

# Linking patterns and processes of tree community assembly across spatial scales in tropical montane forests

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**Abstract.** Many studies have tried to assess the role of both deterministic and stochastic processes in community assembly, yet a lack of consensus exists on which processes are more prevalent and at which spatial scales they operate. To shed light on this issue, we tested two nonmutually exclusive, scale-dependent hypotheses: (1) that competitive exclusion dominates at small spatial scales; and (2) that environmental filtering does so at larger ones. To accomplish this, we studied the functional patterns of tropical montane forest communities along two altitudinal gradients, in Ecuador and Peru, using floristic and functional data from 60 plots of 0.1 ha. We found no evidence of either functional overdispersion or clustering at small spatial scales, but we did find functional clustering at larger ones. The observed pattern of clustering, consistent with an environmental filtering process, was more evident when maximizing the environmental differences among any pair of plots. To strengthen the link between the observed community functional pattern and the underlying process of environmental filtering, we explored differences in the climatic preferences of the most abundant species found at lower and higher elevations and examined whether their abundances shifted along the elevation gradient. We found (1) that greater community functional differences (observed between lower and upper tropical montane forest assemblies) were mostly the result of strong climatic preferences, maintained across the Neotropics; and (2) that the abundances of such species shifted along the elevational gradient. Our findings support the conclusion that, at large spatial scales, environmental filtering is the overriding mechanism for community assembly, because the pattern of functional clustering was linked to species' similarities in their climatic preferences, which ultimately resulted in shifts in species abundances along the gradient. However, there was no evidence of competitive exclusion at more homogeneous, smaller spatial scales, where plant species effectively compete for resources.

**Key words:** altitudinal gradients; community assembly; competitive exclusion; environmental filtering; functional traits; spatial scale; tropical montane forest.

## INTRODUCTION

Which processes determine the structure and composition of communities? This question has generated discussion among naturalists for decades (Clements 1916, Gause 1934, MacArthur and Levins 1967, Wright 2002),

becoming almost an obsession for ecologists and the core of community assembly research (Sutherland et al. 2013). In the quest for answers, scholars have proposed different explanations for the mechanisms shaping the structure and distribution of natural communities, with environmental filtering and competitive exclusion being among the most broadly embraced (Belyea and Lancaster 1999, Götzenberger et al. 2012, Kraft and Ackerly 2014). According to environmental filtering, the abiotic milieu acts as a sieve, allowing only species with certain traits or phenotypes to establish and survive successfully,

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whereas the rest fail (Bazzaz 1991, Weiher and Keddy 1995a, Díaz et al. 1998). However, competitive exclusion posits that coexisting species compete for the resources until one excludes the others. Thus, the less two species compete for resources, the more likely they are to co-occur (Diamond 1975, Abrams 1996, Dayan and Simberloff 2005). As an alternative to these niche-based explanations, the neutral assembly theory considers that all species are ecologically equivalent, and therefore communities would be the result of only dispersal limitation events and stochastic demographic processes (Hubbell 2001).

To address the community assembly issue, functional ecology has emerged as a more powerful and suitable tool than classical taxonomic approaches based on Linnaean binomials, because indices of species composition and abundances provide little information about the ecological strategies of those species (Fukami et al. 2005, Swenson 2012). Instead, the functional approach relies on species functional traits—easily measurable morphological or physiological characters of individuals relevant to growth, survival, or reproduction (Westoby and Wright 2006, Funk et al. 2017)—as proxies of ecological performance and, consequently, capable of explaining how species interact with their abiotic and biotic environment (Keddy 1992, McGill et al. 2006, Violle et al. 2007). By using the functional ecology framework, environmental filtering has been identified as a major force shaping communities across a number of biomes, including drylands (Le Bagousse-Pinguet et al. 2017), alpine (de Bello et al. 2013a, López-Angulo et al. 2018), temperate (Cornwell and Ackerly 2009) and tropical forests (Kraft et al. 2008, Swenson and Enquist 2009, Lebrija-Trejos et al. 2010, Baraloto et al. 2012). Nevertheless, the overwhelming importance of environmental filtering on community assembly has lately been questioned based on a disregard towards spatial scale consideration (Chase 2014) and on the uncertainty regarding whether functional patterns can reliably indicate mechanisms (Mayfield and Levine 2010).

To account for spatial scale is of utmost importance in ecology (Wiens 1989, Levin 1992, McGill 2010), and its implications on community assembly are undeniable (Whittaker et al. 2001, Kneitel and Chase 2004, Snyder and Chesson 2004, Münckmüller et al. 2013). For instance, at a broad spatial scale, environmental filtering seems to prevail over other processes (e.g., cacti do not thrive in arctic regions, nor do polar bears in the rainforest), and competitive exclusion has virtually no effect on individuals that are many kilometers apart, although it may have an effect at a smaller spatial scale, on individuals in close proximity. Nonetheless, ignoring spatial scale-related implications has often led to discrepancies about which processes dominate community assembly (discussed by Chase 2014, Chalmers et al. 2017). To incorporate the scale issue a hierarchical model has been proposed, according to which assembly mechanisms operate sequentially at different spatial scales (Weiher and Keddy 1995b, Götzenberger et al. 2012,

HilleRisLambers et al. 2012). This model encompasses evolutionary and biogeographic processes, such as historical patterns of speciation, extinction, or migration at large/regional scales; to abiotic and biotic processes, like environmental filtering or competitive exclusion at smaller/local scales. The former processes define a regional pool of potential colonizer species over which the latter operate at finer scales, yielding the final assembly of local communities. Under this paradigm, shifting the scope of the studied community and the species pool will allow us to clarify whether distinct assembly processes are restricted to operate at certain spatial scales (Colwell and Winkler 1984, Weiher and Keddy 1995b, Swenson et al. 2007). For instance, environmental filtering may be more prevalent when the species pool is defined from a broad area encompassing strong abiotic heterogeneity, for example, steep environmental or habitat gradients, while the studied community, established at a relatively narrower spatial scale, is constrained to an environmentally homogeneous area (de Bello et al. 2013b, Garzon-Lopez et al. 2014, reviewed in Kraft et al. 2015).

