RESEARCH ARTICLE

# Mechanisms of community assembly explaining beta-diversity patterns across biogeographic regions

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## Abstract

**Aim:** We examined tree beta diversity in four biogeographical regions with contrasting environmental conditions, latitude, and diversity. We tested: (a) the influence of the species pool on beta diversity; (b) the relative contribution of niche-based and dispersal-based assembly to beta diversity; and (c) differences in the importance of these two assembly mechanisms in regions with differing productivity and species richness.

**Location:** Lowland and montane tropical forests in the Madidi region (Bolivia), lowland temperate forests in the Ozarks (USA), and montane temperate forests in the Cantabrian Mountains (Spain).

**Methods:** We surveyed woody plants with a diameter ≥2.5 cm following a standardized protocol in 236 0.1-ha forest plots in four different biogeographical regions. We estimated the species pool at each region and used it to recreate null communities determined entirely by the species pool. Observed patterns of beta diversity smaller or greater than the null-expected patterns of beta diversity implies the presence of local assembly mechanisms beyond the influence of the species pool. We used variation-partitioning analyses to compare the contribution of niche-based and dispersal-based assembly to patterns of observed beta diversity and their deviations from null models among the four regions.

**Results:** (a) Differences in species pools alone did not explain observed differences in beta diversity among biogeographic regions. (b) In 3/4 regions, the environment explained more of the variation in beta diversity than spatial variables. (c) Spatial variables explained more of the beta diversity in more diverse and more productive regions with more rare species (tropical and lower-elevation regions) compared to less diverse and less productive regions (temperate and higher-elevation regions). (d) Greater alpha or gamma diversity did not result in higher beta diversity or stronger correlations with the environment.

**Conclusion:** Overall, the observed differences in beta diversity are better explained by differences in community assembly mechanism than by biogeographical processes that shaped the species pool.

**KEYWORDS**

environmental filtering, Madidi, montane forest, niche partitioning, null model, spatial autocorrelation, species pool, species turnover, temperate forest, tropical forest

# 1 | INTRODUCTION

Beta diversity measures the change in biological composition among sites (Anderson et al., 2011). It reflects a variety of historical, biogeographical, and local mechanisms that control the distribution of species across space and time. The processes that shape local communities within the constraints imposed by the regional species pool (the set of species that could potentially colonize a local community; Pärtel et al., 2011; Lessard et al., 2012a; Lessard et al., 2012b; Carstensen et al., 2013) are called "community assembly processes" (Chase et al., 2011; De Cáceres et al., 2012; Myers et al., 2013). Considerable debate exists about the relative role of species pools and different local community assembly processes in shaping local composition and beta diversity in different biogeographic regions (Kraft et al., 2011; McFadden et al. 2019). Here, we explore several non-mutually exclusive hypotheses about the drivers of beta diversity and their relative importance between regions.

The biogeographical hypothesis (e.g. Kraft et al., 2011) states that local communities solely reflect processes operating at larger scales than the studied community (e.g. long-term historical and biogeographical processes). The biogeographical hypothesis predicts that local communities are randomly-assembled subsets from the species pool. This hypothesis provides a useful null hypothesis in which to explore ecological processes to explain why observed patterns of beta diversity may or may not deviate from random community assembly (e.g. Kraft et al., 2011; Mori et al., 2013; Myers et al., 2013; Tello et al., 2015).

The processes that can cause non-random patterns of community composition can be organized along a continuum ranging from deterministic niche assembly processes to spatial dispersal assembly processes. The "niche assembly hypothesis" (e.g. Condit et al., 2002; Tuomisto et al., 2003b) assumes adaptations of species to specific environmental conditions (Schoener, 1974; Tuomisto et al., 2003a; Levine & HilleRisLambers, 2009; Vellend, 2010; Chase & Myers, 2011). This hypothesis predicts that two sites will have similar species composition (low beta diversity) if their environmental conditions are similar, regardless of where the sites are located within the region. In contrast, the "dispersal assembly hypothesis" (e.g. Hubbell, 2001; Chase et al., 2011) states that dispersal limitation and random changes in species abundances have a stronger influence on community composition than species adaptations to particular environments (Hubbell, 2001, Dexter et al. 2017, Wandrag et al. 2017).

This hypothesis predicts that two sites will have similar species composition (low beta diversity) if they have high connectivity and high rates of dispersal between them, or if they are colonized by the same species from a mainland source or species pool, regardless of their environmental conditions (Chase & Myers, 2011).

The niche assembly and dispersal assembly hypotheses are not mutually exclusive (Gravel et al., 2006; Wang et al., 2012), but we know little about how or why their relative importance differs between regions. Here, we focus on three related hypotheses about the relative importance of niche assembly and dispersal assembly: the "rarity hypothesis" (Hurtt & Pacala, 1995); the "productivity hypothesis" (Chase, 2010); and the "diversity-increases-competition hypothesis" (Karger et al., 2015). First, the rarity hypothesis states that the probability of colonizing an open site is proportional to the abundance of a species (Hurtt & Pacala, 1995). This hypothesis predicts more recruitment-limited communities and a stronger influence of spatial factors on beta diversity when most species are rare. Second, the productivity hypothesis states that the order of species' arrival is less predictable in regions with higher net primary productivity, leading to different final community compositions even when the environment is the same in all localities (Chase, 2003; Chase, 2010). The existence of multiple stable equilibria in composition increases beta diversity (Chase, 2010). This hypothesis predicts both higher beta diversity and a stronger role of stochastic dispersal assembly (relative to deterministic niche assembly) with increasing productivity. The rarity hypothesis and the productivity hypothesis are related because more productive (e.g. tropical) biomes tend to have greater species richness and more rare species. Likewise, both hypotheses predict a stronger correlation between spatial factors and beta diversity in more productive and species-rich regions. Finally, the diversity-increases-competition hypothesis assumes that species-rich regions will contain more habitat specialist species (Karger et al., 2015). Unlike the rarity and the productivity hypotheses, the diversity-increases-competition hypothesis predicts higher beta diversity and a more important role of niche assembly in more productive and species-rich regions.

