



RESEARCH ARTICLE

Water and energy availability mediate biodiversity patterns along an elevational gradient in the tropical Andes

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Abstract

Aim: How tree taxonomic and phylogenetic diversity vary with elevation at multiple spatial scales may provide new insights into the ecological and evolutionary processes influencing biogeographical patterns. The effect of water- and energy-related climatic variables on forests diversity across elevations, as well as how clades have evolved on and established across mountain regions lack consensus. Here, we tested whether changes in biodiversity with elevation are consistent with one of, or multiple, competing hypotheses: the water–energy dynamics (WED), species–energy relationship (SER), Tropical Niche Conservatism (TNC) and Out of The Tropics hypothesis (OTT).

Location: Patia watershed, Colombia

Taxon: Seed plants (trees)

Methods: We used a large dataset of 490 0.1 ha forest plots in nine elevational belts (545–3410 m a.s.l.) that correspond to three different life zones, and quantified alpha and gamma scales using taxonomic and phylogenetic diversity indices. We fitted linear mixed-effects models to evaluate how taxonomic and phylogenetic alpha diversity changed with elevation, precipitation and aboveground biomass. We assessed taxonomic and phylogenetic beta diversity using the Sørensen index and its spatial turnover and nestedness components.

Results: Taxonomic and phylogenetic alpha diversity decrease with elevation. Yet, at the gamma scale, taxonomic and phylogenetic diversity predominantly increased with elevation. Taxonomic and phylogenetic beta diversity were strongly influenced by species turnover, and followed a hump-shaped pattern with elevation.

Main conclusions: Overall, diversity shows a decreasing trend at the local scale, while coarse-scale gamma diversity followed a pattern of nonlinear increases for both taxonomic and phylogenetic diversity. Evidence supports the influence of SER and WED on diversity patterns across elevations, yet neither evolutionary hypotheses had sufficient empirical support to be conclusive.

KEYWORDS

elevational gradient, water–energy dynamics, environmental filtering, evolutionary processes, phylogenetic diversity, spatial scales, taxonomic diversity, tree diversity, tropical Andes

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1 | INTRODUCTION

Since the 18th century, scientists have been fascinated by mountains as biodiversity laboratories, where one can observe how environmental conditions, habitats and communities change with elevation across short geographical distances (Lomolino, 2001; McCain & Grytnes, 2010). Eleven of the world's biodiversity hotspots are located in tropical montane ecosystems (Malhi et al., 2010), with the tropical Andes hotspot—the most biodiverse on the planet—hosting one-sixth of all plant species in the world (Myers et al., 2000). The study of elevational gradients has a long and rich history and remains at the forefront for deepening current understanding of patterns in biodiversity, ecosystem functioning and how species respond to climate change (Antonelli et al., 2018; Bhatta et al., 2021; Bhattarai & Vetaas, 2006; Malhi et al., 2010; McCain & Grytnes, 2010; Vetaas, 2021). There is mounting evidence that tropical biota are more sensitive than species from high latitudes to climate and land-use change, highlighting the importance of tropical mountains as potential refugia for biodiversity (Feeley et al., 2020; Malhi et al., 2010; Rahbek et al., 2019). However, studies on tropical elevational gradients in tree diversity are scarce and tend to be restricted to taxonomic measures of biodiversity at local spatial scale. In contrast, evaluating multiple facets of diversity, that is, taxonomic, phylogenetic and functional diversity (Craven et al., 2018; Tucker et al., 2018), at multiple spatial scales has the potential to provide new insights to ecological processes influencing biodiversity patterns along elevational gradients (Antonelli et al., 2018).

Along elevational gradients, certain abiotic changes are expected to vary monotonously: land area, nutrient availability, atmospheric pressure, temperature, radiation and UV-B radiation (Givnish, 1999; Homeier et al., 2010; Körner, 2007). In contrast, particular climatic variables such as precipitation, wind velocity and seasonality may exhibit nonlinear or unimodal relationships with elevation (Körner, 2007). The majority of previous studies have shown that trees show a monotonous decrease in species richness with elevation in both temperate and tropical elevational gradients (Aiba & Kitayama, 1999; Brambach et al., 2017; Gentry, 1988; Givnish, 1999; Homeier et al., 2010; Kessler, 2002; Lieberman et al., 1996; Peters et al., 2019). The decline in diversity is mostly attributable to a decrease in temperature with elevation, directly impacting nutrient availability (Givnish, 1999; Homeier et al., 2010; Leuschner et al., 2007; but see Bhatta et al., 2021; Vetaas et al., 2019). Decreased habitat area and forest structure impact diversity negatively as well (Givnish, 1999; Vazquez & Givnish, 1998). However, in regions with lower precipitation at lower elevations, changes in precipitation and nutrient availability may support an initial increase in tree diversity with elevation, followed by a subsequent decrease towards higher elevations (i.e. hump-shaped pattern) (Givnish, 1999; McCain & Grytnes, 2010; Rahbek, 2004). Furthermore, some studies have shown little to no change in tree species richness with changes in elevation (Tallents et al., 2005; Vazquez & Givnish, 1998). Nevertheless, differences in spatial scale (Antonelli et al., 2018; Rahbek, 2004), sampling design and effort and anthropogenic disturbances may also

influence the direction and shape of elevational diversity patterns (Laiolo et al., 2018; McCain & Grytnes, 2010).

Two prominent ecological hypotheses offer an explanation for the variation in diversity along environmental gradients, such as those found along elevational gradients: (i) species–energy relationship (SER) and (ii) water–energy dynamics (WED). First, the SER posits that total energy availability (i.e. solar radiation and its proxies, such as net primary productivity (NPP), potential evapotranspiration (PET) and actual evapotranspiration (AET)) imposes constraints on population sizes in a given area and therefore influences species richness (Currie, 1991; Wright, 1983). Consequently, areas with lower energy availability are expected to have smaller populations, higher extinction rates and lower species richness than areas with more available energy and vice versa (Carrara & Vázquez, 2010). Second, WED describe diversity (specifically species richness) as a result of the interaction between water availability and energy, where the highest amount of diversity should be reached at peak levels of water availability and intermediate amounts of energy (Hawkins et al., 2003; O'Brien, 1993, 2006; O'Brien et al., 1998; Vetaas et al., 2019). Water variables have been shown to better predict plant diversity patterns in warmer areas, whereas energy-related variables are dominant predictors in colder areas (Hawkins et al., 2003; Kreft & Jetz, 2007). However, the relative importance of SER and WED in determining tree diversity patterns across elevations is uncertain.

