community leads to the general unimodal pattern in the elevation gradient. Thus, we recommend merging ecological and evolutionary approaches, and yet splitting the analyzes into different species scenarios, to advance the comprehension of processes and mechanisms leading to diversity-environment relationships. Finally, in view of the differences of diversity variation patterns among rich tropical families and the delimited spatial distribution of some phylogenetic lineages, that occur in their large majority at highest altitudes (i.e. Cunoniaceae and Winteraceae), we advocate that conservation planning also consider the diversity patterns of rich families to escape more biodiversity losses by the current and future climate scenario.

## 6. Declarations

### Acknowledgements

We thank the National Council for Scientific and Technological Development (CNPq) for the scholarship conceded to VAK (process n° 141781/2016-5) and for the research grant CNPq-FAPESP-PELD 403710/2012-0, to CAPES (Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil) for scholarships granted to PPL (Processes no. PNPd-086/2013 and 88887.583146/2020-00), and Sao Paulo State Research Support Foundation (FAPESP) for the research support (processes FAPESP/Biota n°03/12595-7, n° 10/50811-7 and no 12/51509-8, and ECOFOR n° 12/51872-5). We also express thanks for all researchers that collaborated in the identification of botanical material, as well as the manager and staff of the PESM.

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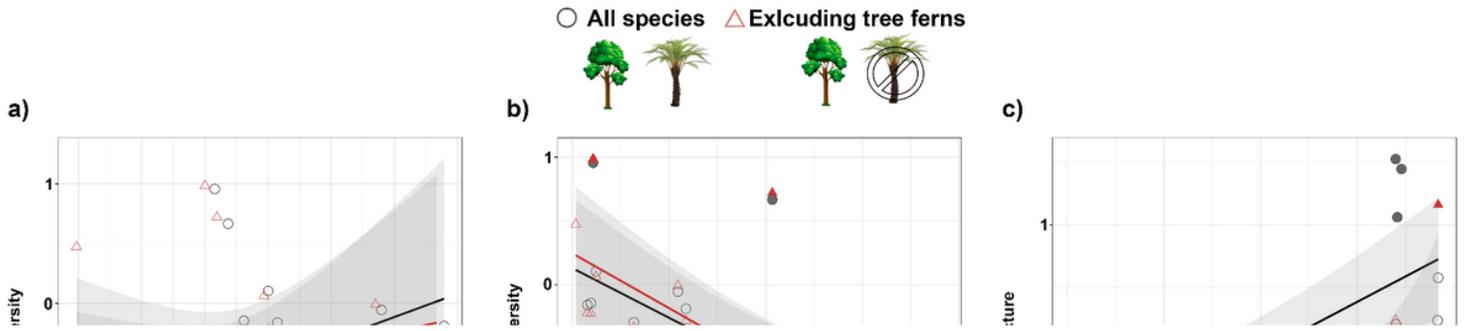
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## Figures

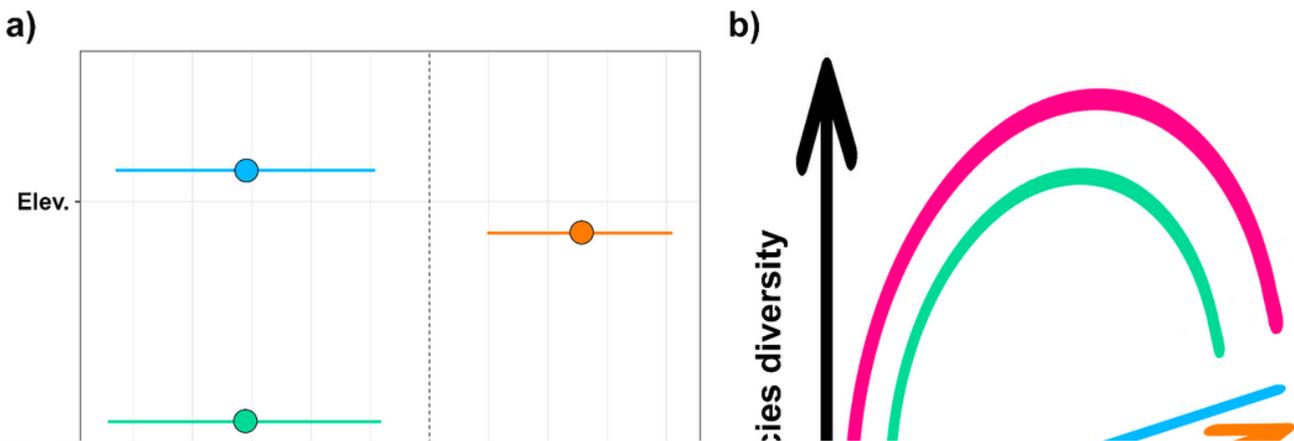
### Figure 1

Effects of elevation on Beta diversity, with species pool of 17 tree communities (plots), using both ecological and evolutionary approaches. Phylobeta diversity was computed as the fraction of PD (phylogenetic diversity or branch-lengths) shared between plots. Species beta diversity was based on species dissimilarity (Sorensen index) between pots.  $r$  – values of Pearson’s correlation from Partial Mantel tests (both  $P < 0.05$  indicated through \*).



**Figure 2**

Correlation between species and phylogenetic diversities (a) and variation across elevation in phylogenetic diversity (b) and phylogenetic structure (c). Phylogenetic diversity was computed by standardized measures of Faith’s diversity. Phylogenetic structure was assessed through standardized effect size of mean pairwise phylogenetic distances. Filled circles and triangles had significantly different phylogenetic diversity structure indexes in relation to the null model. cor – Pearson’s correlation;  $R^2$  - Nagelkerke R-Square.



### Figure 3

Effects of elevation on species diversity of the whole community and three of the richest families along the elevational gradient in the Atlantic Forest, southeastern Brazil (a), and diagram representing their relationships (b). Bars indicate the standard deviations. Two families (Rubiaceae and Melastomataceae) showed no pattern related to elevation and were not shown. Elev. -elevation; Elev.<sup>2</sup> - quadratic function of elevation.

## Supplementary Files

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