In this study, we examined tree beta diversity in four biogeographical regions of contrasting environmental conditions, latitude, and diversity. Within each region, we examined: (a) the influence of the species pool (i.e., the role of the biogeographical hypothesis); (b) the relative contribution of environmental and spatial variables to observed patterns of beta diversity (i.e., niche assembly vs

dispersal assembly hypotheses); and (c) differences in the importance of assembly mechanisms in regions with differing rarity (rarity hypothesis), productivity (productivity hypothesis), or species diversity (diversity-increases-competition hypothesis). Our approach removed methodological biases by using data from forest plots installed following exactly the same field methods, climatic data from the same sources, soil data obtained with comparable laboratory protocols, and standardized statistical procedures. In addition, we controlled for effects of spatial scale and length of environmental gradients by carefully choosing comparable sets of forest plots from larger data sets. To minimize potential biases due to the specific set of forest plots chosen, we replicated our analysis 1,000 times with varying combinations of plots. We also removed possible differences in sampling effort among regions by using complete assemblage-specific species pools including unobserved species.

## 2 | METHODS

In this section, first we present the four studied regions and the plot methods to gather floristic data. The four regions cannot be compared directly, so we also present a plot subsampling procedure. Second, we describe how we obtained environmental and spatial variables for each region. Third, we explain how we estimated complete species pools for the assemblage at each region. Fourth, we describe how we used the species pool to recreate null communities: deviations from the null communities (beta deviations) reflect the importance of local assembly mechanisms; the biogeographical hypothesis is directly tested here at each region. Fifth, we present the methods that we used to compare the alpha, gamma and beta diversities between the four regions. Finally, we present the variation-partitioning analyses that relate beta diversity and beta deviations with the environmental and spatial variables. The results at each region inform about the relative importance of niche assembly and dispersal assembly hypotheses: stronger correlations between beta diversity (or beta deviations) and the environmental variables imply a greater importance of the niche assembly hypothesis; stronger correlations between beta diversity (or beta deviations) and the spatial variables imply a greater importance of the dispersal assembly hypothesis. The comparison between regions (which differ in rarity, productivity and species diversity) informs about the rarity, productivity and diversity-increases-competition hypotheses: the rarity and productivity hypotheses expect lower importance of the environmental variables (relative to spatial variables) in the more diverse/productive regions, whereas the diversity-increases-competition hypothesis expects greater importance of the environmental variables (relative to spatial variables) in the more diverse/productive regions.

### 2.1 | Study regions and botanical inventories

We compared four distinct biogeographic regions: (a) tropical rainforests in northwestern Amazonia (Bolivia), (b) montane tropical

forests in the Bolivian Andes (excluding dry forests), (c) temperate oak–hickory forests in the Missouri Ozarks (USA), and (d) oak–mixed forests on the western side of the Cantabrian Mountains (Spain). Both tropical regions were located in the Madidi area, and are characterized by low seasonality in temperature and high regional species richness (Figure 1). The two temperate regions (the Ozarks and the Cantabrian Mountains) are characterized by high temperature seasonality and low regional species diversity (Figure 1). The Amazon and the Ozarks represent lowland forests (Figure 1a), while the Andes and the Cantabrian Mountains are located at higher elevations with more dissected topography.

In each study region, we installed and evaluated from 22 to 111 forest plots, following standardized methods (Arellano, et al., 2016a). All plots were 20 m × 50 m in size (0.1 ha) and excluded large forest gaps or evidence of recent natural or human disturbances. At each plot, we recorded abundances of all trees with a diameter at breast height ≥2.5 cm. We standardized identifications and morphospecies within each region.

These original data sets could not be compared directly, as they represented very different sampling efforts, different spatial extents, and different ranges of environmental conditions. To remove these effects from our inference, we selected subsets of plots at each region in a way that geographical distances and environmental differences among sites in the different regions were comparable (Ulrich et al., 2017). The sub-setting procedure is described in Appendix S1. To obtain robust results, the whole procedure was repeated 1,000 times, i.e., we analyzed 1,000 times the beta-diversity patterns and drivers in four subsets of plots, one at each of the studied biogeographical regions. The whole data sets were never considered in any of the analyses.

### 2.2 | Environmental and spatial data

We estimated climatic conditions, topographical variables, and soil properties for all plots. Using the location of each plot, we extracted 19 bioclimatic variables from climatic rasters at ~1 km$^2$ resolution from the CHELSA data set version 1.1 (Karger et al., 2016a; http://chelsa-climate.org/). We incorporated into the climatic data sets some topographic variables: elevation and two measurements of aspect (northness and eastness), which is correlated with local microclimate at least in the temperate zone. The topographical variables were measured in the field in the Ozarks and Cantabrian Mountains, and estimated from a ~30-m resolution raster of elevation for the two sets of plots in Madidi (ASTER Global Digital Elevation Map v. 2, http://asterweb.jpl.nasa.gov/gdem.asp). These climatic and topographical variables together are referred to as "climate" in the following.