Elevational diversity gradients have also been explained by evolutionary hypotheses related to temperature changes with elevation, mirroring environmental variations that occur with increases in latitude (Webb et al., 2002). For instance, the Tropical Niche Conservatism hypothesis (TNC) seeks to explain the latitudinal diversity gradient in species richness, which it attributes to (1) tropical lineages having had longer periods to evolve (i.e. older average clade age than non-tropical ones), (2) colonization of extra-tropical environments is both rare and phylogenetically conserved due to a lack of adaptations to harsher conditions (i.e. cold temperatures and water deficit) and that (3) tropical areas covered more area not long ago, which is why many species originated in the tropics (Ramírez et al., 2019; Wiens & Donoghue, 2004; Wiens & Graham, 2005). Importantly, the TNC can also be applied to tropical montane regions like the tropical Andes, where the shorter time for species establishment due to the younger age of these high mountain environments may explain low diversity in some species lineages (Qian et al., 2019; Qian & Ricklefs, 2016; Ramírez et al., 2019), as well as increased relatedness among species with elevation due to strong environmental filtering for phylogenetically conserved traits, leading to phylogenetic clustering (Webb et al., 2002; Wiens & Donoghue, 2004). However, drought may affect phylogenetic diversity patterns along elevational gradients, as dry biomes typically have lower phylogenetic diversity than those that experience less drought (Neves et al., 2021). In contrast, the Out of The Tropics hypothesis (OTT) suggests that despite evolutionary clades having mostly originated in the tropics, some of these clades increased their distributions towards higher latitudes where slow diversification

processes—compared to the ones in the tropics—took place, consequently increasing average clade age with latitude (Jablonski et al., 2006; Qian & Ricklefs, 2016). Similar to the TNC, the OTT hypothesis has been used to elucidate diversity shifts along elevational gradients (Hughes & Eastwood, 2006), leading to phylogenetic overdispersion (Qian et al., 2014; Qian & Ricklefs, 2016). Such phylogenetic overdispersion could arise, for example, due to immigration from non-tropical lineages with adaptations to harsh conditions to tropical highlands (Ramírez et al., 2019).

In contrast to taxonomic diversity patterns along elevational gradients (McCain & Grytnes, 2010), comparatively less is known about phylogenetic diversity patterns, which may provide more mechanistic insights into how diversity shifts across elevations (e.g. Culmsee & Leuschner, 2013; Qian et al., 2014; Segovia et al., 2020). Indeed, phylogenetic diversity is strongly correlated with high-dimensional trait diversity (Tucker et al., 2018), suggesting that it can provide insights to the diversity of resource-use strategies within assemblages, particularly in regions of the world where trait data are not widely available (Cornwell et al., 2019). Phylogenetic diversity patterns, therefore, can reveal the relative importance of biotic and abiotic factors in shaping community assembly of forest ecosystems. Biotic interactions such as competition are expected to increase divergence of traits (i.e. overdispersion) (Webb et al., 2002), and thus are stronger in highly productive and stable environments (e.g. high precipitation and temperature). On the other hand, environmental filtering is likely to be stronger under harsher environmental conditions (e.g. low precipitation and temperature) and selects for similar phenotypes, therefore decreasing trait divergence (i.e. clustering) (Jarzyna et al., 2021; Kraft et al., 2015), a pattern that is consistent with niche conservatism (Wiens & Graham, 2005).

Diversity patterns at biogeographical scales such as the latitudinal diversity gradient or elevational gradients can be driven by multiple processes acting at multiple spatial scales (Ricklefs, 2004). For example, coarse-scale processes (e.g. speciation, extinction and dispersal) can influence local diversity patterns (Gaston, 2000; Ricklefs, 1987), while community assembly processes can drive larger-scale processes as well (Schemske et al., 2009). Beta diversity links landscape-scale gamma diversity with local-scale alpha diversity and can help unveil these multi-scale effects and their underlying ecological processes (e.g. habitat filtering and biotic competition) (Kraft et al., 2011; Qian & Ricklefs, 2007). Across multiple taxa, beta diversity has been shown to decrease with an increase in latitude as environmental conditions become less favourable (Soininen et al., 2018). Furthermore, the spatial turnover component of beta diversity is its largest component and is positively correlated with beta diversity itself, but negatively correlated with its nestedness component (Soininen et al., 2018). However, there are few empirical studies on phylogenetic beta diversity patterns, which can detect terminal or basal turnover among communities (Swenson, 2011). Under the TNC hypothesis, nestedness is expected to be the dominant pattern driving phylogenetic beta diversity because most species originate in the tropical lowlands and only a small subset of phylogenetically conserved lineages disperses into higher elevations

(Ramírez et al., 2019). Under the OTT hypothesis, in contrast, the turnover component is expected to have a stronger influence on phylogenetic beta diversity because elevations have lineages with divergent evolutionary histories (Peixoto et al., 2017). Consequently, the mean clade age of biological communities is expected to increase with elevation and phylogenetic relatedness to decrease, a trend thought to reflect niche convergence (Qian & Ricklefs, 2016).

In this study, we examined taxonomic and phylogenetic diversity from local to landscape scales in tropical forests along a 2865-m elevational gradient in southwest Colombia. We hypothesized that (1) taxonomic and phylogenetic diversity at both alpha and gamma scales exhibit a hump-shaped relationship with elevation, as water availability and temperature likely limit diversity at the lower part of the gradient (Givnish, 1999; McCain & Grytnes, 2010); (2) variation in taxonomic and phylogenetic diversity along the elevational gradient is mediated by annual precipitation, one of the variables tested for WED (Hawkins et al., 2003; O'Brien, 2006), and aboveground biomass, a proxy for SER (Currie, 1991; Wright, 1983); (3) following the OTT, tree communities are phylogenetically overdispersed at both alpha and gamma scales and (4) beta taxonomic and phylogenetic diversity peaks at mid-elevations, and is more strongly determined by the spatial turnover component due to environmental filtering (Kraft et al., 2015; Myers et al., 2013; Socolar et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Study area and data structure

This study was conducted in the Patia watershed in the southwest of Colombia (lat. 1.97, long. -76.81). The 2865-m elevational gradient in Western Andean cordillera ranges from 545 to 3410 m a.s.l, but includes a 1200-m gap between 900 and 2100 m a.s.l without forest plots due to the large-scale conversion to coffee plantations. Consequently, we analysed the elevational gradient in two different ways: (1) across Holdridge life zones (hereon referred to as *ecosystem belts*; Holdridge, 1947) and (2) across 200-m elevation belts (hereon referred to as *elevational belts*). We divided the elevational gradient into three ecosystem belts: (i) the lowest ecosystem belt consists of tropical dry forest (500–1200 m a.s.l.), which transitions to (ii) a lower montane moist forest (1200–2500 m a.s.l.), and (iii) to a montane wet forest (2500–3500 m a.s.l.) comprising the highest ecosystem belt. Overall, both mean temperature and potential evapotranspiration (PET) decrease with increasing elevation (Figure S2), while mean annual precipitation follows a high-plateau pattern along the elevational gradient (Figure 1b).

2.2 | Field data

Trees were measured and identified in a total of 490 0.1 ha forest plots, with 85 plots in the lower ecosystem belt, 141 plots in the middle ecosystem belt and 264 plots in the upper ecosystem belt.