Community patterns based on co-occurring species composition and abundance combined with functional diversity have been broadly trusted to reflect different community assembly processes. However, interpreting them as unequivocal signals of actual assembly processes is arguable. Traditionally and according to the community assembly mechanisms above, two mutually excluding scenarios for species co-occurrence have been proposed: (1) species could diverge in their ecological strategies to achieve co-occurrence by avoiding competitive exclusion, thus functional overdispersion should be observed within the community (Watkins and Wilson 2003, Silvertown 2004, Stubbs and Wilson 2004, Caver-Bares et al. 2009); or (2) species could converge in their ecological strategies such as to enable them to thrive in the same abiotic environment, resulting instead in functional clustering (Keddy 1992, Cornwell et al. 2006, Ackerly and Cornwell 2007). In addition, if the traits are phylogenetically conserved, a phylogenetic overdispersion or clustering pattern should also be observed within the community, respectively (Webb et al. 2002). This dichotomy, nevertheless, is an oversimplification, because both theory (Chesson 2000, Grime 2006, Mayfield and Levine 2010) and practice (Burns and Strauss 2011, Narwani et al. 2013, Godoy et al. 2014) have proven it to be unwarranted, since clustering can also result from competitive exclusion as well as from other biotic processes. For example, the existence of selective herbivores (Uriarte 2000), pathogens (Parker et al. 2015), or pollinators (Sargent and Ackerly 2008) can specifically harm or favor groups of species exhibiting certain traits, thus affecting the whole community structure. Therefore, inferring unequivocally that environmental filtering drives community assembly just on the basis that a clustered functional pattern has been observed could be deluding (Götzenberger et al. 2016, Cadotte and Tucker 2017).

Our study aims to advance the understanding of community assembly accounting for spatial scale implications and avoiding an overreliance on community patterns. To achieve this, we studied functional diversity of woody plant communities along two elevational gradients in Andean tropical montane forests, one of the most complex and diverse ecosystems worldwide. We consider that at a given spatial scale only one single mechanism will have a heavier influence on community assembly. Under this premise we assume that, whereas competitive exclusion would mainly operate at small spatial scales at which the environment is relatively homogeneous, environmental filtering would chiefly emerge as a significant force shaping community assembly at larger scales at which there is enough environmental heterogeneity to trigger a functional community response. Therefore, we hypothesized that (1) if competitive exclusion drives the community assembly at small spatial scales (e.g., across neighboring individuals within a plot), functional patterns would be overdispersed in comparison to a null expectation and (2) if environmental filtering rule at larger scales (e.g., across plots spaced hundreds of meters or at different elevations), functional patterns would be clustered. Furthermore, following the guidelines from Kraft et al. (2015) to state the importance of the processes in the assembly of the community clearly, we sought evidences that link the observed community patterns with the underlying assembly processes (e.g., correlations between thermal gradient and community functional patterns or species abundances, respectively). By doing so, this study will further contribute to unmask the spatial scales at which different assembly processes predominate.

## MATERIALS AND METHODS

### *Study regions and field sampling*

The study was conducted along two elevational gradients of Andean tropical montane forest: one in Podocarpus National Park (Ecuador) and the other in Rio Abiseo National Park (Peru) (Fig. 1). These sites were chosen because both extend along wide elevational ranges (ca. 2,000 m), over a continuous forest cover, each within a single river basin: the Bombuscaro River in Ecuador and the Montecristo-Abiseo River in Peru. Three elevational belts were defined at each site (lower, 800–1,100 m above sea level [a.s.l.]; intermediate, 1,900–2,100 m a.s.l.; upper, 2,700–2,900 m a.s.l.). At each belt, 10 plots of 0.1 ha (50 × 20 m) were established between 2015 and 2017 following Arellano et al. (2016) (Appendix S1: Table S1). Each plot was subdivided in 10 subplots of 0.01 ha (10 × 10 m). Plots were placed at least 300 m apart, avoiding areas visibly affected by natural disturbances (e.g., gaps caused by fallen trees or landslides). In each plot, all woody individuals  $\geq 2.5$ -cm diameter at breast height (DBH) rooted within the plot limit were inventoried and their height estimated, although for this study

solely trees, treelets, shrubs, and lianas were taken into an account. At least one voucher from every taxon was collected for identification. Overall, 18,272 individuals were inventoried in 60 plots: 9,366 in Ecuador and 8,905 in Peru (Appendix S1: Table S1; Data S1).

### *Floristic data and functional characterization*

Voucher specimens were identified at different herbaria from Ecuador (HUTPL, LOJA, QCA) and Peru (HAO, HUT, MOL, USM), acronyms according to Thiers (*n.d.*). After thorough taxonomic effort, 424 individuals from Ecuador (4.5%) and 733 from Peru (8.23%) could not be reliably assigned to a morphospecies level and were therefore excluded from the analysis (Appendix S1: Table S2). For Ecuador, the 8,942 identifiable individuals were assigned to 734 taxa, comprising 471 species and 263 morphospecies. For Peru, the 8,172 identifiable individuals were assigned to 526 taxa, including 189 species and 337 morphospecies. Standardization of taxonomic species names was conducted using the R package ‘Taxonstand’ (Cayuela et al. 2012, 2017).

For each taxon, the following functional traits were measured: specific leaf area (SLA), leaf thickness (LT), and wood density (WD). These traits address key woody plant functional strategy axes on which assembly mechanisms operate (Wright et al. 2004, Kraft et al. 2008, Baraloto et al. 2010). SLA was calculated from five leaves as the ratio of leaf surface area (measured with a portable laser leaf area meter CI- 202, CID Bio-Science, Camas, Washington, USA) to leaf dry mass (after drying at 80°C for 48 h). LT was measured with a digital calliper. Branch wood density was used as a proxy for WD, as both are strongly and positively correlated (Swenson and Enquist 2008). Sections of branches ca. 10 cm in length, as cylindrical as possible, were stripped of bark, and their diameter and length measured in the field with a calliper to determine their fresh volume. Density of the branch section was calculated by dividing its fresh volume by its dry mass (after drying at 80°C for 48–72 h). Mean trait values were calculated for every taxon (Data S1). All these protocols were based on Cornelissen et al. (2003) with just one exception: for SLA and LT, leaves in full sun, at the upper canopy, were avoided in order to make these traits comparable between canopy and understory species. Functional data were collected for 723 taxa in Ecuador (98.5% of the total identified), that include 8,903 individuals (95% of the total inventoried) and for 504 taxa in Peru (95.8% of the total identified), that include 8,016 individuals (90.01% of the total inventoried). For a summary of community functional characterization, see Appendix S1: Table S3.