To characterize edaphic conditions, we collected soil samples (0–30 cm) in each plot. Soil samples were air-dried and sieved through a 2-mm sieve. Soil pH was determined in a 1:2.5 soil:H$_2$O solution in the Amazon, the Andes, and the Cantabrian Mountains; and in a 1:1 soil:CaCl$_2$ solution (0.01 M) in the Ozarks. We standardized these
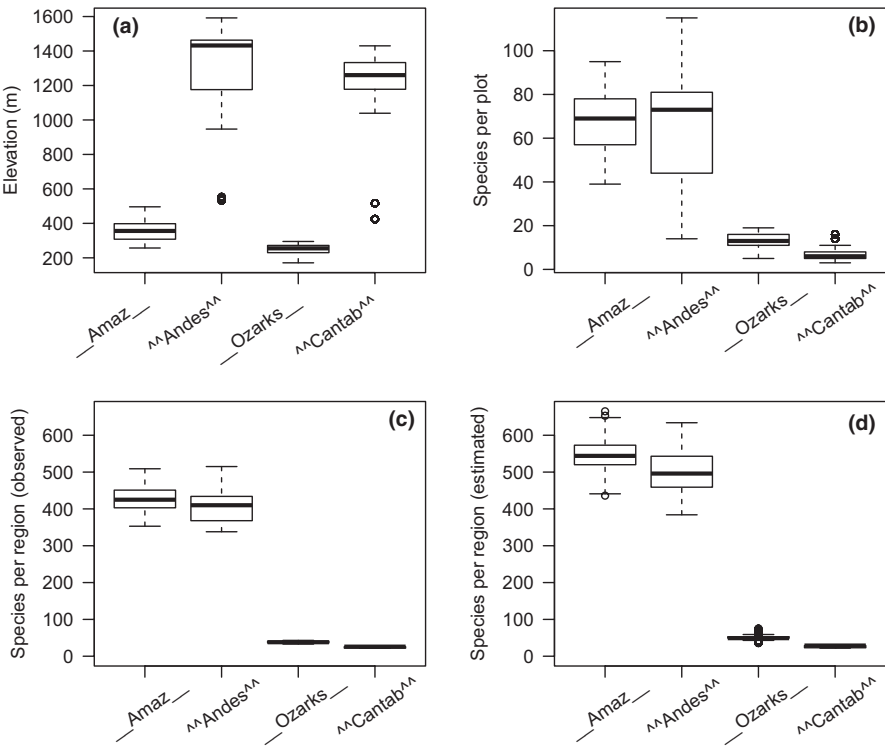
**FIGURE 1** Regional differences in elevation and species richness. (a) Mean elevation of plots in 1,000 sets of four subsets of plots, one subset per region. (b) Mean number of species per plot in 1,000 sets of four subsets of plots. (c) Observed number of species in 1,000 sets of four subsets of plots. (d) Number of species in 1,000 sets of four subsets of plots as estimated with the Chao1 estimator. Table 1 summarizes how much the diversities of many of these 1,000 sets of four subsets of plots differed or were statistically indistinguishable from each other. Amaz, Amazon (Madidi, Bolivia); Andes, Andes (Madidi, Bolivia); Ozarks, Ozarks (USA); Cantab, Cantabrian Mountains (Spain). The lowland regions are indicated by __<code>__ and the mountainous regions by ^^<code>^^

**TABLE 1** Regional comparisons of alpha-diversity (mean number of species per plot) and gamma-diversity (both observed and estimated number of species per region)

| Regions | | Alpha diversity | | | Observed gamma diversity | | | Estimated gamma diversity | | |
|---|---|---|---|---|---|---|---|---|---|---|
| A | B | A > B | A = B | A < B | A > B | A = B | A < B | A > B | A = B | A < B |
| Amazon | Andes | 122 | 703 | 175 | 268 | 656 | 76 | 384 | 521 | 95 |
| Amazon | Ozarks | 1,000 | 0 | 0 | 1,000 | 0 | 0 | 1,000 | 0 | 0 |
| Amazon | Cantabrian | 1,000 | 0 | 0 | 1,000 | 0 | 0 | 1,000 | 0 | 0 |
| Andes | Ozarks | 1,000 | 0 | 0 | 1,000 | 0 | 0 | 1,000 | 0 | 0 |
| Andes | Cantabrian | 1,000 | 0 | 0 | 1,000 | 0 | 0 | 1,000 | 0 | 0 |
| Ozarks | Cantabrian | 1,000 | 0 | 0 | 1,000 | 0 | 0 | 1,000 | 0 | 0 |

*Note:* The table counts how many times two regions were similar ("A = B") or different ("A > B" or "A < B") in 1,000 versions of the same analysis. Each instance of the analysis was based on simple bootstrapped 95% confidence intervals. If A = B in the real world, we would expect 950 in the "A = B" column and 50 somewhere else just by chance. Amazon: Amazon; Andes: Andes; Ozarks: Ozarks, USA; Cantabrian: Cantabrian Mountains, Spain.

measurements into comparable values using conversion methods detailed in Appendix S2. The granulometric analysis was performed with the sedimentation and Bouyoucos' densimeter technique. Total nitrogen (N) was measured with the Kjeldahl method (Reeuwijk, 2002) or with total combustion using an auto-analyzer. Both methods for N result in directly comparable data, because the inorganic N compounds that the Kjeldahl method cannot measure are volatile and typically represent <2% of the total N in surface soils (Arellano et al., 2016a). We also measured calcium (Ca), magnesium (Mg), and potassium (K) using two extractive methods for different sets of samples: (a) the 1-M ammonium acetate solution method, and (b) the Mehlich-3 extraction method (Mehlich, 1984). The results from both methods are linearly correlated; see Appendix 2 for the standardization into comparable values.

To examine the relationship between spatial variables and community composition, we calculated two types of spatial variables

for each region: (a) geographic coordinates (latitude, longitude); and (b) Principal Components of Neighbor Matrices (PCNM) using the function pcnm of the *vegan* package in R (Oksanen et al., 2015). PCNM variables describe spatial structure at all spatial scales that can be fitted in the sampling design (Borcard et al., 2004; Dray et al., 2006). Only PCNMs with positive eigenvalues were included in the analyses.

## 2.3 | Definition of the species pool for the assemblage at each region

The species pool is the set of species that could potentially disperse to, colonize, and establish within a local community, and relates to processes happening at a larger scale than the targeted local

community (Pärtel et al., 2011; Lessard et al., 2012a; Lessard et al., 2012b; Carstensen et al., 2013). Species pools are difficult to estimate in practice (Lessard et al., 2012a; Carstensen et al., 2013; Karger et al., 2016b). Most previous works used the observed total diversity in a set of samples as a proxy for the regional species pool. However, while few plots may capture most of the regional diversity in species-poor regions, they may only capture a fraction of the species in diverse regions (Ulrich et al., 2017). To avoid potential biases when comparing regions of different diversity, the regional species pool employed in our null model included the relative abundances of all species estimated to be present in the regional assemblage (corresponding to the subset of plots considered) including both observed and unobserved species. This involved two steps. First, we estimated the total number of species of the assemblage using the Chao1 estimator, as implemented in Chao et al. (2015). Second, the relative abundance of species in the regional species pool was estimated using Good–Turing sample coverage theory (Chao et al., 2015). This non-parametric technique links the true relative abundance in the entire assemblage with the observed relative abundance in the sample by estimating the probability of finding an object of an unseen class (i.e., an individual of an unobserved species) given a set of past observations of objects from different classes (i.e., given the relative abundances of the observed species). The technique is thoroughly explained in Chao et al. (2015). The code to implement the technique is openly available as a Supplement R script in Chao et al., 2015, as R code in Appendix S1 of Arellano et al., 2017, and as a Shiny app (https://chao.shinyapps.io/GoodTuring/).