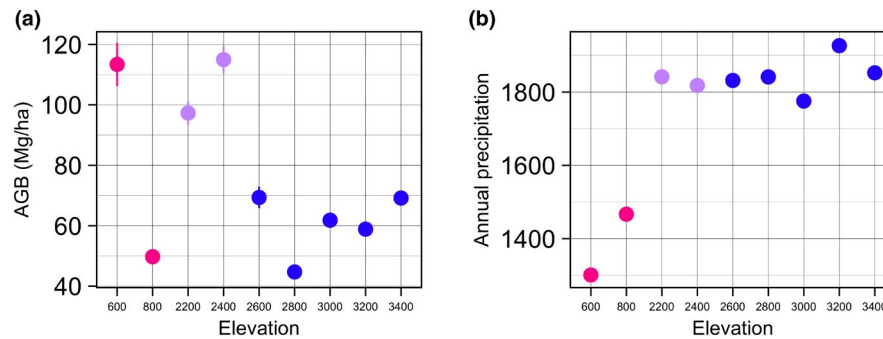


FIGURE 1 (a) Plot-level aboveground biomass (AGB) in megagrams per hectare across elevational belts (m a.s.l.) in the Patia watershed, Colombia. (b) Mean annual precipitation in millimeters per plot across elevational belts in the Patia watershed, Colombia. Note the break in elevation between 800 and 2200 m a.s.l. Points represent mean AGB or annual precipitation and whisker bars are 95% confidence intervals. Each colour represents a life zone subdivision within the elevational gradient: pink is tropical dry forest, purple is lower montane moist forest and blue is montane wet forest

Plots were established in areas with homogeneous forest patches and representative vegetation for each ecosystem belt and without noticeable evidence of recent anthropogenic disturbances (Figure S1). In each plot, all live trees with a diameter at breast height (DBH) ≥ 10 cm were recorded and identified. DBH and total height (m) were measured with a DBH tape and a clinometer respectively. We note that due to the DBH cut-off, we may be excluding proportionately more tree species in the tropical dry forest than from the other ecosystem belts. Species were identified by a local expert, and additionally specimens of all sampled trees were taken to the Universidad del Cauca's herbarium (CAUP) for validation. Across all plots, a total of 280 different tree species were recorded, 246 of which were identified to the species level and 34 to the genus level.

2.3 | Data preparation

2.3.1 | Taxonomic standardization

Species names were standardized based on the Taxonomic Name Resolution Service (Boyle et al., 2013), The Plant List (The Plant List, 2013), Tropicos (Missouri Botanical Garden, 2021) and PLANTS (National Plant Data Team, 2021) using the *tnrs* function of the R package 'TNRS' (Boyle et al., 2021). This step left a total of 270 accepted species. We restricted our analysis to angiosperms only, as the inclusion of gymnosperms may result in unusual phylogenetic measures (Qian et al., 2017). We therefore removed three non-angiosperm species from our dataset, leaving a total of 267 species for all subsequent analyses.

2.3.2 | Phylogeny

We constructed a phylogenetic tree for all tree species in our inventory using the seed plant phylogeny of Smith and Brown (2018) as a backbone, and then conservatively bound species onto the backbone using dating information from congeners in the tree with the

congeneric.merge function of the R package 'pez' (Pearse et al., 2015). This function was chosen because 34 species in the inventory were identified only to the genus level, which were placed on the phylogeny as polytomies. A total of 261 species could be placed on the phylogeny, representing 97.8% of all species.

2.3.3 | Stratified random sampling

We employed stratified random sampling to account for the effects of different numbers of plots per elevational belts on taxonomic and phylogenetic diversity. We therefore randomly sampled 18 plots with replacement per elevational belt 100 times using the *sample_n* function in the R package 'dplyr' (Wickham et al., 2020). All analyses presented here are based on these stratified, random subsamples of the data.

2.3.4 | Energy and climatic variables

We calculated aboveground biomass (AGB) as a direct measure of energy across and within elevations using the R package 'BIOMASS' (Réjou-Méchain et al., 2017) (Figure 1a). To account for the propagation of errors in the estimation of AGB (Molto et al., 2013), we used the function *AGBmonteCarlo*. We estimated AGB per tree using DBH and height measurements from the plot inventory, and wood density values from the global wood density (GWD) database (Chave et al., 2009; Zanne et al., 2009) at the species, genus or family levels.

In our study area, mean annual precipitation (mm/year) (hereafter precipitation) is higher than PET in most (7 of 9) elevational belts (Figure S2b). As a result, PET is equivalent to actual evapotranspiration (AET) and, therefore, AET would be highly correlated with precipitation. For this reason, precipitation is a more parsimonious estimate of water availability than a full WED model (O'Brien, 2006). Furthermore, precipitation regulates water available to plants and therefore has a strong influence on plant diversity (Kreft & Jetz, 2007). Information for precipitation was derived from the

Climatologies at High Resolution for the Earth's Land Surface Areas (CHELSA) dataset at a 1-km resolution (Karger et al., 2017).

2.4 | Taxonomic diversity

We estimated plot (alpha) and elevational belt-level (gamma) taxonomic diversity as species richness (S), rarefied species richness (S_n) and the probability of interspecific encounter (PIE) in terms of the effective number of species (S_{PIE}). In this framework, species richness is the diversity of order zero ($q = 0, {}^0D$) and does not take into account species abundances (Jost, 2006). S is the total number of species present in each plot (alpha) or in each elevational belt (gamma), and gives equal weight to common and rare species. Rarefied number of species (S_n) is the expected number of species for a defined number of individuals (n) (Gotelli & Colwell, 2001). We rarefied species richness using 10 individuals, that is, the lowest of individuals that permitted comparisons among plots, for the alpha scale and 800 (10 individuals \times 80 plots per belt) for the gamma scale. Effective number of species (S_{PIE}) is the effective number of species that is derived from the probability of interspecific encounter (PIE), which is a measure of evenness and is equivalent to Simpson's diversity (McGlenn et al., 2019). All taxonomic diversity indices were estimated using the R package 'mobr' (Xiao et al., 2019).

Baselga (2010) proposes to deconstruct beta diversity into two components: species turnover and nestedness. High nestedness occurs when low-diversity assemblages are subsets of a larger community (Ulrich & Gotelli, 2007). In contrast, species turnover is the replacement of species across space due to changes in environmental conditions or spatial and historical constraints (Qian et al., 2005; Soininen et al., 2018). We calculated taxonomic beta diversity (β SOR) and its turnover (β SIM) and nestedness (β SNE) components using the Sørensen index and the *beta.multi* function of the R package 'betapart' (Baselga & Orme, 2012). This function calculates total dissimilarity and its components across all plots—within one elevational belt—based on a presence-absence matrix (Baselga & Orme, 2012).

2.5 | Phylogenetic diversity

We estimated alpha- and gamma-level phylogenetic diversity using three indices that target different components of evolutionary history because different ecological processes might influence community structure at different evolutionary time-scales (Mazel et al., 2016): (i) Faith's PD (PD; Faith, 1992) provides an evolutionary overview of the relationships among species of an assemblage, (ii) mean pairwise distance (MPD; Webb et al., 2002) and (iii) mean nearest taxon distance (MNTD; Webb, 2000) in turn emphasize different aspects of the phylogenetic structure of assemblages. MPD is more influenced by the basal structure of the phylogenetic tree and reflects older evolutionary relationships, while MNTD highlights the evolutionary relationships at the tips of the phylogeny and therefore captures more recent evolutionary history (Webb et al., 2002). To mirror the taxonomic diversity indices,

we calculated all phylogenetic diversity metrics accounting for species abundances. All PD metrics were calculated using the functions *pd.query*, *mpd.query* and *mntd.query* of the R package 'PhyloMeasures' (Tsirogianis & Sandel, 2016).