### *Community assembly functional patterns*

To elucidate how the consideration of different spatial scales may influence the relative effect of distinct deterministic mechanisms, the observed and the null

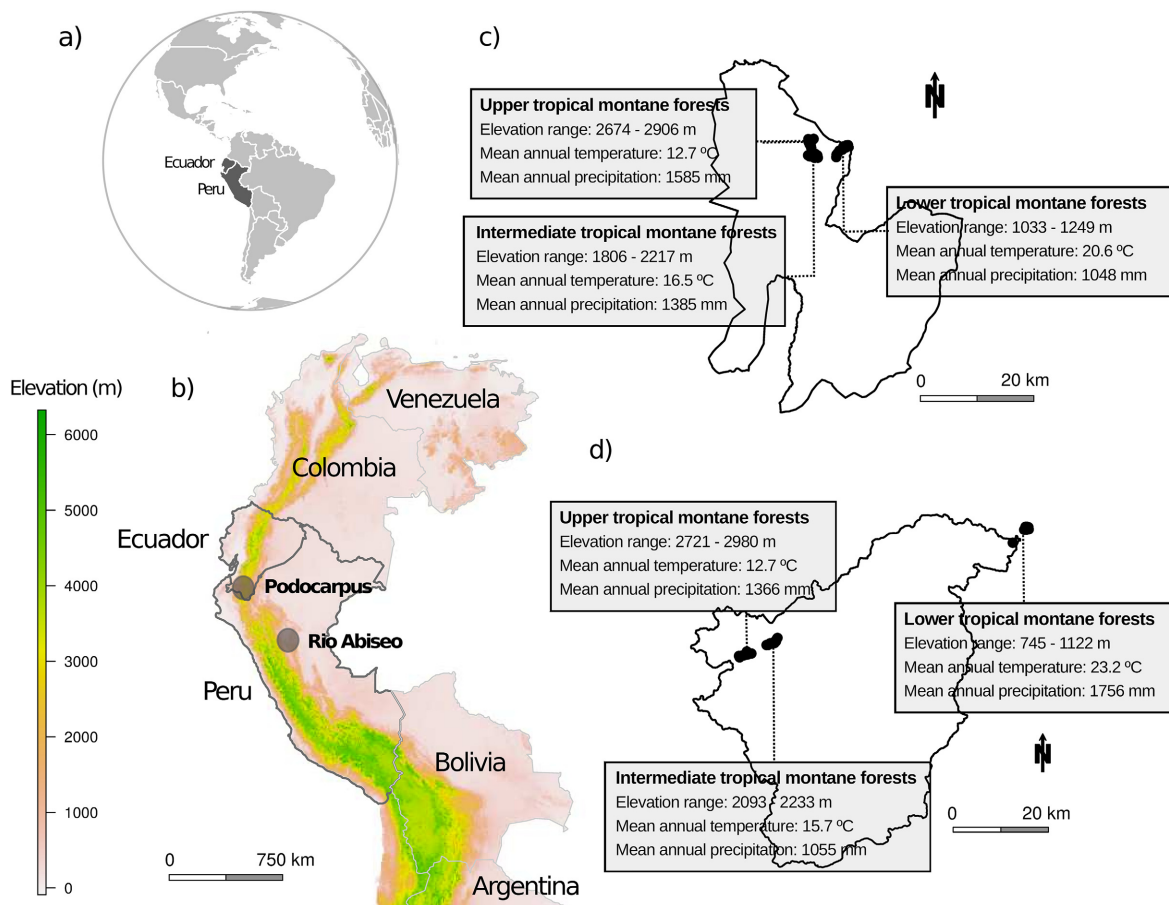


FIG. 1. Location of the study sites. The two tropical montane Andean forests' elevational gradients in Ecuador and Peru (a, b). Outlined areas represent Podocarpus National Park (c) and Rio Abiseo National Park (d), respectively. Ten plots of 0.1 ha were established at each of three elevational belts (lower, intermediate, and upper) for each site, resulting in a total of 60 plots.

community functional trait distribution patterns were calculated for two spatial scale-related hypotheses (Fig. 2): (1) trait distribution within a subplot compared with trait distribution among nonadjacent subplots from the same plot (small spatial scales), and (2) trait distribution within a plot compared with trait distribution among plots located along the elevational gradient (large spatial scales). Deviations in the observed distribution pattern from the null expectation would suggest the existence of different deterministic community assembly processes, such as environmental filtering or competitive exclusion, whereas a close match between distributions could be interpreted as evidence of stochastic community assembly (Connor and Simberloff 1979, Gotelli and Graves 1996).

For both cases, the observed community trait distribution was calculated as  $U_{ST-obs} = 1 - \sum D_w / \sum D_a$ , where  $D_w$  and  $D_a$  are the trait Euclidean distances between pairs of co-occurring individuals (for all the individuals within each site) from distinct taxa randomly paired from within a subplot ( $D_w$ ) and among subplots ( $D_a$ ) for hypothesis 1 and from within a plot ( $D_w$ ) and among plots ( $D_a$ ) for hypothesis 2 (Hardy and Senterre 2007, Baraloto et al.

2012; Data S2). Because the value of  $U_{ST-obs}$  is dependent on the particular selection of a random subset of pairs of individuals, we iterated this procedure 1,000 times and generated a distribution of  $U_{ST-obs}$ . By definition,  $U_{ST}$  can take both positive and negative values, where  $U_{ST} > 0$  indicates trait clustering and  $U_{ST} < 0$  trait overdispersion. To assess the significance of  $U_{ST-obs}$ , a community null functional trait distribution ( $U_{ST-null}$ ) to have random assembly as the null expectation was calculated using the same procedure for each of the hypotheses, but breaking down the community observed functional trait structure by randomly shuffling taxonomic identities among individuals (T1 randomization sensu Götzenberger et al. 2016). As a result, the original community structure remains unaltered because taxa richness and frequency are fixed, but trait values are independently reshuffled across taxa for each trait, thus not preserving the correlation structure across traits. We selected this randomization procedure over others because of its versatility: although it is particularly suitable for detecting competitive exclusion (via limiting similarity), it also performs well in detecting environmental filtering (Götzenberger