These estimations, as all the calculations and analyses presented later, were repeated 1,000 times with varying sets of four subsets of plots, one at each of the studied biogeographical regions.

## 2.4 | Null model to account for the effect of random sampling from the species pool

At each region, we created 999 null assemblages. Each null assemblage was built by taking individuals from the species pool (probability proportional to their estimated relative abundances in the species pool, for both observed and unobserved species) and assigning them randomly to plots until the observed number of individuals at each plot was reached. In this way, the null model recreated a community determined entirely by the local number of individuals and random colonization from the regional species pools. i.e., the null model eliminates the effects of local assembly processes that constrain the membership of individuals into communities.

We measured beta diversity as pairwise Bray–Curtis dissimilarity, which reflects changes in the composition between plots resulting from both species turnover, nestedness in species composition, and differences in species abundances (Baselga, 2013). We compared the observed beta diversity with the beta diversity expected by the null model. The null communities represented 999 values of expected dissimilarities, for each pair of plots. Using that null distribution, we estimated pairwise beta deviations as standardized effect sizes:

$$beta\ deviation = \frac{beta\ observed\ -\ mean(beta\ null)}{sd(beta\ null)}$$

These beta deviations can be interpreted as the relative effect of local assembly mechanisms on beta diversity. Larger beta deviations suggest a greater importance of processes controlling the membership of species into local communities (Schoener, 1974; Ulrich et al., 2017).

## 2.5 | Comparing alpha, gamma, and beta diversities among regions

For a given region, we measured: (a) its alpha diversity as the mean number of species per plot; (b) its observed gamma diversity as the observed number of species in all the selected plots combined; and (c) its estimated gamma diversity as the number of species in the entire assemblage estimated through the Chao1 estimator, as used in the estimation of the species pool. We obtained 95% confidence intervals for these three metrics by bootstrapping the plots and re-calculating the values again with the bootstrapped composition matrix. If the confidence intervals of region A included the central estimate of region B, both regions were considered not different (at the alpha = 0.05 level), for a given diversity metric.

Differences in beta diversity among regions were evaluated using an analysis of multivariate homogeneity of group dispersions (Anderson, 2006, Anderson et al., 2006; betadisper function of R package *vegan*). This analysis represents a multivariate extension of Levenes' test (Anderson, 2006), was described for the comparison of beta diversity among groups by Anderson et al. (2006), and has been used in several recent studies (Myers et al., 2013; Gianuca et al. 2017; Berker-Scarpitta et al. 2019). The main advantages of this analysis are: (a) it avoids the pseudo-replication of pairwise distances while retaining all the information about community variation; and (b) it can be used with any distance measure, including non-Euclidean distances. The analysis applies a principal coordinates analysis (PCoA) to the pairwise Bray–Curtis distances, calculates the centroids of each region (i.e., group) and then estimates the distances from each plot to the centroid of its corresponding region. Higher average distances to centroid represent higher variation in community composition (i.e., higher beta diversity). The statistical significance of the differences between the four regions was tested first. If the test considering all regions was statistically significant, then we conducted separated tests for each pair of regions, to identify which regions were different from one another. This comparison based on the test of homogeneity of group dispersions was applied to: (a) the observed beta diversity; (b) the expected null beta diversity; and (c) the beta deviations.

## 2.6 | Variation partitioning analyses

To examine the role of assembly processes in generating beta-diversity patterns, we conducted variation-partitioning analyses

separately for each region. We performed these analyses for both the observed patterns (beta diversity) and the deviations from the null model (beta deviations). These analyses partitioned variation in community composition into components explained by environmental variables or spatial variables. We also further partitioned the (exclusively) environmental component into the variation associated either to climate or soils. The methods were identical for the four regions and the two response matrices per region (beta diversity and beta deviations):

Step 1. To create a response matrix for our analyses, we conducted a PCoA on the matrix of pairwise Bray–Curtis beta diversity or beta deviations. This resulted in a new matrix composed of the ordination axes from the PCoA, which represents the variation in community composition among plots within a region. In all cases, we used the "Cailliez" correction to avoid negative eigenvalues (Legendre & Legendre, 1998). We retained all ordination axes in our response matrices, so no information was lost except a minimum amount from the "Cailliez" correction.

Step 2. For each group of explanatory variables (climate, soil, spatial variables), we removed variables that were highly correlated with other variables (Pearson's $r > 0.80$).

Step 3. For the remaining variables within each group, we conducted a forward variable selection procedure as described by Blanchet et al. (2008) using the ordiR2step function of the R package *vegan*. This approach controls for type I error rates and overestimation of explained variation. The frequency with which each variable was selected is summarized in Appendix S3.

Step 4. We conducted two variation-partitioning analyses using redundancy analysis (Legendre & Anderson, 1999). For the first analysis, we decomposed variation in community composition (ordination axes from the PCoA in step 1) into fractions: (a) explained solely by environmental predictors (combining the selected climate and soil variables in step 3); (b) explained solely by spatial predictors (also selected in step 3); or (c) explained by both sets of predictors simultaneously. For the second analysis, we decomposed the variation explained solely by environment into the contribution of: (a) climate only; (b) soils only; or (c) climate and soils only (Appendix S4).

