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Research article

Biotic pressures and environmental heterogeneity shape beta-diversity of seedling communities in tropical montane forests

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Many theories have been proposed to explain the high diversity of plants in the tropics. However, we lack an understanding of the processes that drive plant diversity and community assembly at different spatial scales. Here, we applied beta-diversity partitioning to test how biotic and abiotic factors are associated with seedling beta-diversity in a tropical montane forest in southern Ecuador. We recorded seedling communities on 81 subplots in nine plots located at three elevations along a 2000 m elevational gradient. We measured biotic pressures (i.e. herbivory and fungal pathogen attacks) and environmental conditions (i.e. soil moisture and canopy closure) in all subplots and related them to species turnover and richness differences in seedling communities within and between elevations. We found that species turnover increased with differences in biotic dissimilarity within elevations, while differences in species richness within elevations increased with increasing environmental dissimilarity. Between elevations, species turnover increased with increasing environmental dissimilarity. Our findings show that species turnover and changes in species richness are related differently to abiotic and biotic factors, and that the importance of these factors for shaping seedling diversity is scale-dependent. Our study contributes to better understand the processes driving seedling beta-diversity and the assembly of plant communities in highly diverse tropical montane forests.

Keywords: community assembly, plant regeneration, Podocarpus National Park, seedling recruitment, species coexistence, species sorting, tropical diversity

Introduction

The diversity of plant species in the tropics is remarkably high (Slik et al. 2015). Many theories have been formulated to explain this phenomenon (Janzen 1970, Giles et al. 2004), principally by seeking to understand the role of environmental filtering (Jones et al. 2008, Stein et al. 2014, Murphy et al. 2016) and spatio-temporal



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patterns of species coexistence (HilleRisLambers et al. 2012, Murphy et al. 2017, Usinowicz et al. 2017). One of the key mechanisms related to environmental filtering is species sorting (Clappe et al. 2018). Plant communities assemble through this mechanism, as species with different functional traits respond differently to changes in local environmental conditions. Eventually, local adaptations in some communities can result in habitat specialization (Leibold et al. 2004, Questad and Foster 2008). Accordingly, environmental heterogeneity can act as a driver of species richness and community composition (Stein et al. 2014). Another important concept of tropical plant diversity is based on the Janzen–Connell hypothesis (Janzen 1970, Connell 1971), which has been extensively tested in many tropical and temperate forests (Bagchi et al. 2010, Comita et al. 2014, Jia et al. 2020). It centres around the interactions between plants and their herbivores and fungal enemies that can moderate plant coexistence and shape diversity patterns in space and time (Bell et al. 2006, Rodríguez-Castañeda et al. 2010, Bachelot et al. 2016, Forrister et al. 2019). Consequently, the variability in biotic pressures plays a major role in shaping tropical plant diversity and the assembly of plant communities (Bagchi et al. 2014, Spear and Broders 2021). Yet, to what extent environmental heterogeneity and biotic interactions drive the diversity and assembly of highly diverse tropical plant communities is not yet resolved (Harms et al. 2000, Arellano et al. 2016a, Johnson et al. 2017).

Beta-diversity concepts facilitate studies of the patterns and drivers of spatial variation in community composition (Whittaker 1972). Beta-diversity, defined as variation in species identities in space, provides effective measures to test the magnitude at which different factors drive dissimilarities in species composition (Anderson et al. 2011). As such, beta-diversity can uncover valuable information on the factors underpinning species turnover and species loss or gain between studied sites (Baselga 2010, Legendre 2014). Effective methods have been established to partition original beta-diversity (i.e. dissimilarity) into two different components, i.e. species turnover (i.e. species replacement) and richness differences (Legendre 2014). While dissimilarity provides quantitative information on how communities resemble each other, species turnover and richness differences provide complementary information on how often species are replaced by each other, and on how locations differ in terms of the number of species. This approach can yield insight into how communities vary across environmental gradients (Baselga 2010, Anderson et al. 2011). The use of beta-diversity partitioning is particularly helpful in revealing factors driving plant diversity. For instance, Pinto-Ledezma et al. (2018) showed that high turnover of plant species occurred mainly in stable climates with higher species richness, while richness differences contributed to beta-diversity of plant communities in less diverse biomes with high environmental variability. So far, most studies investigated the role of environmental filtering to explain regional patterns of beta-diversity (Condit et al. 2002, Swenson et al. 2011, Worthy et al. 2021). However, cross-scale comparisons of beta-diversity are needed to disentangle the effects of

environmental factors and biotic interactions on local and regional diversity in plant communities (Kraft et al. 2011).