We also calculated phylogenetic beta diversity (β SOR) and its turnover (β SIM) and nestedness (β SNE) components based on Faith's PD using the Sørensen index with the function *phylo.beta.multi* of the R package 'betapart' (Baselga & Orme, 2012). As for phylogenetic gamma and alpha diversity, we calculated phylogenetic beta diversity accounting for species abundances.

We used null models to compare observed and randomized species assemblages to evaluate differences in community structure (Kembel & Hubbell, 2006; Kluge & Kessler, 2011). We generated null communities using the 'frequency.by.richness' model of the R package 'PhyloMeasures', which holds species richness per plot constant while randomizing species co-occurrence (Tsirogianis & Sandel, 2016). We generated 1000 null communities for each subsample of the data.

We then calculated standardized effect sizes (SES) to test for phylogenetic clustering and overdispersion, where values higher than 0 show overdispersion (i.e. species are less related than expected) and values lower than 0 show clustering (i.e. species are more related than expected). For each phylogenetic metric, that is, Faith's PD, MPD and MNTD, we calculated SES at the alpha and gamma scales as follows (Gotelli & Rohde, 2002):

$$SES = \frac{\text{Observed value} - \text{Mean value (null model)}}{\text{Standard deviation (null model)}}$$

SES estimations were made using the function *pd.query*, *mpd.query* and *mntd.query* of the R package 'PhyloMeasures' (Tsirogianis & Sandel, 2016). We only interpreted SES values that are significantly greater than ± 1.96 .

2.6 | Statistical analysis

At the beta and gamma scales, we estimated means and 95% confidence intervals for each elevational belt using all subsamples of the data for all metrics of taxonomic and phylogenetic diversity. We interpreted statistically significant differences across elevational belts if confidence intervals did not overlap.

At the alpha scale, we examined the influence of elevation, precipitation and AGB on the different indices of taxonomic and phylogenetic diversity using linear mixed-effects models with the R package 'lme4' (Bates et al., 2015). In all models, we used a random intercept term for subsample (Bates et al., 2015). Wald Chi-square tests were calculated for fixed effects with the *Anova* function in the R package 'car' (Fox & Weisberg, 2019). Model assumptions, that is, homogeneity of variance and distribution of model residuals, were evaluated visually. We visualized the relationship between diversity indices and the variables tested using the R package 'ggeffects' (Lüdtke, 2018). To investigate how spatial autocorrelation between plots might affect our results, we calculated Moran's I for the residuals of all models using the *correlog* function of the 'pgrmness' package

(Giraudoux, 2021). Residuals from all models show no significant levels of spatial autocorrelation (Figure S3).

All analysis were conducted in R version 3.6.0 (R Core Team, 2019), using packages: 'dplyr' (Wickham et al., 2020), 'tidyr' (Wickham & Henry, 2019), 'stringr' (Wickham, 2019), 'Hmisc' (Harrell Jr., 2019), 'TNRs' (Boyle et al., 2021), 'Taxonstand' (Cayuela et al., 2021), 'BIOMASS' (Réjou-Méchain et al., 2017), 'mobr' (Xiao et al., 2019), 'betapart' (Baselga & Orme, 2012), 'pez' (Pearse et al., 2015), 'picante' (Kembel et al., 2010), 'PhyloMeasures' (Tsirogianis & Sandel, 2016), 'lme4' (Bates et al., 2015), 'ggeffects' (Lüdecke, 2018), 'ggplot2' (Wickham, 2016), 'cowplot' (Wilke, 2019), 'patchwork' (Pedersen, 2020), 'car' (Fox & Weisberg, 2019) and 'pgirmess' (Giraudoux, 2021).

3 | RESULTS

3.1 | Effects of elevation, precipitation and aboveground biomass on taxonomic and phylogenetic alpha diversity

At the local scale, all three taxonomic diversity indices showed a statistically significant relationship with elevation (Table 1; $p < 0.01$). Species richness, rarefied number of species and effective number of species followed a similar overall decreasing trend with elevation, however, diversity values fluctuated greatly along the gradient (Figure 2a,d,g). Furthermore, for all taxonomic diversity indices, both the highest and the lowest diversity values were found in the tropical montane wet forest (Figure 2a,d,g; blue

points). While all indices were significantly affected by mean annual precipitation (Table 1; $p < 0.01$), rarefied number of species (Figure 2e) was not associated with this variable, species richness had a nonlinear decrease (Figure 2b) and effective number of species exhibited subtle yet positive linear relationships with mean annual precipitation (Figure 2h). Moreover, as for elevation and precipitation, all three taxonomic diversity indices had a statistically significant relationship with AGB (Table 1; $p < 0.01$). Species richness showed a saturating trend (Figure 2c), effective number of species had a subtle negative linear relationship with AGB (Figure 2i) and rarefied number of species had no relationship with this variable (Figure 2f).

At the local scale, PD, MPD and MNTD showed a statistically significant relationship with elevation, mean annual precipitation and AGB (Table 1; $p < 0.01$). All three phylogenetic diversity indices followed a general decreasing pattern of alpha diversity across elevations (Figure 3a,d,g). In all cases, the 2500–2700 m a.s.l. elevational belt (Figure 3a,d,g) displayed the lowest values of diversity. Additionally, we found the elevational belts with the highest phylogenetic diversity were in the tropical dry forest and the montane wet forest for PD (Figure 3a), and the lower montane moist forest for MPD and MNTD (Figure 3d,g). Although MPD and MNTD were not associated with mean annual precipitation (Figure 3e,h), PD showed a U-shaped relationship with this variable (Figure 3b). Similarly, PD was the only index with a saturating relationship with AGB (Figure 3c), while MPD and MNTD did not have an association with this variable (Figure 3f,i).

At the local scale, standardized phylogenetic diversity indices were significantly influenced by elevation, annual precipitation and

TABLE 1 ANOVA summaries of the mixed-effects models examining variation in taxonomic diversity, phylogenetic diversity and standardized values of phylogenetic diversity across elevations (m a.s.l.), annual precipitation (mm/year) and aboveground biomass (AGB; Mg/ha) in tropical forests in the Patia watershed, Colombia. Each summary shows the Wald chi-square (Statistic), degrees of freedom (df) and the p value for each effect

	Species richness (S)			Rarefied number of species (Sn)			Effective number of species PIE (SPIE)		
	Statistic	df	p value	Statistic	df	p value	Statistic	df	p value
Elevation	2129.467	8	<0.001	1924.281	8	<0.001	2166.522	8	<0.001
Scale AGB	6430.716	2	<0.001	78.61762	2	<0.001	131.801	1	<0.001
Scale precipitation	124.8348	2	<0.001	58.76603	2	<0.001	86.09208	1	<0.001
	Faith's PD			MPD			MNTD		
	Statistic	df	p value	Statistic	df	p value	Statistic	df	p value
Elevation	2398.707	8	<0.001	2002.928	8	<0.001	1724.334	8	<0.001
Scale AGB	5119.918	2	<0.001	19.71698	2	<0.001	2673.28	2	<0.001
Scale precipitation	207.2034	2	<0.001	549.2473	2	<0.001	872.6401	2	<0.001
	Standardized faith's PD			Standardized MPD			Standardized MNTD		
	Statistic	df	p value	Statistic	df	p value	Statistic	df	p value
Elevation	2751.241	8	<0.001	2508.821	8	<0.001	2528.534	8	<0.001
Scale AGB	388.232	2	<0.001	378.3632	2	<0.001	365.1416	2	<0.001
Scale precipitation	1251.663	2	<0.001	551.0255	2	<0.001	1281.82	2	<0.001