## 3 | RESULTS

All the analyses were repeated 1,000 times on varying sets of four subsets of plots, one at each of the studied biogeographical regions. Because of that, each result (e.g. "A > B") has a weight of evidence or support (e.g. "A > B in 900 cases out of 1,000 versions of the analysis"). Here and in the *Discussion* section we will use notation like "900/1,000" to refer to these weights of evidence or support. The frequency of occurrence of a given result across 1,000 subsets is not a measure of effect size (i.e. how "extreme" a result is). It is a measure of how robust or general a given result is, i.e., how transferable the results are from one specific instance of a sampling effort to an equivalent sampling in the same study regions.

### 3.1 | Regional differences in alpha and gamma diversities

Both tropical regions (the Amazon and Andes) had greater species richness than their temperate counterparts (Ozarks and Cantabrian Mountains) at local scales (Figure 1b). This was a very consistent result obtained 1,000/1,000 times in our repeated analyses (Table 1). In turn, the Ozarks had greater alpha diversity than the Cantabrian Mountains (Figure 1a, 1,000/1,000 times in Table 1). Both tropical regions, however, had similar alpha diversity (Figure 1b; in 703/1,000 cases they were not significantly different from each other).

Similar results were obtained for observed gamma diversity (Figure 1c): in 1,000/1,000 cases the tropical regions had greater gamma diversity than the temperate regions, and the Ozarks greater than the Cantabrian Mountains. The same happened with estimated gamma diversity (Figure 1d). In terms of gamma diversity, the Amazon and the Andes were also relatively similar to each other (656/1,000 times in observed gamma diversity, 521/1,000 times in estimated gamma diversity), but the Amazon more frequently showed greater values than the Andes (268/1,000 times in observed gamma diversity, 384/1,000 times in estimated gamma diversity).

### 3.2 | Regional differences in beta diversity and beta deviations

Observed beta diversity often differed significantly among regions (845/1,000 times in our repeated analyses). These differences were most often due to a lower observed beta diversity in the Ozarks region compared with the other three regions (Figure 2a, Table 2). Other than the Ozarks the regions had similar observed beta diversity overall (Figure 2a; Table 2).

In all regions, the observed beta diversity was higher than the expected or null beta diversity (Figure 2a), i.e. beta deviations were mostly positive (Figure 2b). Beta deviations varied among regions (Figure 2b; Table 2). Beta deviations were often (740/1,000 times) higher in the montane temperate region (Cantabrian Mountains) than in the lowland temperate region (Ozarks). In contrast, beta deviations were higher in the montane tropical region (Andes) than in the tropical lowland region (Amazon) 307/1,000 times only. For a given elevation, beta deviations were indistinguishable between the Amazon and the Ozarks (1,000/1,000 times) but were often higher in the Cantabrian Mountains compared to the Andes (689/1,000 times).

### 3.3 | Environmental and spatial correlations with beta diversity and beta deviations

Total explained variation in observed beta diversity, averaged across the 1,000 repetitions of the analyses, was higher in the Cantabrian Mountains (45%) than in the other three regions (27–29%; Figure 3a, Appendix S5). The environment was a stronger
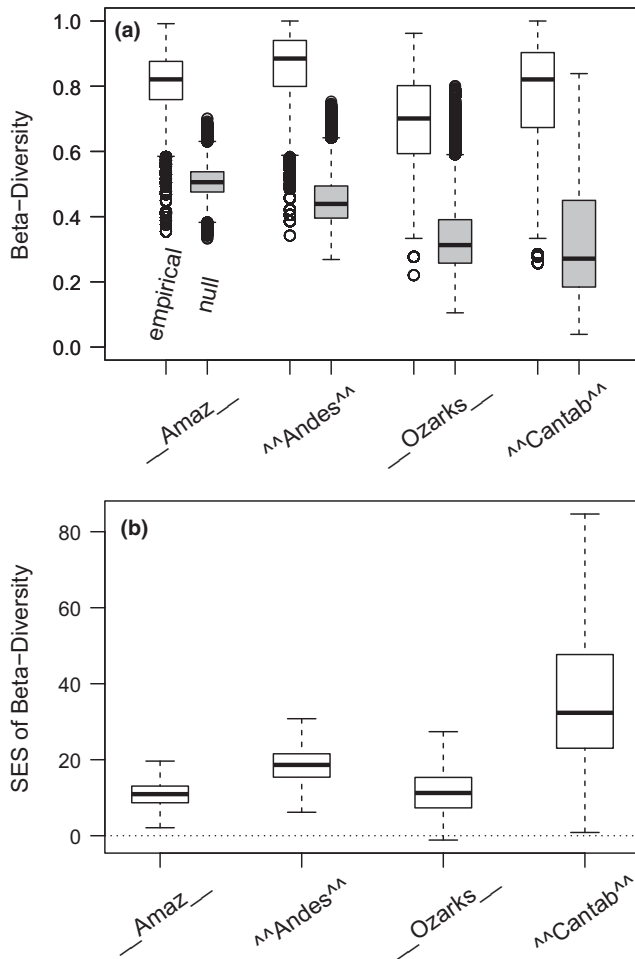
**FIGURE 2** Regional differences in beta diversity (variation in community composition). (a) Empirical beta diversity and expected (null) values from the null model, in white and gray boxplots respectively. (b) Beta deviations (standardized effect sizes, SES). The null model controls for sampling from the estimated regional species pools, while removing effects of assembly processes (see *Methods* for further details). The boxplots reflect all the values pooled together for 1,000 versions of the same analysis. A summary of the results of statistical comparisons at each instance of the analyses can be found in Table 2. Amaz: Amazon (Madidi, Bolivia); Andes: Andes (Madidi, Bolivia); Ozarks: Ozarks (USA); Cantab: Cantabrian Mountains (Spain). The lowland regions are indicated by __<code>__ and the mountainous regions by ^^<code>^^

predictor of observed beta diversity than spatial variables in all forest types (15–43% vs 12–18% of explained variation, respectively); Figure 3c). With the exception of the Ozarks, the importance of the environment was due to the importance of climate more than soils (Figure 3e). The environment was more important in the temperate regions (24–43%) than in the tropical regions (15–24%) and more important in the mountains within a given latitude (24% in the Andes vs 15% in the Amazon, and 43% in the Cantabrian mountains vs 24% in the Ozarks). There were only small differences in how important the space was in explaining observed beta diversity in the four regions.