Seedling recruitment processes are key for shaping plant community composition (Leck and Outred 2008, Terborgh et al. 2014), because at early life stages plants are particularly exposed to environmental filtering and biotic pressures (Leck and Outred 2008, Browne et al. 2021). Indeed, seedlings of some species are more prone to environmental stress than others. For instance, seedlings with short roots may experience higher mortality under limited water conditions than seedlings developing long roots early on in the establishment phase (Harrison and LaForgia 2019). Likewise, seedlings of species recruiting from large seeds can cope better with pressures by herbivores and pathogens (Moles and Westoby 2004). Because the seedling establishment phase comprises short periods of time relative to plant life span, it is possible to study the processes shaping seedling diversity with observations and experiments over short time periods (Bagchi et al. 2014, Inman-Narahari et al. 2014, Bachelot et al. 2016). Given the critical importance of the seedling life stage, such studies can help to unravel the mechanisms underpinning the assembly of plant communities (Bachelot et al. 2016, Larson and Funk 2016). Studying seedlings in tropical forests is, however, a challenging task, because of the lack of identification tools, high morphological diversity and high seedling mortality (Browne et al. 2021). Given these difficulties, only few studies have sought to disentangle the effects of environmental factors on beta-diversity in tropical seedling communities (Murphy et al. 2016, Worthy et al. 2021).

Tropical mountain ecosystems harbour an extremely high diversity of plant species but, at the same time, they remain relatively little explored (Perrigo et al. 2020). Tropical montane forests offer a unique, natural laboratory to investigate the extraordinary diversity of plants due to high environmental heterogeneity and broad environmental gradients (Malhi et al. 2010, Arellano et al. 2016b). In particular, elevational gradients are very useful to compare processes operating at local and regional scales (Arellano et al. 2016a), as environmental conditions and biotic pressures differ within and between elevations and may contribute to the high diversity of plants in tropical mountains (Arellano et al. 2017, Sam et al. 2020, Wallis et al. 2021). Yet more studies on beta-diversity are required to better understand processes of community assembly in seedling communities (Arellano et al. 2016a, Conradi and Kollmann 2016, Gianuca et al. 2017).

Here, we study the drivers of beta-diversity in seedling communities within and between elevations of tropical montane rainforest in the southern Ecuadorian Andes. Specifically, we attempt to disentangle to what extent species turnover and richness differences are associated with environmental heterogeneity and biotic pressures at two spatial scales (i.e. within and between elevations). We quantified seedling recruitment along a 2000 m elevational gradient over a one-year period and quantified environmental dissimilarity (i.e. soil moisture and canopy closure) and biotic dissimilarity (i.e. herbivory and fungal attacks). We expected

high species turnover in seedling communities within elevations (Swenson et al. 2011) and prominent differences in species richness between elevations (Albrecht et al. 2021). In particular, we expected that differences in species turnover were primarily promoted by 1) environmental dissimilarity between elevations (Johnson et al. 2017) and by 2) biotic dissimilarity within elevations (Bagchi et al. 2014). We further expected 3) an increase in species richness differences associated with environmental dissimilarity, primarily within elevations (Homeier et al. 2010).

Material and methods

Study area

This study was conducted in tropical montane forests in the protected areas of the Podocarpus National Park and adjacent San Francisco Reserve. The Podocarpus National Park spans over 1000 km² in southern Ecuador, bordering on the Amazon Basin at around 1000 m asl and reaching the main ridge of the Andes above 3600 m asl. Main habitats comprise evergreen premontane forest, lower montane forest and upper evergreen tropical montane forest and subpáramo, and are mostly undisturbed due to low human activity (Homeier et al. 2008). The mean annual precipitation ranges between 2000 and 4500 mm with a less rainy season between September and December (i.e. 2432 mm annual precipitation at low elevations, 2079 mm at mid elevations and 4522 mm at high elevations, Santillán et al. 2018). The mean annual temperature ranges between 20°C at 1000 m asl, 15.5°C at 2000 m asl and 10°C at 3000 m asl (Bendix et al. 2008).

Our research was carried out on nine 1 ha plots established in the frame of the DFG Research Unit “RESPECT” along an elevational gradient ranging from 1000 m to 3000 m asl in the primary montane forest (Bendix et al. 2021). Three study plots were located along the Bombuscaro River (1000 m asl, 4°6’S, 78°58’W), three in the San Francisco Valley (2000 m asl, 3°58’S, 79°4’W) and three at Cajanuma (3000 m asl, 4°6’S, 79°10’W) (Homeier et al. 2008). Within each elevation, the three plots represented corresponding forest type (above) and were located at least 100 m apart from each other.