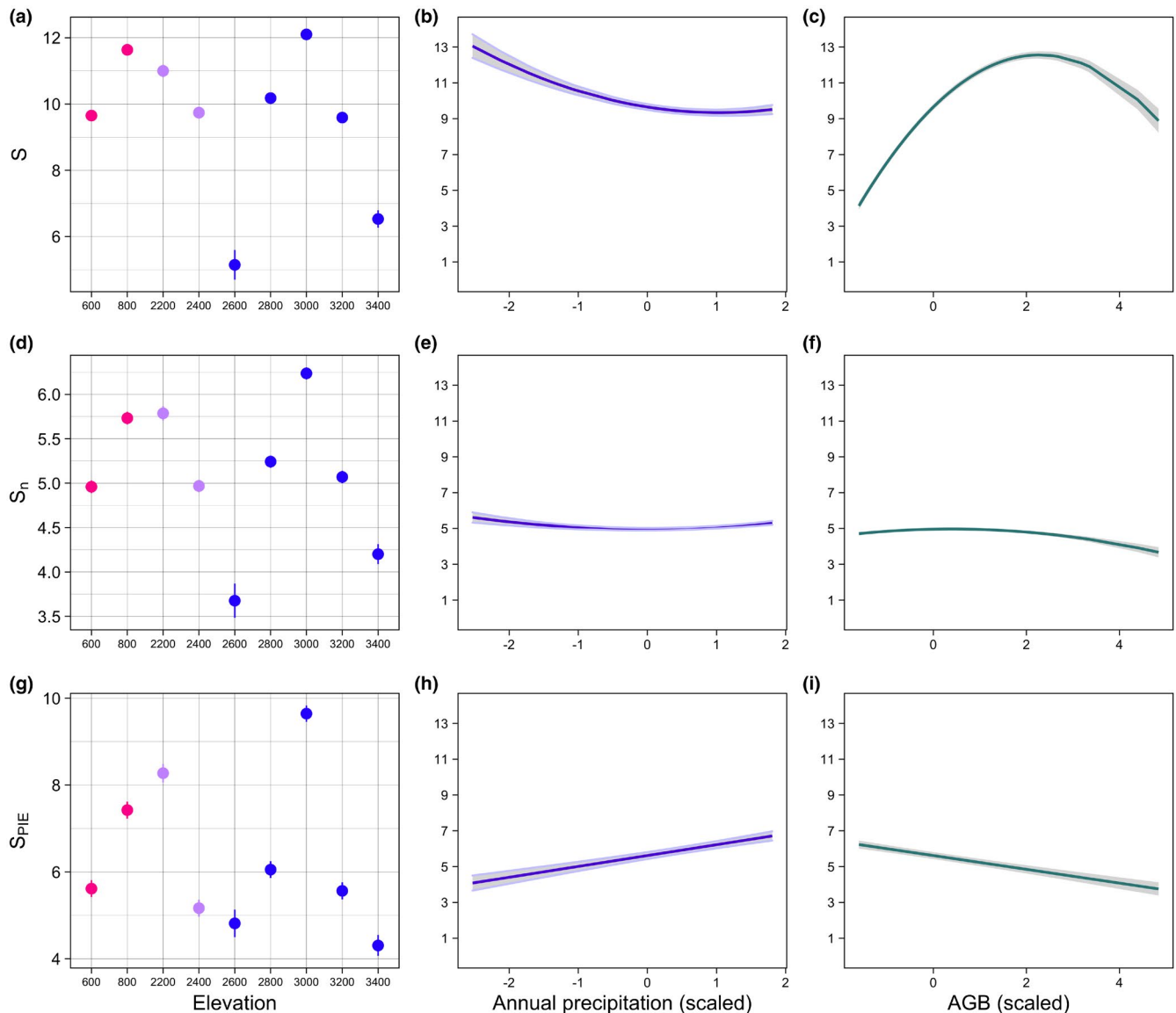


FIGURE 2 Effects of elevation (m a.s.l.), annual precipitation (mm/year) and aboveground biomass (AGB; Mg/ha) on species richness (S ; panels a–c), rarefied number of species (S_n ; panels d–f) and the probability of interspecific encounter (PIE) in terms of effective number of species (S_{PIE} ; panels g–i) of tropical forests in the Patia watershed, Colombia. Note the break in elevation between 800 and 2200 m a.s.l. Precipitation and AGB were standardized with a z-transformation. Points (left column; panels a, d & g) and curves (centre and right columns; panels b, c, e, f, h & i) are mixed-effects model fits, and shaded bands are 95% confidence intervals (centre and right columns). Linear mixed-effects models were fitted to 100 subsamples, each with 18 plots per elevational belt. Each colour represents a life zone subdivision within the elevational gradient: pink is tropical dry forest, purple is lower montane moist forest and blue is montane wet forest

aboveground biomass (Table 1; $p < 0.01$). All three indices followed a similar, yet variable pattern of diversity across elevations, with an overall decreasing trend (Figure S4a,d,g). PD, MPD and MNTD showed a nonlinear ‘U’ relationship of standardized phylogenetic diversity with precipitation (Figure S4b,e,h). Similarly, the relationship of standardized phylogenetic diversity with AGB was a nonlinear ‘U’ trend across all three indices. Furthermore, all standardized phylogenetic diversity indices at most elevational belts displayed values with 95% confidence intervals that overlapped with zero, showing no support for phylogenetic clustering or overdispersion (Figure S4). Yet, there were exceptions to this trend for the 2500–2700 m a.s.l.

elevational belts for all indices and the highest elevational belt for MPD, where values were negative; patterns consistent with phylogenetic clustering (Figure S4a,d,g).

3.2 | Effects of elevation on taxonomic and phylogenetic beta diversity

Across elevations, taxonomic beta diversity (β_{SOR}) was dominated by its turnover component (β_{SIM}) (Figure 4). Taxonomic beta diversity (β_{SOR}) and its spatial turnover component (β_{SIM})