The total explained variation in beta diversity tended to increase 13–14% after accounting for sampling effects from species pools (i.e., when using beta deviations; Figure 3b). The only exception was the Cantabrian Mountains, where the total explained variation decreased from 45% to 8% for beta deviations (Figure 3b). With the exception of this great reduction in total explained variance in the Cantabrian mountains (Figure 3b), the results of the variation-partitioning analyses were generally consistent when using observed beta diversity or beta deviations in all regions (Figure 3d, f).

## 4 | DISCUSSION

We tested several hypotheses related to how environmental, spatial, and regional factors shape beta diversity. We found that: (a) species pools alone cannot explain the observed patterns of beta diversity (we reject the biogeographical hypothesis); (b) except in the Amazon, the environment explains more of the variation in beta diversity than the space (stronger support for the niche assembly hypothesis than for the dispersal assembly hypothesis); (c) the space explains more of the beta diversity in more diverse/productive regions with more rare species (in tropical regions more than in temperate regions, at lower elevations more than at higher elevations; we accept the rarity and productivity hypotheses); and (d) greater alpha or gamma diversity does not result in higher beta diversity or tighter correlations with the environment (we reject the diversity-increases-competition hypothesis).

As expected, we found a high degree of idiosyncrasy in the quantitative results that come from different regions. However, we used comparable field methods (exactly the same tree diameter cut-off and plot shape), environmental variables (including comparable lab methods for soil analyses), equivalent spatial and environmental dispersions, and the same statistical analyses. Besides, we replicated all our analyses 1,000 times over varying subsets of plots from each region. Overall, the contingencies in our results very likely come from ecological differences, and are not spurious or driven by methodological choices.

## 4.1 | Regional differences in beta-diversity patterns and the influence of the species pools

Previous studies have observed a positive relationship between the size of the species pool and beta diversity across latitudes and elevation (Kraft et al., 2011; Myers et al., 2013; Tello et al., 2015). This relationship is hypothesized to underlie the latitudinal (e.g. Qian & Ricklefs, 2007) and elevational (e.g. Sabatini et al., 2018) gradients in beta diversity. Such gradients in beta diversity are expected to be less steep than the gradients in species richness: climate may be more homogeneous at higher latitudes (e.g. Qian & Ricklefs, 2007) and species may have broader niches and be less responsive to geographical changes in temperate regions and at higher elevations (Janzen, 1967; Stevens, 1989, 1992; Wang et al., 2012). In our case, we did not find a clear difference in observed beta-diversity values between the studied regions, with the exception of the temperate

**TABLE 2** Regional comparisons of beta diversity (Bray–Curtis dissimilarities)

| Regions | | Observed beta diversity | | | Null beta diversity | | | Beta deviations | | |
|---------|---|---|---|---|---|---|---|---|---|---|
| A | B | A > B | A = B | A < B | A > B | A = B | A < B | A > B | A = B | A < B |
| Amazon | Andes | 6 | 585 | 254 | 431 | 558 | 0 | 0 | 693 | 307 |
| Amazon | Ozarks | 795 | 50 | 0 | 171 | 818 | 0 | 0 | 1,000 | 0 |
| Amazon | Cantabrian | 1 | 844 | 0 | 684 | 305 | 0 | 0 | 253 | 747 |
| Andes | Ozarks | 536 | 309 | 0 | 525 | 464 | 0 | 821 | 179 | 0 |
| Andes | Cantabrian | 367 | 478 | 0 | 272 | 717 | 0 | 0 | 311 | 689 |
| Ozarks | Cantabrian | 0 | 824 | 21 | 0 | 989 | 0 | 0 | 260 | 740 |

*Note:* Comparisons are made for observed beta-diversity values, as well as for null expectations and beta deviations (standardized effect sizes [SES] from the null model). The table counts how many times two regions were similar ("A = B") or different ("A > B" or "A < B") in 1,000 versions of the same analysis. Each instance of the analysis was based on a two-step test of homogeneity of multivariate dispersion. The first step compared the four regions. If such a test was significant, tests were conducted in a second step for each pair of regions. If A = B in the real world, we would expect around 50 significant results outside the "A = B" column just by chance. Note that the counts do not sum to 1,000 in all cases: the remaining were non-significant tests of comparisons of the four regions together. Amazon: Amazon; Andes: Andes; Ozarks: Ozarks, USA; Cantabrian: Cantabrian Mountains, Spain.

lowland forest in the Ozarks, which had the lowest values compared to the other three regions. Even in this case, the differences were not great. Our work supports the idea that obvious latitudinal gradients in beta diversity do not exist beyond the local scales (0–0.1 ha; Sreekar et al., 2018). Similarly, we cannot conclude either that obvious beta-diversity differences exist between forests at different elevations, at the scales considered.

Due to the confounding effect of species richness at alpha and gamma scales, the processes that generate and maintain beta diversity cannot be studied by looking at observed beta diversity (Kraft et al., 2011). When we controlled for the effects of the species pools on beta diversity, we found that communities were much more different than expected. Therefore, our study found no support for the (null) biogeographical hypothesis that random sampling from the species pool alone determines variation in local community composition. The same has been found by most studies exploring this issue to date (e.g. De Cáceres et al., 2012; Mori et al., 2013; Myers et al., 2013; Tello et al., 2015; Sabatini et al., 2018). Studies on functional ecology in temperate forests (e.g. Weiher et al., 1998; Cavender-Bares et al., 2004) and tropical forests (e.g. Kraft et al., 2008; Swenson & Enquist, 2009) have also rejected the purely stochastic model of community assembly. Among the well-known works, only Kraft et al. (2011) reported a lack of elevational gradient in beta deviations, which could be due to their small sample size (n = 8) or because differences in beta deviations emerge only at larger extents than the within-0.1-ha scale that they examined.