Monitoring of seedling communities

On each of the nine 1 ha plots, we established nine 1 m² subplots with no trees inside, resulting in a total of 81 subplots (Fig. 1). All subplots were situated inside the plots with a distance of 40 m between each other. Prior to the seedling survey starting in May 2019, we manually cleared existing vegetation from the subplots to better spot newly established seedlings and to focus our assessment on the early stages of seedling recruitment. Every four months until July 2020, we recorded all recently recruited seedlings (i.e. at least cotyledons had been developed) and classified them into species and morphotypes. Eventually, we compiled a community matrix, in which columns indicated the presence/absence of

each seedling (morpho)species and rows specified the experimental subplots. In the community matrix, all species identified at the level of genera were treated as distinct (morpho) species for each elevation. The matrix embraced all seedlings encountered at least once over the study period and, thus, comprised seedling species emerging at different times over the study period. Hence, we integrated data over the entire study period and focussed the analyses on our hypotheses concerning spatial patterns in seedling beta-diversity.

Environmental conditions and biotic pressures

Daily measurements of temperature and precipitation were recorded along the entire years 2019 and 2020 at automatic climate stations and were downscaled to the plot scale with the use of remote sensing techniques and a regionalization tool developed for the study area (Fries et al. 2009, Rollenbeck and Bendix 2011). The climatic conditions across the study period were, thus, calculated for each plot separately, but they varied very little within elevations (Supporting information). We therefore calculated the mean annual temperature and precipitation for each elevation and used this value for all plots of an elevation in the analyses. However, the effects of climate on seedling beta-diversity were never significant ($p > 0.1$ in all cases) and we therefore discarded the climatic dissimilarity between elevations from further analyses.

To measure environmental heterogeneity, we recorded soil moisture and canopy closure in all subplots during the less rainy season (October 2019). Average soil moisture was measured using a tensiometer by taking five single measurements inside each subplot. To obtain canopy closure, we took hemispherical photos 0.7 m above ground, with a Nikon Coolpix 4500 digital camera fitted with a Nikon FC-E8 fish-eye converter lens. All photos were taken in the mornings with overcast sky. The hemispherical photos were analysed in Gap Light Analyzer ver. 2.0 (1999, SFU/IES, Canada/USA). We considered soil moisture and canopy closure to be the most relevant proxy for environmental heterogeneity, as they are proxies for two crucial resources exploited by plants: water and light (Leck and Outred 2008).

To assess the degree of biotic pressures, we recorded herbivory traces and fungal pathogens on the seedlings at each of our three visits. As herbivory traces, we considered any kind of external leaf damage including bites, leaf mining and cuts (Muehleisen et al. 2020). As fungal pathogen traces, we considered any kind of leaf damage, including internal changes in leaf colour or external fruiting bodies (Benítez-Malvido and Lemus-Albor 2005).

For each seedling, we recorded the presence or absence of these biotic pressures, corresponding to the presence/absence data on species composition. Based on these data, we calculated the proportion of seedlings with signs of herbivory or fungal pathogens to quantify biotic pressures on seedlings for each subplot and census.

We computed the dissimilarity in environmental conditions and biotic pressures between all pairs of subplots. To this end, we calculated Gower’s distances to quantify the