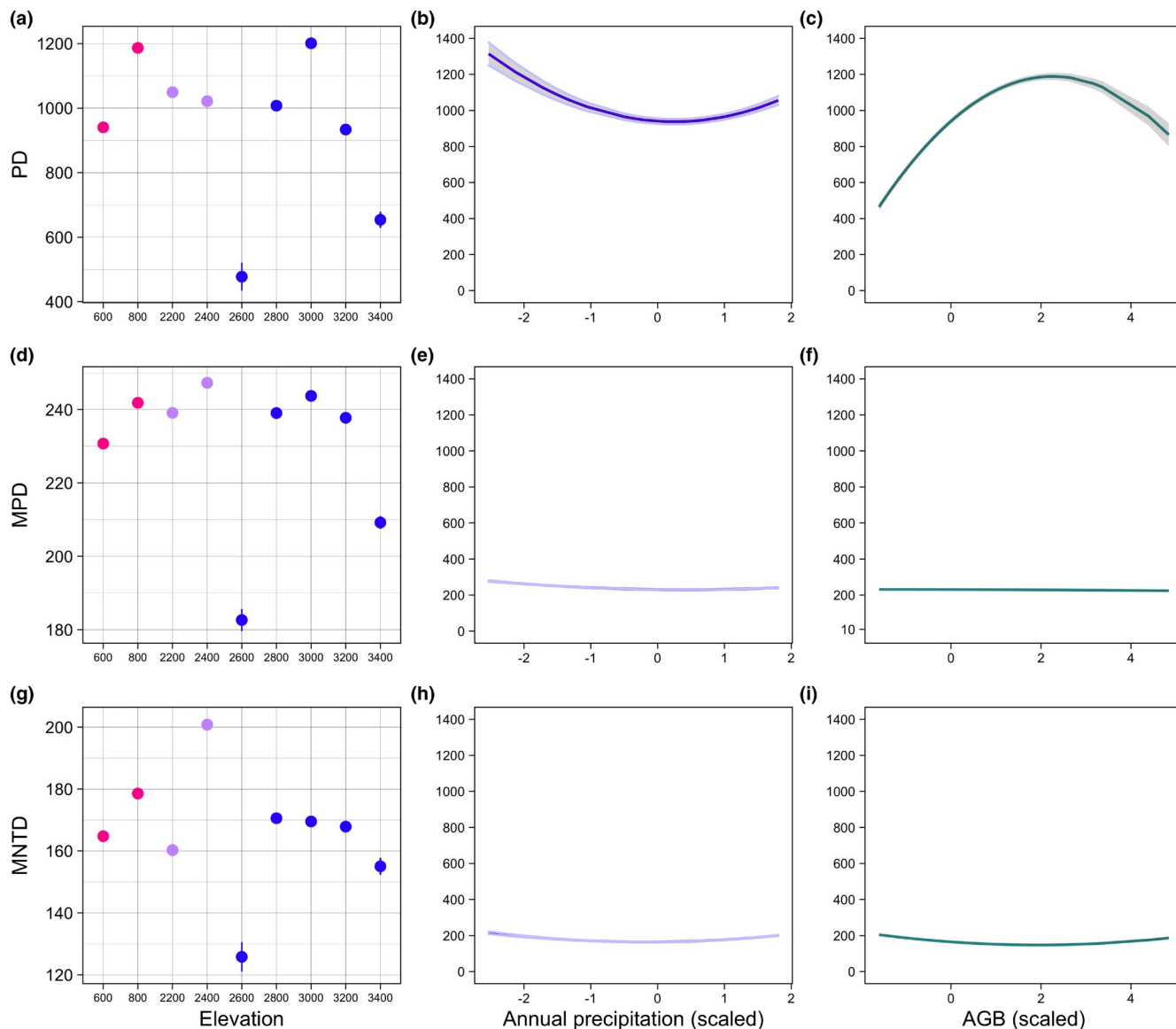


FIGURE 3 Effects of elevation (m a.s.l.), annual precipitation (mm/year) and aboveground biomass (AGB; Mg/ha) on three different phylogenetic diversity indices: Faith's PD (PD; panels a–c), mean pairwise distance (MPD; panels d–f) and mean nearest taxon distance (MNTD; panels g–i) of tropical forests in the Patia watershed, Colombia. Note the break in elevation between 800 and 2200 m a.s.l. Precipitation and AGB were standardized with a z-transformation. Points (left column; panels a, d & g) and curves (centre and right columns; panels b, c, e, f, h & i) are mixed-effects model fits, and shaded bands are 95% confidence intervals (centre and right columns). Linear mixed-effects models were fitted to 100 subsamples, each with 18 plots per elevational belt. Each colour represents a life zone subdivision within the elevational gradient: pink is tropical dry forest, purple is lower montane moist forest and blue is montane wet forest

followed a hump-shaped pattern with the lowest values towards lower elevations (Figure 4a,b). In contrast, the nestedness component of beta diversity (β SNE) decreased with elevation, until reaching a low plateau towards the upper part of the elevational gradient (Figure 4c).

As found for taxonomic beta diversity, phylogenetic beta diversity (β SOR) was dominated by its turnover component (β SIM) (Figure 4). Both β SOR and β SIM followed a hump-shaped pattern with their lowest values at lower elevations, peaking at mid-elevations with only a slight decrease towards higher elevational belts (Figure 4d,e). As with taxonomic beta diversity, the nestedness component (β SNE)

of phylogenetic beta diversity showed a low-plateau pattern, with an initial decrease followed by low variability towards higher elevations (Figure 4f).

3.3 | Effects of elevation on taxonomic and phylogenetic gamma diversity

Gamma diversity (Figure 5) exhibited a general increasing trend with elevation for all taxonomic diversity indices tested (Figure 5a), while displaying different intensities of variation

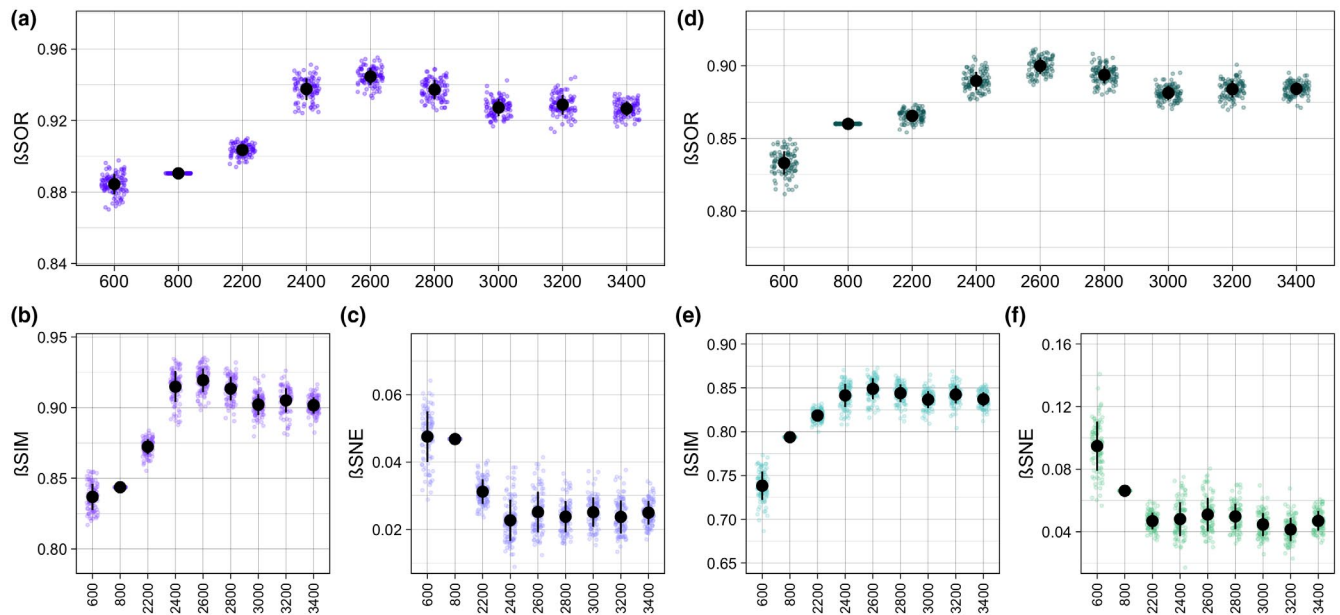


FIGURE 4 Taxonomic and phylogenetic beta diversity across elevations (m a.s.l.) of tropical forests in the Patia watershed, Colombia. (a) Taxonomic beta diversity (β SOR) using the Sørensen index and its two components, spatial turnover (b; β SIM) using the Simpson index and nestedness (c; β SNE). (d) Phylogenetic beta diversity (β SOR) using the Sørensen index and its two components, spatial turnover fraction (e; β SIM) using the Simpson index and nestedness (f; β SNE). Note the break in elevation between 800 and 2200 m a.s.l. Black points represent average phylogenetic beta diversity and its two components derived from 100 randomly sampled subsets of 18 plots within each elevational belt. Coloured points are individual values of each subsample, and whisker bars are the 95% confidence intervals

across the gradient. Species richness was the index with the steepest increase with elevation, while rarefied species number and effective number of species increased to a lesser degree (Figure 5a).