Controlling for the effects of species pools eliminated the latitudinal differences in beta diversity in the lowland, and reversed the latitudinal differences in beta diversity in montane forests. Within a given latitude, beta deviations were higher at higher elevations, suggesting that montane ecosystems are floristically much more heterogeneous than expected given their regional species pools. Previous studies controlling for the size of the species pool also found higher levels of observed beta diversity and beta deviations at higher elevations in temperate (Mori et al., 2013; Sabatini et al., 2018) and tropical (Tello et al., 2015) forests. Surprisingly, we found greater beta deviations in the Cantabrian forest which has the smallest species pool, suggesting that sites can have high beta diversity and small species pools.

## 4.2 | Regional differences in the relative importance of community assembly processes

Niche assembly and dispersal assembly hypotheses are not mutually exclusive (Gravel et al., 2006). Although both mechanisms seem to explain beta-diversity or beta-deviation patterns to some degree in all regions, environmental factors were more important overall. These results are congruent with most previous results on temperate forests (e.g. Myers et al., 2013) and tropical forests (e.g. Macía et al., 2007; Jones et al., 2008), which found niche processes to be more important than neutral processes.

The space was more important at low elevations (for a given latitude) and in the tropics (for a given elevation), both in beta diversity and beta deviations, suggesting a greater importance of stochastic processes in more diverse/productive systems (Myers et al., 2013). In particular, our results suggest that recruitment limitation may play a more important role in more species-rich communities with many rare species, as predicted by the rarity hypothesis (Hurtt & Pacala, 1995; Hubbell et al., 1999; Hubbell, 2001; De Cáceres et al., 2012; Myers et al., 2013). Alternatively, contingencies resulting from stochastic arrival order of species may be more important in tropical environments and areas of higher productivity, as suggested by the productivity hypothesis (Chase, 2010; Mori et al., 2013). Finally, tropical and lowland forests may be more dynamic (greater rates of colonization and mortality rates, more frequent interspecific interactions, etc.). This dynamism can result in a broader range of local compositions, regardless of the environment, and therefore greater beta diversity of stochastic origin (Steiner & Leibold, 2004; Chase, 2010). The lower importance of space in mountain landscapes
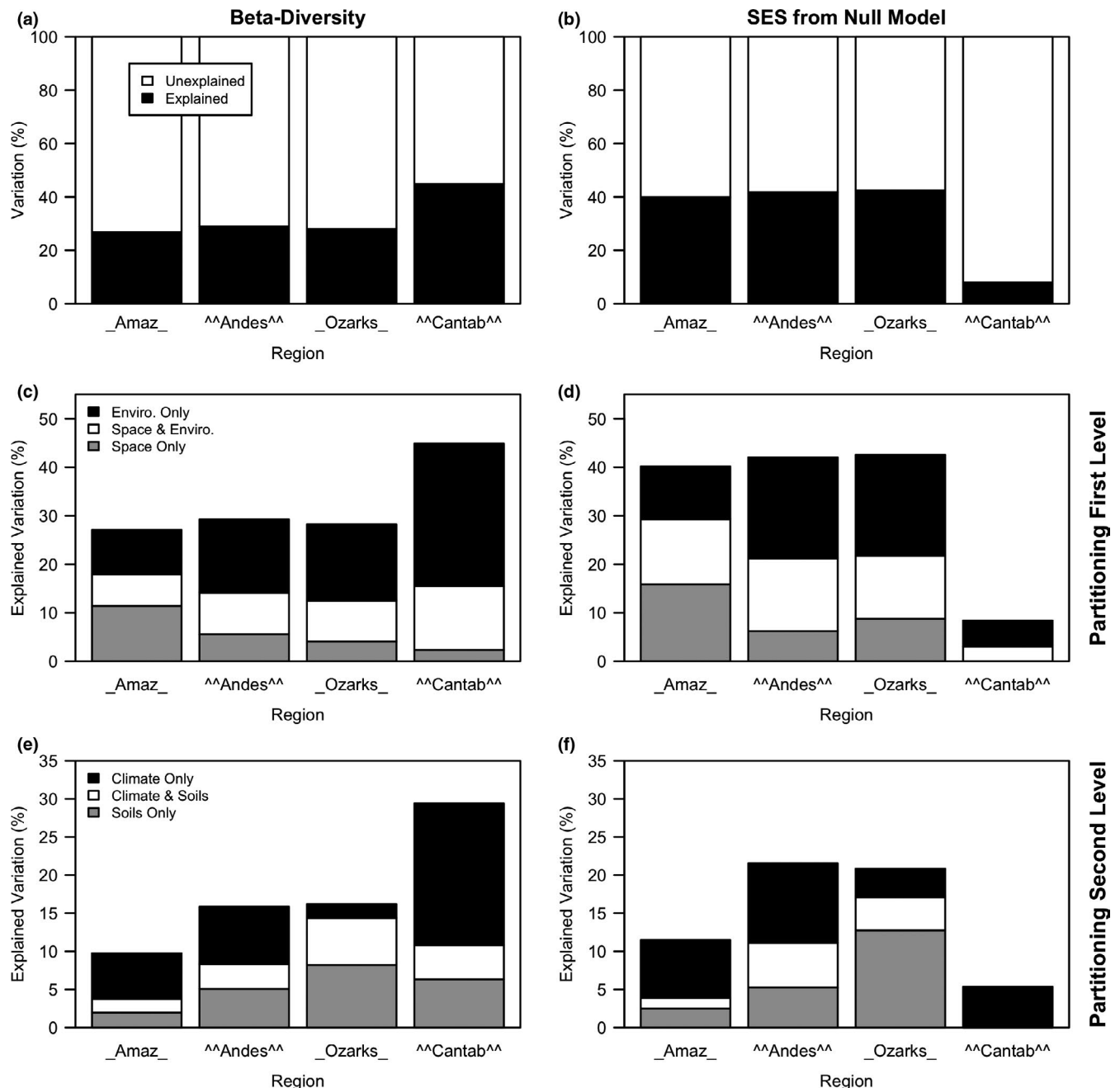
**FIGURE 3** Partitioning of beta diversity (variation in community composition) among sets of spatial and environmental predictors. For each region, partitioning was conducted on observed values of beta diversity (first column: a, c and e), as well as on beta deviations (standardized effect sizes – SES) from a null model (second column: b, d and f). The results are presented for the total amount of variation explained by all predictors (first row: a and b), the partitioning of the explained variation between spatial and environmental predictors (second row: c and d), and the partitioning of environmental variation into climatic and soil predictors (third row: e and f). Enviro. Only: variation explained exclusively by environment after accounting for space; Space Only: exclusively by space after accounting for environment; Enviro. & Space: simultaneously by environment and space. Climate Only: exclusively by climate after accounting for soils and space; Soils Only: exclusively by soils after accounting for climates and space; Climate & Soils: simultaneously by climate and soils after accounting for space. See also Appendix S4 for a conceptual diagram. Amaz: Amazon (Madidi, Bolivia); Andes: Andes (Madidi, Bolivia); Ozarks: Ozarks (USA); Cantab: Cantabrian Mountains (Spain). The lowland regions are indicated by _<code>_ and the mountainous regions by ^^<code>^^. The results are averaged values across 1,000 repetitions of the same analysis