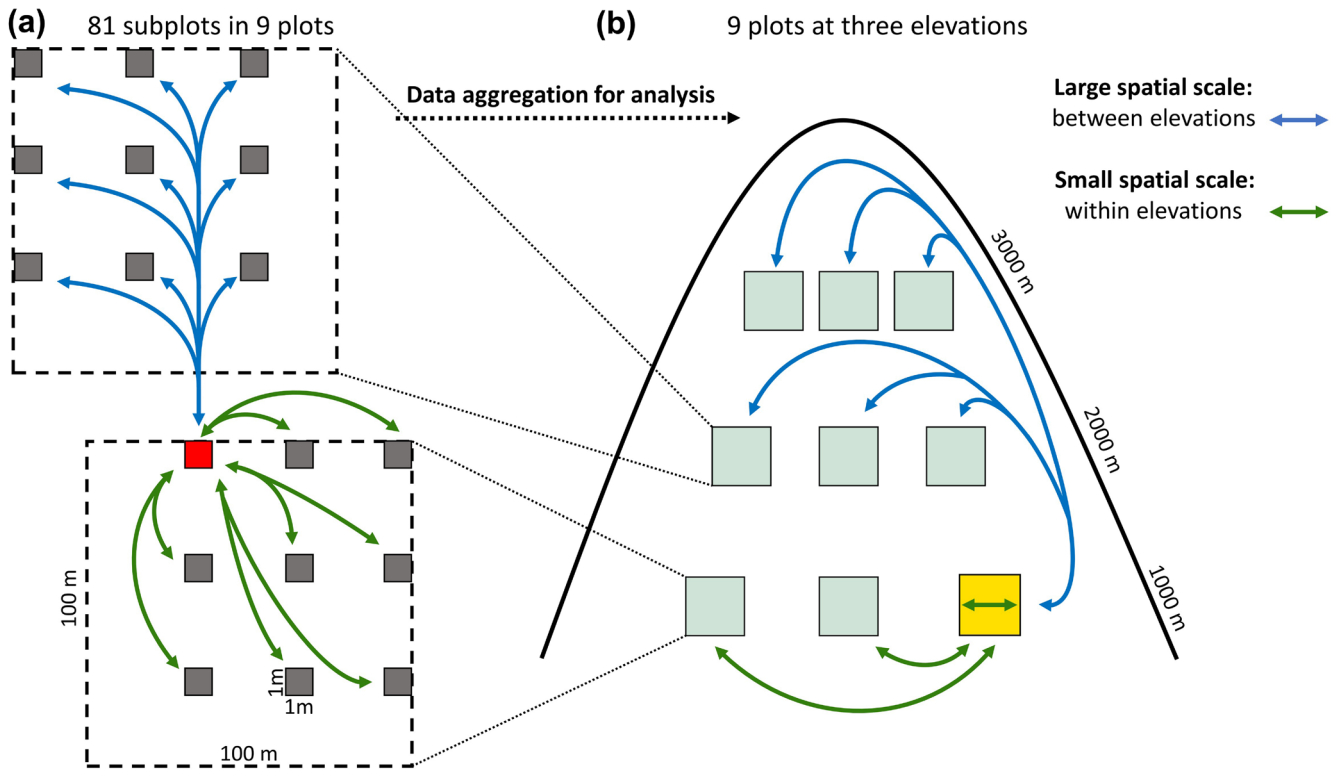


Figure 1. Study design for the analyses of biotic pressures, environmental conditions and seedling communities. We established 81 subplots within nine plots located along an elevational gradient from 1000 to 3000 m asl. (a) Pairwise comparisons of subplots were calculated within each plot, between plots located at the same elevation and between plots located at different elevations. Shown are all pairwise comparisons for an exemplary subplot (red) in relation to subplots within the same plot (green arrows) and to subplots of another plot at another elevation (blue arrows). (b) All subplot comparisons in biotic pressures, environmental conditions and seedling communities were aggregated at plot level for the analysis. The aggregation resulted in a total of 45 plot-based comparisons, both within elevations ($n = 18$) and between elevations ($n = 27$). Shown are all comparisons for an exemplary plot (yellow) within the same elevation (green arrows) and between elevations (blue arrows).

dissimilarity in environmental conditions (i.e. soil moisture and canopy closure) and biotic pressures (i.e. herbivory attacks and fungal pathogens at each census) between all pairs of subplots. Such data handling allowed matching of the dissimilarity measures and seedling recruitment data, concurrently accounting for temporal variability in biotic pressures typically observed among tropical plant communities (Norden et al. 2007, Pereira Martins et al. 2020). The two dissimilarity matrices were uncorrelated (Mantel tests, $n = 9999$, $r = -0.01$, $p = 0.529$).

Beta-diversity components

We applied beta-diversity partitioning based on the presence-absence of seedlings at subplot level. We calculated the pairwise Jaccard dissimilarities between subplots according to the methods of Legendre (2014) (Eq. 1):

$$D_j = (b + c) / (a + b + c) \quad (1)$$

with a referring to the shared number of species between subplot 1 and subplot 2, and b and c defined as the number

of species present only in subplot 1 and subplot 2, respectively. Thus, a gives the minimum number of species in each pairwise comparison; b is the number of species in subplot 1 minus a ; and c is the number of species in subplot 2 minus a .

Furthermore, we computed the species turnover (replacement) and species richness differences as two components of beta-diversity by decomposing the Jaccard dissimilarities with equations (2) and (3):

$$\text{Repl}_j = 2 \times \min(b, c) / (a + b + c) \quad (2)$$

$$\text{RichDiff}_j = |b - c| / (a + b + c) \quad (3)$$

Repl_j describes turnover of species between two different sites, showing the number of species that have been replaced in one community to another. Turnover, known also as replacement, describes the tendency of species to replace each other according to their distinct ecological requirements (Baselga 2010, Swenson et al. 2011).

RichDiff_j defines richness differences between a pair of sites. Richness differences refer to how many species

can coexist together, reflecting differences in the diversity of available niches at different locations (Baselga 2010, Legendre 2014).

Given the fact that species turnover and richness differences derive from beta-diversity partitioning, they complement each other (Legendre 2014) as follows (Eq. 4):

$$D_j = \text{Repl}_j + \text{RichDiff}_j \quad (4)$$

We used the code provided by Legendre (2014) to compute overall beta-diversity (D_j) and to partition beta-diversity into turnover (Repl_j) and richness differences (RichDiff_j). We calculated beta-diversity as well as species turnover and richness differences for all pairwise comparisons of subplots (Fig. 1a).