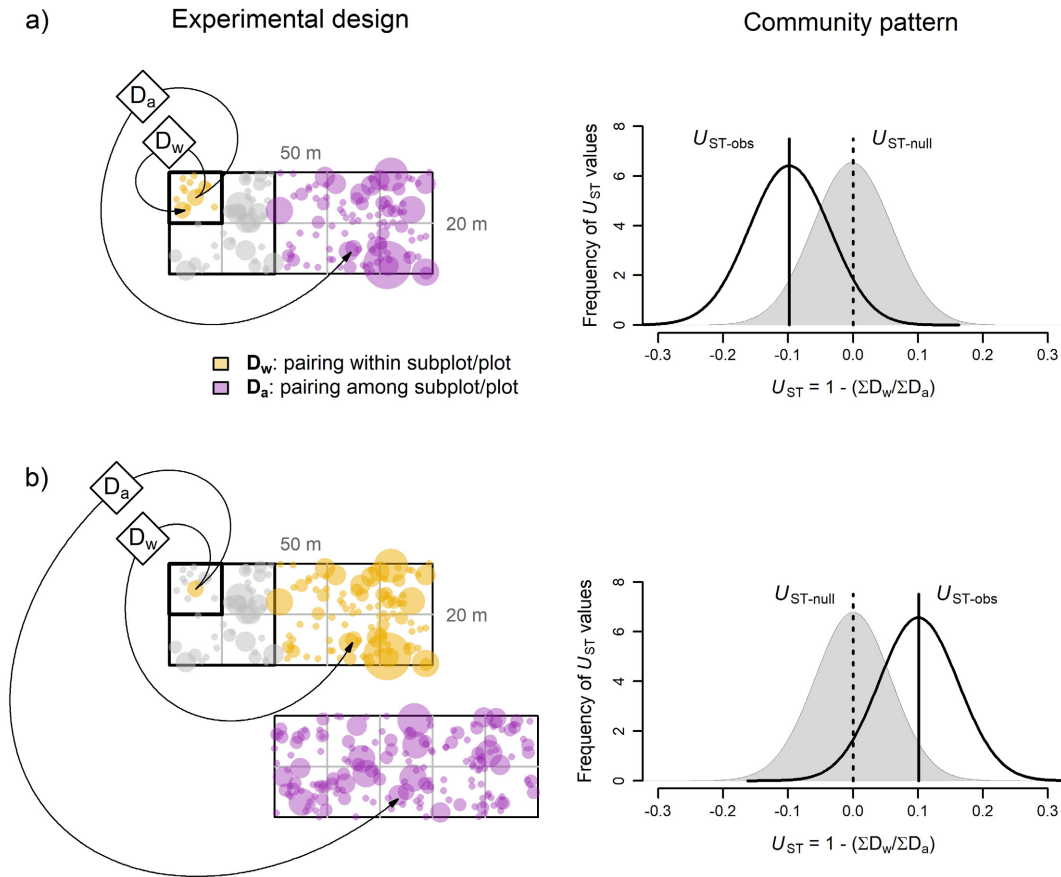


FIG. 2. Sampling design and the respective community functional pattern for testing the existence of different community assembly processes at different spatial scales and the expected community functional patterns. (a) According to hypothesis 1, at small spatial scale within plots, an overdispersed functional pattern occurs, which would be consistent with competitive exclusion. Conversely, (b) in accordance with hypothesis 2, at larger spatial scale among plots, a clustered functional pattern arises, which would suggest the existence of environmental filtering.  $U_{ST}$  is the mean functional trait Euclidean distance between pairs of co-occurring individuals from distinct taxa randomly paired within subplots ( $D_w$ ) and among subplots ( $D_a$ ) for hypothesis 1 and within plot ( $D_w$ ) and among plots ( $D_a$ ) for hypothesis 2.

et al. 2016). For each of the 1,000  $U_{ST-obs}$  and  $U_{ST-null}$  distributions we extracted the mean value as a summary statistic. Then, the distributions of the means of both the observed and null  $U_{ST}$  were compared using a one-tailed  $t$  test, with a critical significance level of  $\alpha = 0.05$ , because tests for the null hypothesis were unidirectional (Götzenberger et al. 2016). The whole analytic procedure was conducted independently for each site and replicated for two cohorts of co-occurring individuals: saplings (DBH < 10 cm) and adults (DBH  $\geq$  10 cm).

#### *Assembly processes underlying community functional patterns*

For environmental characterization of each plot we used the bioclimatic variables from CHELSA climate data set (Karger et al. 2017). Mean annual temperature (hereinafter MAT) was selected, as small changes in this variable along our altitudinal gradients (spanning thermal ranges between 9 and 12°C in Ecuador and Peru,

respectively; see Appendix S1: Table S1) are expected to have a strong effect on species distribution, because in the tropics species have evolved to have narrow thermal tolerances (Janzen 1967). In addition, MAT was highly correlated ( $r > 0.86$ ) with most bioclimatic variables, both in Ecuador and Peru. We used Mantel tests to analyze statistically the correlation between the observed community functional pattern for any pair of plots ( $U_{ST-obs}$ , sensu hypothesis 2) and the plots' environmental distance, calculated as the pairwise difference in MAT (Data S2). To estimate the statistical significance of the correlation between MAT and  $U_{ST-obs}$  we used a Monte Carlo test, permuting 200 times the elements of one of the distance matrices while holding the other constant.

The climatic preferences of the most abundant taxa in the lower and upper elevational belts (i.e., at both extremes of the elevational gradient) were computed for each one of the two study sites. To achieve this, we defined the most abundant species as those with 10 or more individuals within a single elevational belt

(morphospecies excluded). In total we recognized 65 of such species for the lower tropical montane forest belt (henceforth, LTMF species) and 66 for the upper belt (UTMF species) for Ecuador, whereas there were 26 and 27, respectively, for Peru (Appendix S1: Table S4; Data S1). We then we retrieved occurrence data across the Neotropics for each of those species from the Global Biodiversity Information Facility (GBIF) and extracted the bioclimatic information from CHELSA for the locations where species were reported. The climatic preference of LTMF and UTMF species was defined as the mean  $\pm 1.96$  standard deviation of the MAT from those species' locations (Data S2). Finally, the significance of the differences in climatic preferences between sets of LTMF and UTMF species was estimated comparing the mean MAT value for each set of species' locations with a one-tailed  $t$  test, using a significance level of  $\alpha = 0.05$ . All analyses were conducted using the 'vegan' R package (Oksanen et al. 2006).