contrasts with prior results suggesting that low connectivity among sites and landscape roughness make spatial factors relatively more important at higher elevations (Condit et al., 2002; Bjorholm et al., 2008; Arellano et al., 2016b).

Our results provide little support for the two predictions of the diversity-increases-competition hypothesis (Karger et al., 2015). Beta diversity or beta deviations were not always higher in regions of higher species richness, and their links with the environment

were not stronger. The assumption of narrower niches and higher degrees of environmental specialization in communities with more species may be questionable in the light of the evidence provided here. Numerous studies suggest that beta diversity in species-poor temperate forests is strongly influenced by niche-based processes across environmental gradients (Gilbert & Lechowicz, 2004; Qian & Ricklefs, 2007; Gilbert & Bennett, 2010). Other results in the tropics indicate that species niche overlap tends to overlap more in areas with high diversity (Arellano et al., 2017), at least when niches are measured in macroscale environmental variables as those used here. Unfortunately, it is difficult to conclude from observed patterns of beta diversity what the underlying environmental tolerances of the species are. Local-scale and/or experimental studies may be better suited to quantify environmental niches and competition (which requires spatial proximity between individuals of different species).

## 4.3 | Strengths and limitations

Results from comparisons among regions with different species pools should be taken with caution due to the interdependence of species richness and beta diversity and the influence of differences in the environmental heterogeneity between regions (Ulrich et al., 2017). We minimized this potential interdependence by using a null model that includes unobserved species from the species pool. Also, our regions were defined in such a way that they did not differ in spatial or environmental heterogeneity. However, our specific choice of spatial and environmental scale limits the comparison of our result with other studies. To date, most studies of regional influences on beta diversity have focused on small-scale patterns of beta diversity that differ from regional-scale studies traditionally examined in the beta-diversity literature. Kraft et al. (2011) and Mori et al. (2013) defined a "region" as an area of 0.1 ha, and De Cáceres et al. (2012) defined a "region" as an area between 20 and 50 ha. The spatial extent evaluated here is much larger, in the order of 100–1,000 $km^2$. To describe the latitudinal gradient in beta deviations in the same way as the gradient in observed beta diversity (e.g. Brown, 2014), future studies should use scale-explicit comparisons to infer the roles of environmental and spatial influences on beta diversity (e.g. Zhang et al., 2020).

Although it is easier to find relationships with the space or the environment when using larger scales, the link with specific mechanisms is blurred, as we necessarily include more heterogeneous assemblages, life strategies, and external factors (human influence, fragmentation, habitat loss) that are easier to control in studies made at more local scales. This could be the case for the Cantabrian Mountains; in spite of having the greatest beta deviations, these were practically impossible to explain with the used variables. Although we did not observe any recent evidence of fire or management (e.g. snags, charcoal in the soils), forests in the Cantabrian mountain range have been exposed to both natural and anthropogenic disturbances that have created heavily fragmented forests in recent centuries (García et al., 2005; Pérez-Obiol et al., 2016).

Finally, although variation-partitioning provides key insights into environmental and spatial influences on community composition, it has limitations (Smith & Lundholm, 2010). For example, the explanatory variables used to partition variance may not be equally relevant in all regions. In addition, spatial variables could reflect processes other than dispersal limitation, such as unmeasured, spatially structured environmental gradients (Legendre et al., 2009; Peres-Neto & Legendre, 2010; Smith & Lundholm, 2010; Anderson et al., 2011). The effects of climate on beta diversity could also be underestimated because of the relatively coarse spatial resolution (1 $km^2$) of the climate variables. Besides, anything that makes species appear or disappear randomly in local communities without affecting the species pool (e.g. disturbance) will change beta-diversity patterns in ways that variation-partitioning analysis may not capture (Chase & Myers, 2011; Catano et al., 2017).

## AUTHOR CONTRIBUTIONS

GA, MJM and VC designed the research. MM and GA collected the data in Spain. JAM collected the data in the US. GA, MJM, PMJ, and AFF collected data in Bolivia. VC analyzed soils. MM, ST, JAM and GA designed and implemented the statistical analyses. MM, GA and ST wrote the manuscript, with contributions from all the other authors.

## DATA AVAILABILITY STATEMENT

Data from the Madidi are stored in the TROPICOS database, and are shared under the Policy to Share, Use and Publish Data of the Madidi Project (https://madidiproject.weebly.com/). Data from Ozarks are available from Vela Díaz et al. (2021), Data from: Untangling the importance of niche breadth and niche position as drivers of tree species abundance and occupancy across biogeographic regions, Dryad, Dataset, https://doi.org/10.5061/dryad.80gb5mknx. Data from Spain are available from Muñoz et al. (2021), Data from the Cantabrian Mountains used in 'Mechanisms of community assembly explaining beta-diversity patterns across biogeographic regions' [Data set]. Zenodo. http://doi.org/10.5281/zenodo.4675670.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**Appendix S1**. Selection of subsets of plots at each region.

**Appendix S2**. Conversions between different methods of soil analyses.

**Appendix S3**. Results of variable selection.

**Appendix S4**. Diagram of hierarchical variation partitioning.

**Appendix S5**. Results of the variation partitioning analyses.