Across indices, phylogenetic gamma diversity showed different patterns across elevations (Figure 5b). MPD exhibited no change across the entire gradient. In contrast, MNTD increased initially at lower elevations, followed by a low plateau. Lastly, PD exhibited a high-plateau pattern, showing an increase at lower elevations that later stagnated (Figure 5b).

Variation in standardized phylogenetic gamma diversity with elevation (Figure 5c) followed a similar overall increasing trend across indices, yet with different intensities. With the exception of the lowest elevational gradient (500–700 m a.s.l.), the 95% confidence intervals for most elevational belts for PD, MPD and MNTD overlapped with zero (Figure 5c), indicating neither phylogenetic overdispersion nor phylogenetic clustering.

4 | DISCUSSION

In this study, we find contrasting patterns in taxonomic and phylogenetic diversity with elevation across spatial scales—patterns that are most likely driven by meso-climatic conditions. Furthermore, we find that environmental filtering has a stronger influence on community assembly across spatial scales, especially at the lower ecosystem belt, and that biotic interactions strengthen towards higher elevations.

4.1 | Taxonomic and phylogenetic diversity patterns with elevation

Taxonomic and phylogenetic diversity indices showed similar patterns for alpha diversity across elevations. All three taxonomic diversity indices showed an overall decreasing diversity trend across elevations, which has been found previously in tropical mountains. However, there were considerable fluctuations across elevational belts, mainly in montane wet forest ecosystems, which displayed both the highest and lowest values of diversity for all indices. This suggests that montane wet forests host on average both the more locally rare species and the less locally rare species, while the tropical dry forest and the lower montane moist forest exhibited less variation. In contrast to previous studies (see González-Caro et al., 2020), PD followed an overall decreasing (yet highly variable) pattern with elevation which, as expected, correlates with the one found for species richness (Tucker & Cadotte, 2013). MPD and MNTD also showed a similar trend.

In contrast to the frequently reported pattern of decreasing taxonomic species diversity with increasing elevation in tropical forests (Brambach et al., 2017; Culmsee & Leuschner, 2013; Gentry, 1988; Givnish, 1999; Kraft et al., 2011; Rosenzweig, 1995), we found that taxonomic gamma diversity increased with elevation for all diversity indices. This finding might be explained by the fact that the lower elevational belts in our study are dominated by tropical dry forests, whereas most tropical elevational studies start in the humid lowland forests (e.g. Aiba & Kitayama, 1999; Brambach et al., 2017; Griffiths et al., 2020; Ramírez et al., 2019). Tropical dry forests are strongly constrained by water availability (Allen et al., 2017), and in

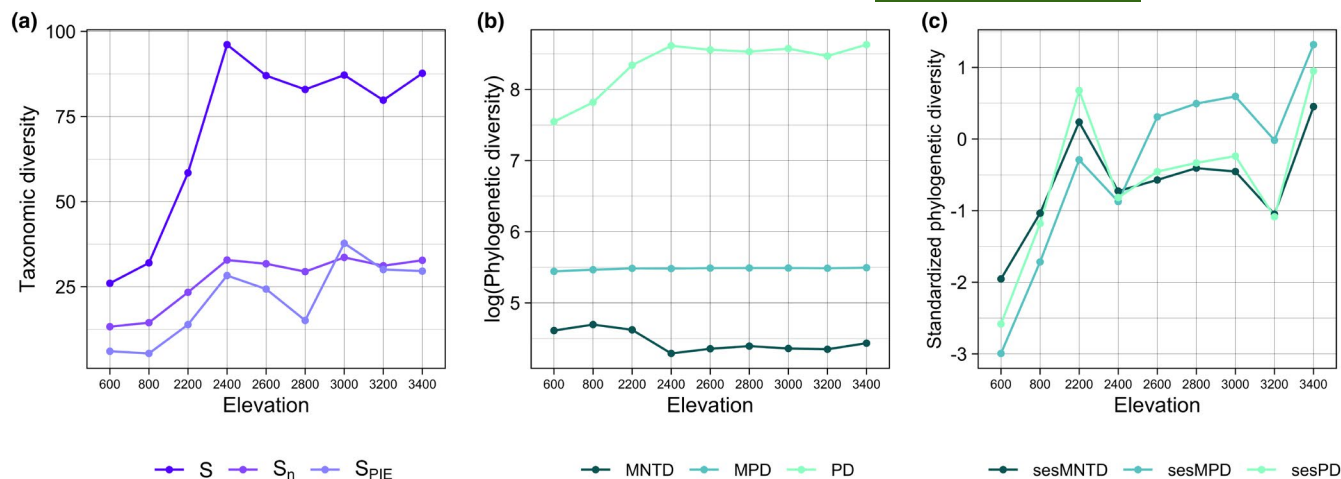


FIGURE 5 Gamma diversity of tropical tree communities across seven elevational belts (m a.s.l.) in the Patia watershed, Colombia, derived from 100 randomly sampled subsets of 18 plots per elevational belt. (a) Taxonomic gamma diversity showing variation in patterns of: tree species richness (S), rarefied number of species (S_n) and the probability of interspecific encounter (PIE) in terms of the effective number of species (S_{PIE}). (b) Phylogenetic gamma diversity, weighted by species abundances of: Faith's PD (PD), mean pairwise distance (MPD) and mean nearest taxon distance (MNTD). Note the break in elevation between 800 and 2200 m a.s.l. Phylogenetic diversity indices were natural log transformed for visual clarity. (c) Standardized phylogenetic gamma diversity for Faith's PD (sesPD), mean pairwise distance (sesMPD) and mean nearest taxon distance (sesMNTD)

this elevational gradient, precipitation increases towards higher elevations where lower montane moist and montane wet forests occur. For this reason, it is likely that the increase in diversity with elevation reflects the moisture gradient rather than the elevational one (Cavieres et al., 2006; Hawkins et al., 2003; Körner, 2007). Similarly, phylogenetic gamma diversity showed an increasing pattern for PD and MPD, which is in line with studies in tropical mountains in Asia and the Americas (Culmsee & Leuschner, 2013; Qian, 2014). Furthermore, high values of phylogenetic diversity at higher elevations support the idea that tree communities in higher elevations of the gradient are a mixture of species that originated in the lowland tropics (i.e. trait conservatism in distant lineages that have developed adaptations to lower temperatures) together with extra-tropical lineages adapted to harsh environmental conditions (Culmsee & Leuschner, 2013; Donoghue & Edwards, 2014; Neves et al., 2021). Neither taxonomic nor phylogenetic diversity patterns were consistent across spatial scales, suggesting that underlying drivers of these patterns may have shifted over time.