Statistical analysis

For statistical analyses, we aggregated the pairwise comparisons of subplots at plot level to compare beta-diversity patterns within and between elevations. For within-elevation comparisons, we calculated the mean dissimilarities between subplots of each plot ($n=9$) and for each pair of plots located at the same elevation ($n=9$), totalling 18 plot-based comparisons within elevations (green arrows in Fig. 1b, exemplified for one plot). We further calculated the mean dissimilarities between subplots for each pair of plots between elevations ($n=27$) (blue arrows in Fig. 1b, exemplified for one plot). In total, this resulted in 45 plot-based comparisons for environmental and biotic dissimilarities and the respective components of seedling beta-diversity (Fig. 1b). The aggregation was necessary to account for the non-independence of subplot comparisons within the same plots, and helped to reduce the noise of environmental, biotic and beta-diversity data at the subplot level. The resulting matrices were scaled to zero mean and unit variance to facilitate the further analyses. We used Wilcoxon rank-sum tests to test for differences in environmental and biotic dissimilarities between two spatial scales (within versus between elevations). We also applied Wilcoxon rank-sum tests by comparing the means of the general beta-diversity (D_j) and the two beta-diversity components (Repl_j , RichDiff_j) between the two spatial scales. Additionally, we used a Kruskal–Wallis test to test for differences in the species richness of seedlings among elevations (Supporting information).

We performed linear mixed models (LMMs) to test how beta-diversity components were associated with dissimilarity in environmental conditions and biotic pressures at the two spatial scales. The model included either species turnover or richness differences as response variable tested against the spatial scale (within or between elevations) and the dissimilarities in environmental conditions and biotic pressures, respectively. We included both their respective main effects and their interaction term with spatial scale into the analysis to test for scale-dependent effects of environmental conditions and biotic pressures on seedling beta-diversity. To control for the spatial design of our analysis, we included plot

identities of each plot-based comparison as random effects to the models; the same plot identity was included twice for the nine data points based solely on within-plot comparisons. We focussed the interpretation of these models on the positive associations between beta-diversity components and environmental heterogeneity and biotic pressures, respectively, as we expected positive relationships between species turnover/richness differences and environmental/biotic dissimilarity. This was justified because turnover and richness differences generally related to explanatory variables in opposite directions, given their interdependence (see beta-diversity partitioning in Eq. 4). All analyses were run in R ver. 4.0.2 (www.r-project.org) and the associated packages ‘ggplot2’ (Wickham 2016), ‘lme4’ (Bates et al. 2015), ‘lmerTest’ (Kuznetsova et al. 2017), ‘plyr’ (Wickham 2011), ‘reshape2’ (Wickham 2007), ‘tidyverse’ (Wickham et al. 2019) and ‘vegan’ (Oksanen 2016).

Results

We recorded 156 morphospecies of seedlings belonging to more than 40 families along the 2000 m elevational gradient. Species richness at the subplot level did not differ significantly across elevations (Kruskal–Wallis test, $n=81$, $\text{Chi}^2=5.49$, $p=0.064$; Supporting information) and species composition barely overlapped between different elevations. As expected, beta-diversity (D_j) was significantly higher between elevations than within elevations (Wilcoxon rank-sum test: $n=45$, $W=485$, $p<0.001$). While species turnover was significantly higher between elevations ($n=45$, $W=357$, $p=0.008$, Fig. 2a), no significant differences between the spatial scales were detected for species richness differences ($n=45$, $W=226$, $p=0.705$, Fig. 2b). Environmental dissimilarity was also significantly higher between elevations than within elevations ($n=45$, $W=385$, $p<0.001$, Fig. 3a). In turn, biotic dissimilarity was similar at both scales ($n=45$, $W=292$, $p=0.264$, Fig. 3b).

Associations between environmental factors and beta-diversity

Overall, we found a strong indication for scale-dependent effects of environmental and biotic dissimilarity on beta-diversity of seedlings (Table 1). Environmental dissimilarity was positively related to species turnover between elevations (Fig. 4a, Table 1) and to richness differences in seedling communities within elevations (Fig. 4b, Table 1). Biotic dissimilarity was positively related to species turnover within elevations (Fig. 5a). That is, species turnover increased between plots characterized by dissimilar values of biotic pressures. In contrast, biotic dissimilarity was not significantly associated with species turnover between elevations (Table 1). Further, biotic dissimilarity was not significantly related to differences in species richness neither within elevations, nor between elevations (Table 1, Fig. 5b).