As consequence of environmental filtering the species adapted to certain climatic preferences would be filtered out along the elevational gradient as climatic conditions change. To explore this, we quantified the number of individuals of LTMF and UTMF species at each of the three elevational belts (lower, intermediate, and upper) and then analyzed how they changed with elevation in each of the two study sites using generalized linear mixed models

(GLMMs) with a negative binomial error distribution (to account for statistical overdispersion; not to be confounded with functional overdispersion). Mean elevation at each belt, climatic preference (LTMF or UTMF) and their interactions were used as fixed terms, whereas species identity was used as a random factor. A random slope structure was used for mean elevation, indicating that the slope of the relationship between abundance and elevation may change randomly among species. We built all possible combinations of fixed and random factors. Overall, we fitted 15 models, including null models for both fixed and random effects (Appendix S1: Table S5), using the R packages 'glmmADMB' (Skaug et al. 2013) and 'MASS' (Venables and Ripley 2002). All models were compared using Akaike's information criterion, corrected for small sample sizes ( $AIC_c$ ), with the R package 'MuMIn' (Barton 2018; Data S2). Models with a difference in  $AIC_c > 2$  indicate that the worse model had virtually no support and could be omitted.

## RESULTS

### Community assembly functional patterns

No statistically significant evidence ( $U_{ST-obs} \approx U_{ST-null}$ ) of functional overdispersion was found at small spatial scales for any of the three traits in either site (Fig. 3).

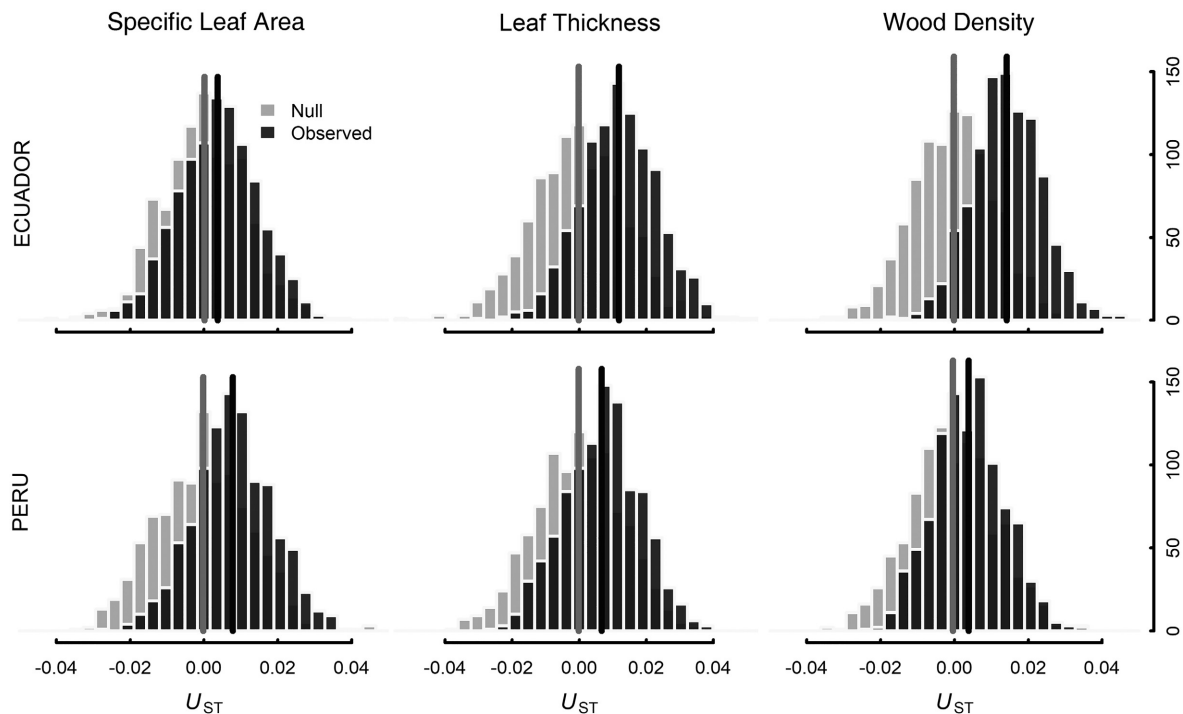


FIG. 3. Hypothesis 1: community functional distances distribution patterns at small spatial scale (within plot). Frequency of distribution of  $U_{ST-obs}$  (black) and  $U_{ST-null}$  (gray) values at two geographical sites (Ecuador, upper charts; Peru, lower charts) as measured based on three functional traits (specific leaf area [SLA], left; leaf thickness [LT], center; wood density [WD], right) after 1,000 randomizations, in all six cases. There were no significant differences ( $\alpha = 0.05$ ) between  $U_{ST-obs}$  and  $U_{ST-null}$  for any of the traits at any of the sites.

Thus, individuals within a subplot were not functionally more different from the rest of individuals of the same plot than expected by chance ( $U_{ST-obs}; D_w \approx D_a$ ). The same overall results were obtained when the analyses were conducted independently for saplings and adults (Appendix S1: Fig. S1).

Instead, when larger spatial scales were considered, there was statistically significant evidence ( $U_{ST-obs} > U_{ST-null}$ ,  $P \leq 0.01$ ) of functional clustering for all traits at both sites (Fig. 4). Thus, the individuals within a plot were functionally more similar from the individuals of different plots than expected by chance ( $U_{ST-obs}; D_w < D_a$ ). The same overall results were obtained when the analyses were independently conducted for saplings and adults (Appendix S1: Fig. S2).

#### ASSEMBLY PROCESSES UNDERLYING COMMUNITY FUNCTIONAL PATTERNS

Trait clustering pattern ( $U_{ST-obs} > 0$ ) among pairs of plots increased when increasing differences in MAT (Fig. 5). Those differences, as expected, were greater when comparing plots from lower and upper elevational belts (i.e., greater MAT differences) than when comparing among plots within the same elevational belt (i.e.,

smaller or no MAT differences). The correlation between MAT differences and trait clustering was positive and statistically significant ( $P \leq 0.01$ ) for all three functional traits at both sites. The only exception was SLA in Peru, for which no significant variations in community trait pattern appeared in relation to differences in MAT.

The climatic preferences of the LTMF and UTMF species, defined using their MAT values across their entire Neotropical distribution ranges, were clearly segregated both in Ecuador and Peru (Fig. 6a, b). LTMF species showed a mean temperature optimum of 22.8°C in Ecuador and 24°C in Peru, whereas these optima were 15.5° and 18.2°C, respectively, for UTMF species. There were statistically significant ( $P \leq 0.01$ ) differences in MAT for LTMF and UTMF species, both in Ecuador and Peru.