4.2 | Influence of WED and SER on diversity across elevations

Our results suggest that the impacts of both annual precipitation, a proxy for WED, and aboveground biomass, a proxy for SER, on both taxonomic and phylogenetic diversity are consistent at the local scale, yet not across all indices. When sampling effort was not accounted for, we found that taxonomic diversity decreased with precipitation and saturated with aboveground biomass across elevations. However, after accounting for sampling effort, taxonomic diversity showed a very mild or no association with both variables. We observed similar patterns for phylogenetic diversity indices,

suggesting that PD is more sensitive to sampling effort than MPD and MNTD. Together, these results indicate the sensitivity of WED and SER hypotheses to sampling effort (Chase et al., 2020), which may mask how environmental factors shape diversity patterns within and across elevations. Additionally to all variables having consistent effects on alpha diversity patterns, there may be an effect of the sum of multiple macro-scale factors (e.g. temperature and soil characteristics) that change (linearly or nonlinearly) with elevation on diversity.

While the level of anthropogenic activity in low-elevation tropical dry forests is likely higher than in the higher ones (McCain & Grytnes, 2010), it is possible that anthropogenic activity also impacted forest structure and diversity patterns in the lower montane moist and montane wet forests. Consequently, variation in anthropogenic activity within elevational belts may have introduced unexpected variability in the relationships among diversity, mean annual precipitation and aboveground biomass. Furthermore, landscape fragmentation may have indirectly shaped our results, as diversity of smaller patches can be disproportionately lower than expected by chance (Chase et al., 2020). However, as we did not sample forest patches proportionately, we were not able to detect indirect sampling effects. This variability is consistent with a recent study on the interactive effects of elevation and anthropogenic activity on multiple facets of biodiversity of tropical forests in Mexico, which showed that the impacts of anthropogenic activity were inconsistent across elevations (Monge-González et al., 2021).

4.3 | Diversity-generating mechanisms along the elevational gradient: TNC versus OTT

Among standardized phylogenetic diversity estimates at the alpha scale, none of the three indices tested (PD, MPD and MNTD)

exhibited a consistent pattern of either phylogenetic clustering or overdispersion across elevations. However, all three standardized indices showed a slight tendency towards clustering, indicating that environmental filtering may have a stronger influence on diversity patterns where PET is higher (tropical dry forest, Figure S2) and temperature is lower (tropical montane wet forest; Figure S2). Yet, biotic interactions such as exploitative trophic relationships (e.g. predation and herbivory) and mutualistic interactions (Cadotte & Tucker, 2017) also appear to contribute to shaping coexistence on this gradient. Overall, the lack of conclusive evidence for phylogenetic clustering or overdispersion across elevations does not provide strong support for OTT or TNC as the mechanisms driving local-scale diversity patterns in the Patia watershed.

As for the local scale, all standardized phylogenetic diversity indices at the gamma scale did not show a definitive pattern for phylogenetic clustering or overdispersion. Nevertheless, all three standardized phylogenetic diversity indices had negative values in the lowest elevational belt (tropical dry forest), resulting in a consistent pattern of phylogenetic clustering, that is, individuals at the lowest elevational belt are more closely related than expected by chance and likely share similar environmental niche requirements (Qian & Ricklefs, 2016), both at fine (MNTD; i.e. newer) and large (MPD; i.e. older) evolutionary time-scales (Mazel et al., 2016; Webb et al., 2002). This result supports the notion of environmental filtering being the main driver of community assembly at lower elevations, where water availability is more limiting (Cavender-Bares et al., 2004; Mazel et al., 2016; Webb et al., 2002). As a result, at the landscape scale, phylogenetic clustering and therefore the TNC hypothesis is likely the predominant mechanism influencing diversity in tropical dry forests (Griffiths et al., 2020; Segovia et al., 2020). Furthermore, it is important to note that phylogenetic clustering disappeared with elevation as water availability increases towards the lower montane moist and montane wet forests. Therefore, there is a weak and inconsistent signal of both TNC and OTT across elevations.

4.4 | Taxonomic and phylogenetic beta diversity

We found similar patterns for taxonomic and phylogenetic beta diversity along the elevational gradient. Contrary to our predictions, we found a weak hump-shaped pattern in taxonomic beta diversity with elevation. This finding differs from those of previous studies (Kraft et al., 2011; Vazquez & Givnish, 1998), which reported a decrease in spatial turnover with elevation. The stronger influence of the turnover component of beta diversity could be attributed to the high endemism in montane forests, as well as the role of the Andes as refugia during the past glaciation (Muellner et al., 2005). Furthermore, the stronger influence of spatial turnover could be related to the relaxation of environmental filtering with high elevations and the high climatic variability in montane areas (Malhi et al., 2010), which influences ecological processes, such as niche partitioning (Soininen et al., 2018). Consistently with taxonomic beta diversity, phylogenetic beta diversity shows a weak hump-shaped

pattern, indicating a low overlap of the major clades between the lower ecosystem belts with the middle and upper belts of the gradient (Ramírez et al., 2019). Moreover, the overriding influence of the turnover component establishes a link to the OTT because it is believed that the immigration of extra-tropical lineages is more common in upper elevations than in lower ones (Gentry, 1982; Peixoto et al., 2017; Ramírez et al., 2019; van der Hammen & Cleef, 1983). The high variation in elevation and temperature that takes place along small distances in mountainous regions (McKnight et al., 2007; Melo et al., 2009) may create barriers that expedite diversification events (Weir, 2006) and consequently increase the turnover component of phylogenetic beta diversity (Peixoto et al., 2017). This likely suggests that ecological processes such as niche convergence play an important role in shaping community assembly along this gradient, allowing old, distantly related species with convergent adaptations to tolerate cooler temperatures (Qian & Ricklefs, 2016; Segovia et al., 2020).

5 | CONCLUSIONS

Overall, our results show contrasting taxonomic and phylogenetic diversity across spatial scales. While local-scale diversity showed a decreasing trend with elevation for both facets, coarse-scale gamma diversity followed an unusual pattern of nonlinear increases for both diversity facets. Furthermore, local-scale diversity patterns were consistently mediated by factors associated with SER and WED. Our findings for landscape and local scales did not lend strong support to the TNC hypothesis that environmental filtering is the principal mechanism driving diversity patterns and community assembly processes. However, we found evidence that the effect of environmental filtering may weaken as water availability increases. Our results indicate that the OTT hypothesis may influence evolutionary processes at higher elevations, where phylogenetic diversity increased for most indices. Yet, neither evolutionary hypotheses had sufficient empirical support to be conclusive. Our study highlights the value of studying multiple facets of diversity across elevations and scales, and helps to further understand the threat climate change poses for these highly endangered ecosystems.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at <https://doi.org/10.6084/m9.figshare.13360658>.

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BIOSKETCH

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Authors' contributions: JR and RO designed field study and collected the data; MLT and DC designed and performed the data analysis; MLT, DC and HK contributed to the interpretation of the results and MLT led the writing process with contributions from all authors.

SUPPORTING INFORMATION

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