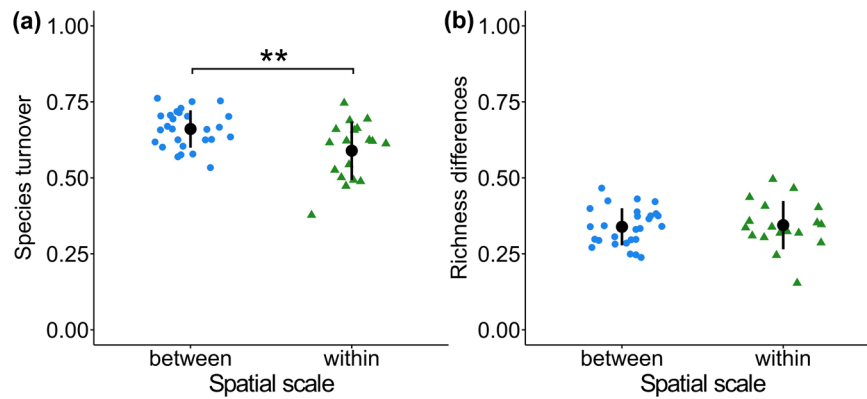


Figure 2. Variation of beta-diversity in seedling communities at two spatial scales in tropical montane forests, showing variability in (a) species turnover and (b) richness differences between seedling communities. Blue dots depict the beta-diversity between elevations, while green triangles correspond to variation within elevations. Values represent 45 plot-based comparisons between elevations ($n=27$) and within elevations ($n=18$) (Fig. 1). Whiskers show 25th and 75th percentiles, with the median indicated with black dots. The asterisks represent statistical significance ($p < 0.01$).

Discussion

We assessed the scale-dependent patterns of species turnover and richness differences in tropical seedling communities and related these to variation in key abiotic and biotic factors. We found that species turnover increased with increasing environmental dissimilarity between elevations and with increasing biotic dissimilarity within elevations. In turn, richness differences in seedling communities increased with environmental dissimilarity within elevations. Our findings show that scale-dependency may be key to understand how different mechanisms shape beta-diversity of seedling communities and, ultimately, the assembly of plant communities in tropical montane forests.

At the large spatial scale, species turnover increased with increasing environmental dissimilarity (Fig. 4a). That is, species turnover between elevations was significantly higher between plots differing in environmental conditions

than between plots with similar environmental conditions. Environmental heterogeneity has been described as a dominant driver of biodiversity for many taxa in the tropical montane forest of Ecuador (Wallis et al. 2021). In line with our findings, beta-diversity patterns in Andean forests are driven by environmental heterogeneity (Arellano et al. 2016b). Essentially, in many tropical forests, high species turnover is associated with changing environmental conditions (Condit et al. 2002, Davidar et al. 2007, Tello et al. 2015). At the same time, a study comparing tree beta-diversity between North and South America found that soil and topography influence species sorting more strongly in temperate forests than in tropical forests, due to the seasonal changes in environmental filtering in temperate ecosystems (Myers et al. 2013). Accordingly, cross-scale dissimilarities in species composition are generally driven by species sorting along steep environmental gradients (Myers et al. 2013, Tello et al. 2015, Zhang et al. 2020). Our findings add to

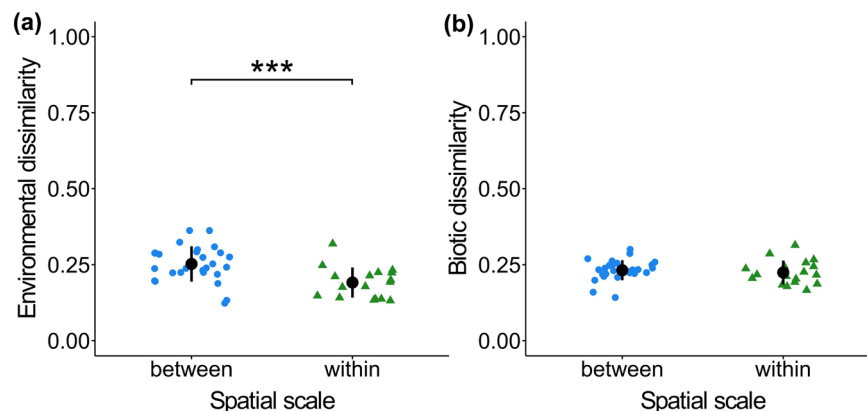


Figure 3. Variation of environmental and biotic dissimilarities at two spatial scales in tropical montane forests, showing (a) environmental dissimilarities based on soil moisture and canopy closure and (b) biotic dissimilarities based on herbivory and fungal pathogens. Blue dots depict the dissimilarities between elevations, while green triangles respond to the dissimilarities within elevations. Values represent 45 plot-based comparisons between elevations ($n=27$) and within elevations ($n=18$) (Fig. 1). Whiskers show 25th and 75th percentiles, with the median indicated with black dots. The asterisks represent statistical significance ($p < 0.001$).

Table 1. Linear mixed models testing the main and interaction effects of biotic and environmental dissimilarities on (a) species turnover and (b) richness differences within and between elevations. Plot identities were included as random factors ($n=45$ plot-based comparisons). Estimates, standard errors, degrees of freedom, t values and probability of tested effects are shown in columns. Estimates give the differences between the factor variable (within versus between elevations), as well as the linear estimate for the continuous predictor variables (biotic and environmental dissimilarity). The respective interaction terms indicate the effect of biotic and environmental dissimilarity within elevations relative to the effect between elevations (i.e. the differences to the respective main effect of biotic and environmental dissimilarity). Significant values ($p < 0.05$) are marked with*.