The abundances of LTMF and UTMF species shifted across the different elevational belts (Fig. 6c, d). Best-fit models for both sites included the most complex structure for both fixed effects and the simplest for random effects (Appendix S1: Table S5). Model predictions indicated that LTMF species were significantly more abundant at lower elevations than at the intermediate or, especially, higher elevations, from which some species

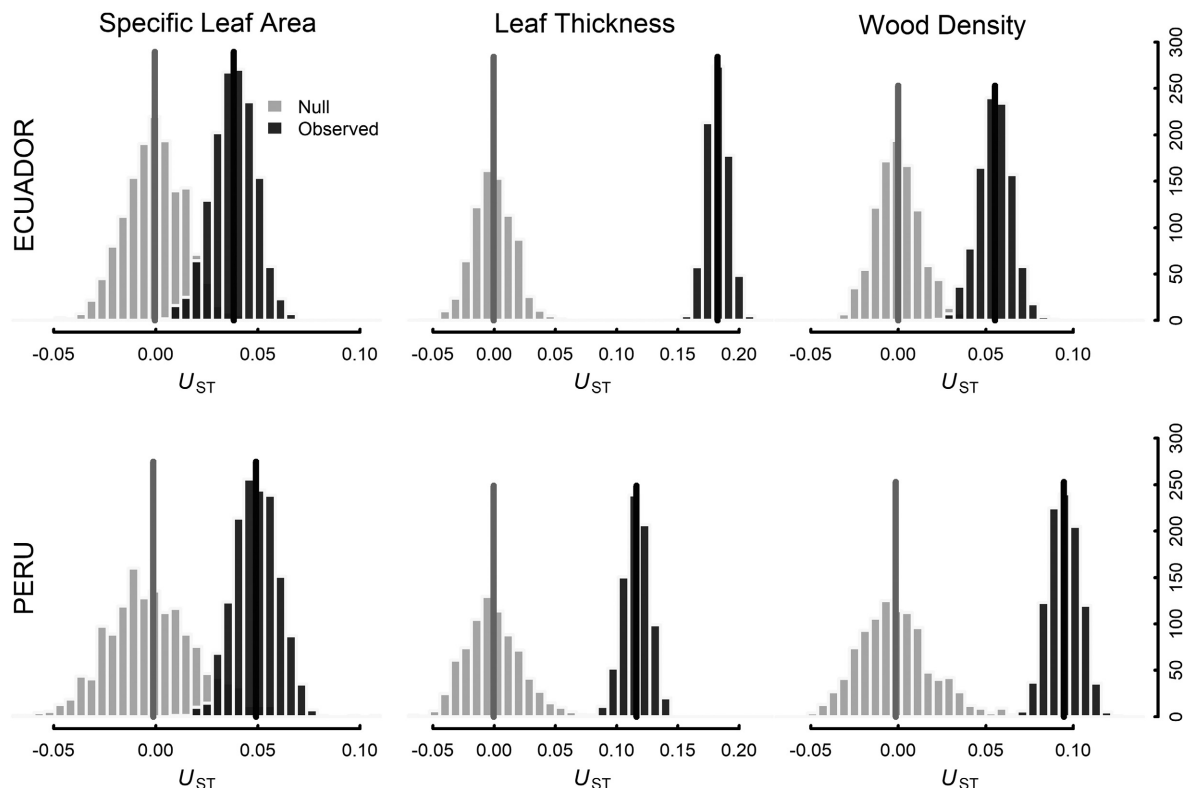


FIG. 4. Hypothesis 2: community functional distances distribution patterns at large spatial scale (among plots). Frequency of distribution of  $U_{ST-obs}$  (black) and  $U_{ST-null}$  (gray) values at two geographical sites (Ecuador, upper charts; Peru, lower charts) as measured based on three functional traits (specific leaf area [SLA], left; leaf thickness [LT], center; wood density [WD], right) after 1,000 randomizations, in all six cases. Differences between  $U_{ST-obs}$  and  $U_{ST-null}$  were significant ( $P \leq 0.01$ ) for all traits at both sites.

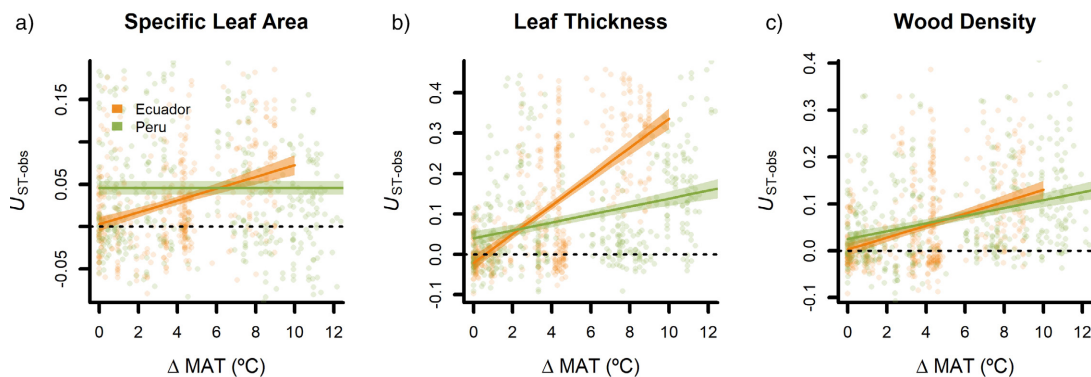


FIG. 5. Plots pairwise functional and environmental comparison. The x-axes represent environmental differences (in terms of mean annual temperature; MAT) between pairs of plots. The y-axes represent differences in observed functional traits patterns ( $U_{ST-obs}$ ) among plots for (a) specific leaf area [SLA], for (b) leaf thickness [LT], and (c) wood density [WD]. Trait clustering pattern ( $U_{ST-obs} > 0$ ) increased positively as MAT differences increased. This correlation was significant ( $P \leq 0.01$ ) for all traits at both sites, excepting for SLA in Peru.

were absent. Conversely, UTMF species were significantly more abundant at higher elevations than at the intermediate or, especially, lower ones, where some were missing.

#### DISCUSSION

Our study approaches a fundamental question in ecology: identifying the ecological mechanisms shaping community assembly. Overall, we found that taking into account spatial scale is key for detecting the functional fingerprint of the underlying mechanisms driving community assembly. Although we found no evidence of competitive exclusion at the smallest spatial scale, we detected strong evidence of environmental filtering at larger scales. In addition, further analyses conducted to link the community observed functional pattern with its underlying assembly process allows us to endorse the role of environmental filtering for community assembly.

##### *No evidence of competitive exclusion at small spatial scales*

In this study we detected no evidence of competitive exclusion at small spatial scale. Competitive exclusion has been hypothesized to occur at small spatial scales, where individuals from different species effectively compete for local resources (Weiher and Keddy 1995b, Stoll and Weiner 2000), thus a pattern of trait divergence is expected as a consequence of limiting similarity (Watkins and Wilson 2003, Stubbs and Wilson 2004). Nevertheless, as obvious as may seem, scale dependence has sometimes been ignored. For instance, Baraloto et al. (2012) rejected the importance of competitive exclusion as an assembly process by comparing functional distances of species within 1-ha plots ( $D_w$ ) and among plots separated by tens of kilometers ( $D_a$ ). In our opinion, their results ought to be interpreted with caution for two

reasons. First, it makes little sense to test for competitive exclusion between plant individuals that are very spatially distant (e.g., up to 140 m apart from each other), so are hardly competing for the same resources (e.g., light, soil nutrients). In relation to this, the scale at which competition between species operates is certainly organism dependent, thus whereas sessile organisms like plants mostly compete for key resources at small spatial scales (up to a few tens of meters), motile organisms such as birds or mammals can compete at much larger scales (up to a few tens of kilometers). Consequently, studies need to consider the spatial scales at which community assembly processes are most likely to operate in relation to the group of organisms under study; for example, if the organisms were plants, a checkerboard pattern noticed at large spatial scales (Diamond 1975, 1982) could be misinterpreted as the effect of competitive exclusion. Second, even if competitive exclusion existed between individuals within such a large plot, its trait overdispersion signal would be masked by the effect of among-plots environmental differences on functional distance.

To avoid spatial scale biases, we searched for evidence of competitive exclusion at small spatial scale (i.e., within  $10 \times 10$  m subplots). At this scale, co-occurring individuals can be assumed to compete directly for the same resources, and the effect of environmental filtering on functional distance can be ruled out because environmental conditions within a subplot are essentially the same (de Bello et al. 2013b). However, conversely to our expectation, we detected no evidence of a functional overdispersion pattern resulting from competitive exclusion for the traits we measured (Fig. 3). Instead, our results suggest a random community assembly at this small scale, although there could be cryptic nonrandom dispersion with respect to traits that we did not measure (Gallien 2017). In addition, because most of the assembly processes operate more strongly at early stages of

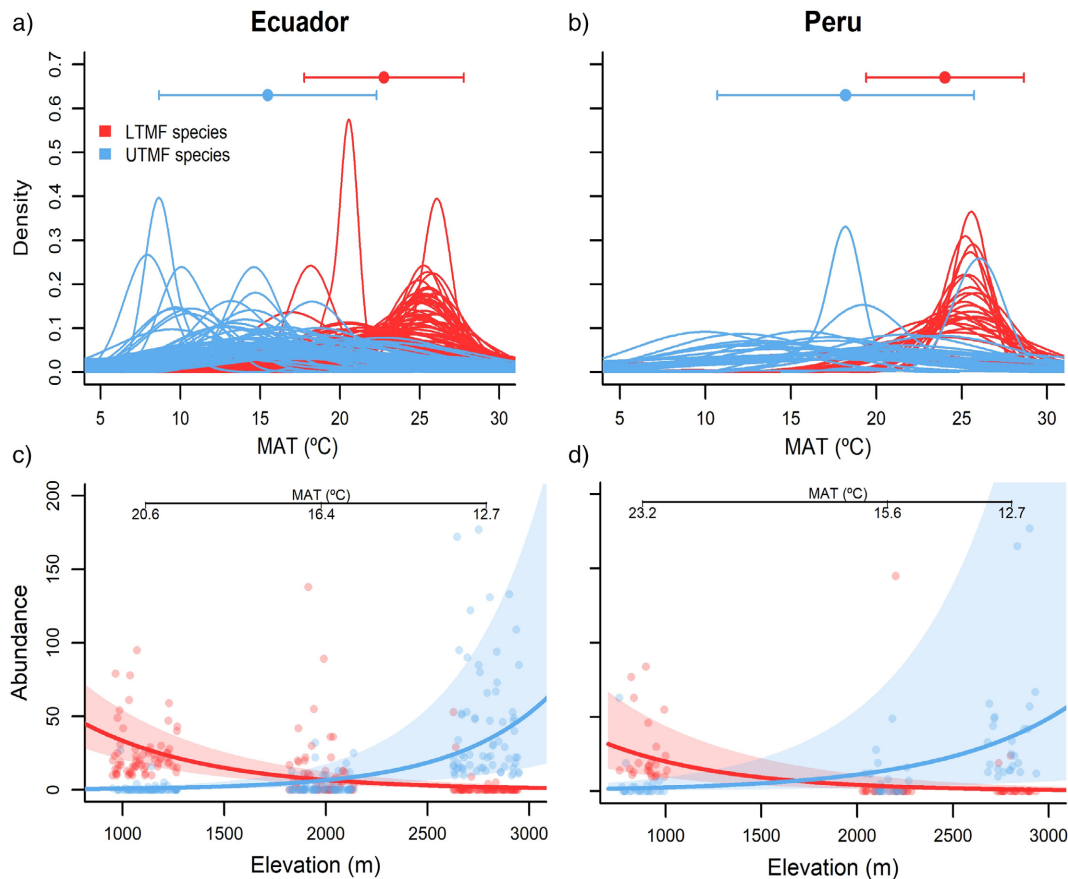


FIG. 6. Climatic preferences for the upper and lower tropical montane forest most abundant ( $N \geq 10$ ) species (upper tropical montane forest [UTMF] and lower tropical montane forest [LTMF] species, respectively) and their abundances along the elevational gradients. Climatic preferences in terms of mean annual temperature (MAT) of the UTMF and LTMF sets of species were segregated at the edges of the thermal gradient when the MAT values for those species' occurrences across their entire distribution range in the Neotropics were considered, both in (a) Ecuador and (b) Peru. Dots represent the mean MAT and horizontal lines the 95 % confidence interval of the MAT for each set of species' climatic preferences. Difference in the means of MAT for LTMF and UTMF species' climatic preferences was statistically significant ( $P \leq 0.01$ ) in both sites. Shifts in UTMF and LTMF species' abundances along the elevation gradients in (c) Ecuador and (d) Peru. Lines represent best fit model predictions with a 95% confidence interval. Best-fit models for both sites included altitude, climatic preference, and their interaction as fixed terms, and species as a random factor.

plant life cycles (Green et al. 2014), a functional pattern suggesting competitive exclusion may only become revealed when only considering saplings in the community, as they are most sensitive to competition (Falster and Westoby 2003, Wagg et al. 2017). To test this hypothesis, we checked whether functional overdispersion emerged for saplings but disappeared for adults. Again, no evidence of functional overdispersion was found for either saplings or adults (Appendix S1: Fig. S1).