	Estimate	SE	df	t value	p
a) Species turnover					
(Intercept)	0.63	0.02	12.19	25.61	< 0.001***
Within elevations	-0.05	0.02	37.78	-2.32	0.026*
Biotic dissimilarity	0.003	0.01	36.13	0.21	0.834
Environmental dissimilarity	0.047	0.01	36.13	0.21	0.002**
Biotic dissimilarity \times within elevations	0.04	0.02	36.78	2.45	0.019*
Environmental dissimilarity \times within elevations	-0.08	0.02	33.67	-3.79	< 0.001***
b) Richness differences					
(Intercept)	0.38	0.02	12.79	15.64	< 0.001***
Within elevations	-0.02	0.02	37.70	-0.86	0.396
Biotic dissimilarity	-0.001	0.01	35.23	-0.08	0.935
Environmental dissimilarity	-0.04	0.01	33.95	-3.45	0.002**
Biotic dissimilarity \times within elevations	-0.03	0.02	36.68	-1.72	0.094
Environmental dissimilarity \times within elevations	0.07	0.02	33.23	4.12	< 0.001***

these studies and show that the environmental heterogeneity between elevations in tropical mountains is a main driver of species turnover in seedling communities.

At the small spatial scale, species turnover increased with increasing biotic dissimilarity (Fig. 5a). In other words, high species turnover within elevations corresponded to increasing differences in biotic pressures on seedlings. Previous field studies revealed the importance of fungal pathogens and insects for community composition of seedlings (Bagchi et al. 2014, Spear and Broders 2021). In line with these findings, the positive association between species turnover and dissimilarity in biotic pressures may be related to differences in the intensity and type of biotic pressures at each plot. This would suggest that herbivores and pathogens drive the detected changes in species composition. However, our findings may also suggest that high species turnover results in changing biotic pressures on seedlings. This interpretation would suggest that different

seedling communities attract different enemies because biotic interactions are often highly specialized, especially in tropical mountains (Rodríguez-Castañeda et al. 2010, Bachelot et al. 2016). While our correlative analyses cannot determine the ultimate mechanism underpinning the reported pattern, both suggested mechanisms are contingent on the host specificity of herbivores and pathogens on specific plant species (Novotny et al. 2006, Bachelot et al. 2016). Independent of the exact mechanism, our findings demonstrate that biotic interactions are more likely to shape species beta-diversity at small than at large spatial scales, consistent with previous concepts (Novotny et al. 2006, Wisz et al. 2013, Cohen et al. 2016). In the future, experimental studies on seedling communities and their enemies could contribute to identify the mechanisms promoting species turnover at small spatial scales.

While the effects of environmental heterogeneity and biotic pressures on plant diversity have been predominantly

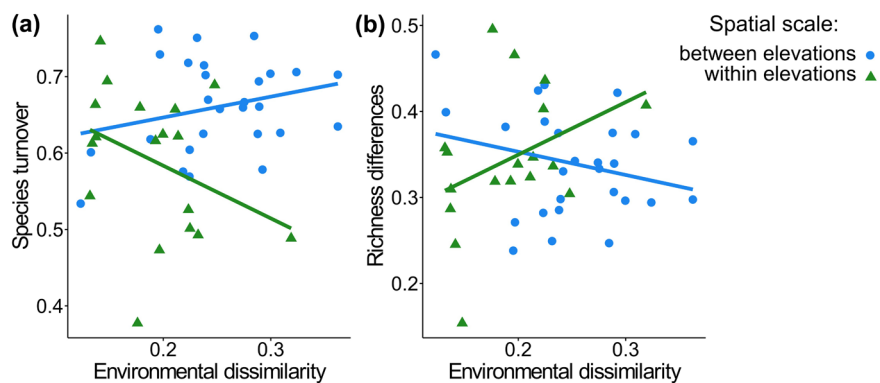


Figure 4. The relationships between environmental dissimilarity (based on soil moisture and canopy closure) and two beta-diversity components: (a) species turnover and (b) species richness differences in seedling communities. Each dot represents the corresponding dissimilarity measure at two different spatial scales (blue – between elevations, green – within elevations), based on 45 plot-based comparisons (Fig. 1). Fitted lines correspond to the univariate association between beta-diversity and the respective predictor variable. Partial effects of environmental dissimilarity on beta-diversity components are given in Table 1.