Whereas some studies have also found no evidence of functional overdispersion between co-occurring species at small spatial scale (Schamp et al. 2008, Thompson et al. 2010), others have. However, those studies that did find functional overdispersion typically did not find it for all the analyzed traits, and it was sometimes the case that functional overdispersion and clustering were both

simultaneously reported within the same study system (Cavender-Bares et al. 2004, Mason et al. 2007, Kraft et al. 2008, Cornwell and Ackerly 2009, Swenson and Enquist 2009, Kraft and Ackerly 2010, de Bello et al. 2013b). The few studies that systematically reported the existence of limiting similarity (see Wilson 2007) were based on evidence found in relatively low-diversity communities, for example, sand dunes (Stubbs and Wilson 2004), lawns (Mason and Wilson 2006), or salt marshes (Wilson and Stubbs 2012). Our results, in agreement with the lack of consensus found in earlier studies, suggest that in hyperdiverse plant communities, limiting similarity may not be a paramount force driving community assembly (Grime 2006) because in hyperdiverse systems, the functional hyperspace would be limited to be parsed out into many discrete and differentiated functional niches, each for one of the co-occurring species.

*Evidence of environmental filtering clearly linked to environmental heterogeneity at large spatial scale*

In this study, we did find strong evidence of environmental filtering at large spatial scale. Given the more abiotically homogeneous and restrictive environment existing at small spatial scales, the potentially successful functional strategies that allow the survival of community members are narrowed, thus decreasing the role of environmental filtering for community assembly. But at large spatial scales that encompass different habitat conditions, such as topography or edaphic variables, or that expand environmental gradients, there is consensus on the importance of environmental filtering. Under this scenario, the selection of just the suitable set of traits that allows species to thrive under certain environmental conditions would result in a functional clustering pattern (Fig. 4). Nevertheless, the reliability of clustering patterns, in themselves widely accepted as indicators of environmental filtering, has been questioned lately, because some biotic processes can also render clustering patterns (Sargent and Ackerly 2008). We agree with Kraft et al. (2015) on their assertion that experimental manipulations aimed to assess species' failure to establish and persist in the absence of biotic interactions are the most robust proof of environmental filtering *sensu stricto*. We argue, however, that this is not only impractical in field studies, especially at logistically challenging tropical montane forests, it is also not necessarily meaningful from an ecological perspective. Instead, we trust that, according to Cadotte and Tucker (2017), as long as we can correlate changes in community functional clustering patterns, species abundances, or population growth with the underlying shifts in environmental conditions, we can infer and advocate for the existence of a *sensu lato* environmental filtering process ongoing, regardless of simultaneously occurring biotic phenomena.

Our results show that only when large spatial scales that truly encompass environmental differences are considered (e.g., among pairs of plots from different elevational belts and, thus, affected by notable MAT differences) is environmental filtering revealed as an overriding influence for community assembly. Thus, the evidence of environmental filtering does not merely lay in the traditionally admitted clustering pattern itself, but in the fact that the pattern only arises when underlying environmental heterogeneity exists (Fig. 5). In addition, our study reveals how such environmental differences cause changes in community features other than the clustering pattern. For instance, for the most abundant species in the lower and upper tropical montane forest—LTMF and UTMF species, respectively—(1) their abundances dramatically shift between elevations (Fig. 6c, d) and (2) their climatic preferences are segregated at the edges of the thermal gradient (Fig. 6a, b). Those facts suggest that species distribution is mainly a consequence of species abiotic preferences resulting from environmental filtering, and unlikely the result of other factors, such

as dispersal limitation, which is expected to play a negligible role in the continuous, nonfragmented forests within single river basins, as is the case in both our sites (Young 1990, Pennington et al. 2010). In addition, the fact that the climatic preferences of the LTMF and UTMF species are maintained across their entire distribution range in the Neotropics (Fig. 6a, b) reinforces the role of environmental filtering as a broadly prevalent mechanism for community assembly.

Thus far, indications of an environmental filtering fingerprint on tropical community assembly across different habitats have been reported mainly by considering habitat differences as a surrogate for environmental differences (e.g., topography in the Yasuní megaplot, Ecuador, by Kraft et al. 2008, or forest age and geological formation in Barro Colorado Island, Panama, by Garzon-Lopez et al. 2014). Besides, identifying the effect of environmental filtering has remained particularly challenging in species-rich forests, where, as a result of stochastic dilution, the signal of deterministic assembly processes may not be detectable, even if those processes are operating (Wang et al. 2016). However, our study provides robust scale and environmentally based evidence supporting the importance of environmental filtering for community assembly.

#### SUMMARY AND FURTHER PROSPECTS

The effect of environmental filtering in community assembly has been traditionally inferred from trait clustering patterns, as found by several studies targeted at various systems and taxonomic groups (e.g., trees in tropical forests, Baraloto et al. 2012; rockfishes in the ocean, Ingram and Shurin 2009; bees in mountains, Pellissier et al. 2013). However, in order to be properly addressed, pertinent spatial scale-related implications need to be taken into account (e.g., de Bello et al. 2009, Swenson and Enquist 2009, Münkemüller et al. 2013, Garzon-Lopez et al. 2014, Mori et al. 2015). Our results demonstrate a clear link between the pattern and the mechanism by showing that the pattern is only revealed when environmental differences exist, and by demonstrating how those differences correlate with species' climatic preferences, maintained across their entire distribution range in the Neotropics, and abundances, along elevation. This study thus contributes to emphasizing the importance of considering the implications of spatial scale to detect the extent at which assembly mechanisms act. In addition, it highlights the undeniable role of environmental filtering in community assembly and the usefulness of such a concept, demonstrating that neither excluding biotic potentially confounding processes nor identifying abiotic tolerance ranges are strictly necessary for validating its effect. Future studies have the challenge of advancing the discussion and shedding light on the remaining details, such as whether the effect of environmental filtering equally influences low- and high-diversity communities.

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