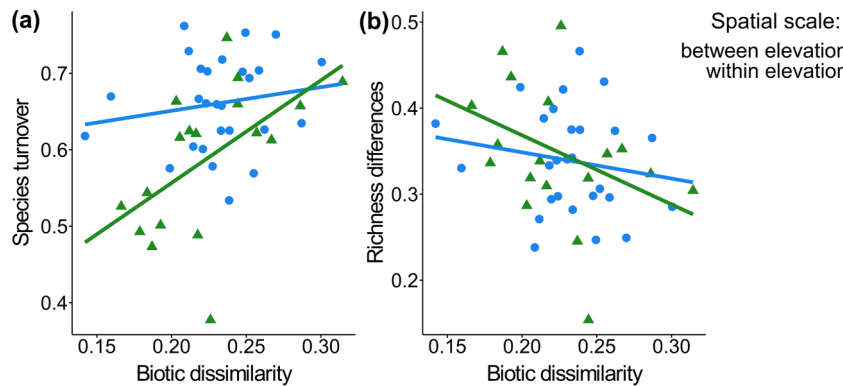


Figure 5. The relationships between biotic dissimilarity (based on herbivory and fungal pathogens) and two beta-diversity components: (a) species turnover and (b) species richness differences in seedling communities. Each dot represents the corresponding dissimilarity measure at two different spatial scales (blue – between elevations, green – within elevations), based on 45 plot-based comparisons (Fig. 1). Fitted lines correspond to the univariate association between beta-diversity and the selected environmental variable. Partial effects of biotic dissimilarity on beta-diversity components are given in Table 1.

reported for tropical lowland forests (Svenning 1999, Bagchi et al. 2014), there is little evidence of how species turnover varies at different spatial scales in tropical montane forests. A previous study from the Bolivian Andes showed that environmental processes contribute to shaping the community composition of trees regardless of the spatial scale (Arellano et al. 2016a). In contrast, a study from a temperate forest showed a strong correlation between environmental filtering and tree species turnover across latitudes (Zhang et al. 2020). Future studies on different growth forms and life stages of plants are required to obtain a more complete picture of species turnover as a result of scale-dependent processes of community assembly (Swenson 2013, Murphy et al. 2016).

We found that species richness differences increased with increasing environmental dissimilarity at the small spatial scale (Fig. 4b). That is, richness differences were particularly high between environmentally heterogeneous localities within elevations. Environmental heterogeneity has been described as very important for species richness across many taxa and at different spatial scales (Stein et al. 2014, Worthy et al. 2021). Additionally, topography has been reported as a prominent driver of the high local diversity of trees in the study area (Homeier et al. 2010). Similarly, coexistence of seedlings was related to niche differences in a tropical montane forest (Inman-Narahari et al. 2014) and to niche partitioning among seedlings in different habitats of tropical lowland forests (Johnson et al. 2017). Thus, certain environmental conditions, e.g. a high light availability under an open canopy, may determine the amount of available niches and therefore promote the coexistence of many species, at least at the early stage of plant regeneration (Giles et al. 2004).

Our study focused on early seedling recruitment, because this initial recruitment phase is especially prone to environmental filtering and biotic pressures (Bagchi et al. 2014, Murphy et al. 2016) and sets a blueprint of community composition for later life stages (Visser et al. 2016, Forrister et al. 2019). Given the high seedling mortality in tropical rainforests, initial seedling recruitment is also considered to be

particularly important for the assembly of tropical plant communities (Maron et al. 2019). In fact, in spite of the relatively short period of our study, we were able to capture a high number of seedling species (Supporting information) and a large variation in beta-diversity (Fig. 2). Despite the asynchrony in seed production in the tropics (Connell and Green 2000), this suggests that our one-year study of seedling communities was able to capture scale-dependent differences in community assembly at this very early stage of plant recruitment. Nevertheless, future long-term studies will be required to test whether patterns in beta-diversity are similar for seedlings and later recruitment stages. In particular, it will be interesting to test whether the importance of abiotic and biotic drivers changes across life stages and subsequent demographic processes (Murphy et al. 2016, Pereira Martins et al. 2020).

We conclude that the processes promoting species turnover and richness differences in seedling communities are scale-dependent and that abiotic and biotic factors shape seedling beta-diversity differently within and between elevations in tropical montane forests. In particular, we reveal that the effects of biotic pressures on seedling communities are particularly pronounced at the local scale within elevations. We conclude that these scale-dependent processes are likely to play a key role in shaping the assembly of seedling and plant communities in tropical montane forests.

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Author contributions

Maciej K. Barczyk: Conceptualization (equal), Data curation (lead), Formal analysis (lead), Investigation (lead), Methodology (equal), Writing – original draft (lead). **Diana C. Acosta-Rojas:** Conceptualization (equal), Investigation-Supporting, Methodology-Supporting, Writing – review and editing-Supporting. **Carlos I. Espinosa:** Funding acquisition-Supporting, Methodology-Supporting, Writing – review and editing-Supporting. **Matthias Schleuning:** Conceptualization (equal), Funding acquisition (equal), Methodology (equal), Supervision (equal), Writing – review and editing (equal). **Eike L. Neuschulz:** Conceptualization (equal), Funding acquisition (equal), Methodology (equal), Supervision (equal), Writing – review and editing (equal).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.3r2280gmh> (Barczyk et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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