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Niche-based processes outperform neutral processes when predicting distance decay in co-dominance along the Amazon – Andes rainforest gradient

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Abstract

Question: Dispersal limitation (neutral hypothesis) and deterministic factors (niche hypothesis) shape floristic gradients including between-site patterns of species' dominance (co-dominance). Because their relative importance remains poorly known, we ask how their comparative contribution to co-dominance changes with elevation and geographical extent.

Location: Madidi region, NW Bolivia.

Methods: We analysed floristic composition and environmental factors of 90 plots spanning the gradient from Amazonian (<1,000 m) to montane forests at three elevations (1,200–1,500; 2,000–2,300; and 2,800–3,200 m) and two geographical extents: local (plots <12 km apart) and regional (38–120 km apart). We modelled distance decay within each elevational band with a neutral model, using two parameters (speciation rate and dispersal distance). Subsequently, we related the model's residuals to environmental differences using flexible machine learning models.

Results: We found that 5–44% of the variability in floristic differences along the gradient studied can be explained by a neutral model of distance decay, while 18–50% can be explained by environmental differences. Montane forests showed an overall gradient in floristic composition that is congruent with an increase in elevation for both dispersal limitation and environmental filtering. However, Amazonian forest was more niche-structured and more dispersal-limited relative to its elevation and topography.

Conclusions: Environmental differences explained floristic differences better than the neutral model, even giving preferential attribution to the more parsimonious neutral processes.

KEYWORDS
Amazon, Andes, Bolivia, environmental determinism, Madidi, neutral theory, niche partitioning, oligarchy hypothesis, species co-dominance, species turnover, tropical montane forests

1 | INTRODUCTION

Communities differ from site to site in many aspects and at multiple scales. Understanding why is a central goal of community ecology. Species' turnover, i.e., how species presences/absences differ between sites, is a common measure of compositional change (Anderson et al., 2011; Tuomisto, 2010). Another key aspect is how the relative abundances of species vary from one site to another. For example, two communities may be made up of exactly the same species, while their relative abundances could be dramatically different. The opposite can be also true; two communities may share just a small fraction of species, but most of its individuals belong to the same suite of dominant species. In the latter situation, both communities are very similar in important ecological aspects, especially those affecting interactions between individuals. The occurrence of such pattern in forests is known as "the oligarchy hypothesis" (Arellano et al., 2015; Condit et al., 2002; Macía & Svenning, 2005; Pitman, Silman, & Terborgh, 2013; Pitman et al., 2001), which states that tropical forest communities tend to be dominated by the same set of locally abundant and geographically widespread species. There is ample empirical evidence supporting this pattern (see Pitman et al., 2013 and references therein) but the underlying causes remain understudied.

Two hypotheses have been formulated to address the question of changes in plant communities across space: the neutral hypothesis (Hubbell, 2001) and the niche hypothesis (Gilbert & Lechowicz, 2004). The neutral hypothesis predicts differences between communities should occur related to their spatial separation, based on neutral speciation and dispersal limitation, irrespective of environmental conditions or of functional differences among species (Chave & Leigh, 2002; Condit et al., 2002; Gilbert & Lechowicz, 2004). The niche hypothesis states that two sites will show high (or low) floristic similarity depending on their similar (or dissimilar) environmental conditions, a deterministic process (Gilbert & Lechowicz, 2004). These two complementary hypotheses generate straightforward qualitative predictions on co-dominance patterns: species from two sites that are either spatially close or environmentally similar should be similar in their relative abundances. How the relative importance of these two hypotheses changes between different forest types and/or different geographical extents remains unknown. From a neutral perspective, the greater topographic variability and landscape fragmentation of montane regions should impose stronger dispersal limitation (Arellano, Umaña et al., 2016; Brehm, Colwell, & Kluge, 2007; Ghalambor, Huey, Martin, Tewksbury, & Wang, 2006). From the niche perspective, increasing habitat patchiness and variability, with locally abrupt changes in elevation, should also increase the absolute importance of the niche hypothesis (Brehm et al., 2007; Hutter, Guayasamin, & Wiens, 2013; Kozak & Wiens, 2010; Qian & Ricklefs, 2012; Wiens, 2004). Additionally, geographical extent may determine the relative importance of the environment if niche plays a disproportionately greater role at larger extents because longer and steeper environmental gradients allow a more marked

sorting of species by their different preferences (Kristiansen et al., 2012; Pansonato, Costa, de Castilho, Carvalho, & Zuquim, 2013). In contrast, some authors suggest that geographic distances shape regional floristic patterns, while environmental differences operate mostly at local scales (Normand, Vormisto, Svenning, Grández, & Balslev, 2006). These differences between forest types and geographical extents remain unresolved.

In this study, we analysed data from four elevation bands along the eastern slopes of the Bolivian Amazon–Andes transition (300–3,200 m in elevation), each band containing a well-defined forest type. Note that floristic changes across elevations are obvious due to the magnitude of the elevational gradient in the area, so it would be trivial to perform any floristic comparison between elevation bands. For that reason, our analyses were always confined to within discrete elevation bands. We address the following questions:

1. To what degree do neutral processes predict the pattern of distance decay in floristic similarity?
2. Is there any effect of elevation on the importance of the neutral processes?
3. Do environmental factors explain differences in floristic composition beyond what geographic distance does?
4. Is the importance of these factors consistent across elevations and between local and regional extents?

2 | METHODS

2.1 | Floristic data

The study was conducted in the Madidi region, Bolivia, within or adjacent to the Madidi National Park (Figure 1). Within an area of 100 km × 120 km, we established 90 plots of 0.1 ha (20 m × 50 m) (Arellano & Macía, 2014; Macía, 2008). Plots were grouped into ten sites (6–10 plots/site) at four elevational bands, each hosting a different forest type: (a) Amazonian forest, below 1,000 m (36 plots in four sites); (b) lower montane forest, at 1,200–1,500 m (18 plots in two sites); (c) intermediate montane forest, at 2,000–2,300 m (18 plots in two sites); and (d) upper montane forest, at 2,800–3,200 m (18 plots in two sites). The minimum distance between plots was 500 m in Amazonian forests and 250 m in the montane forests. All plots were located in apparently mature rain forests without recent human disturbance.

We censused all tree stems with a diameter ≥2.5 cm at 130 cm height. All individuals were assigned to a morphospecies in the field, and >6,500 voucher specimens were collected and deposited in the Herbario Nacional de Bolivia in La Paz (LPB). All stems of the small shrub *Psychotria carthagenensis* Jacq. were removed from analyses because their extremely high density in two plots (most likely clonal ramets), which would overestimate the species' co-dominance, distorting the model. In all, <3% of total stems were eliminated. The final dataset contained 27,431 individual trees belonging to 1,128 species, 374 genera and 109 families (Appendix S1).
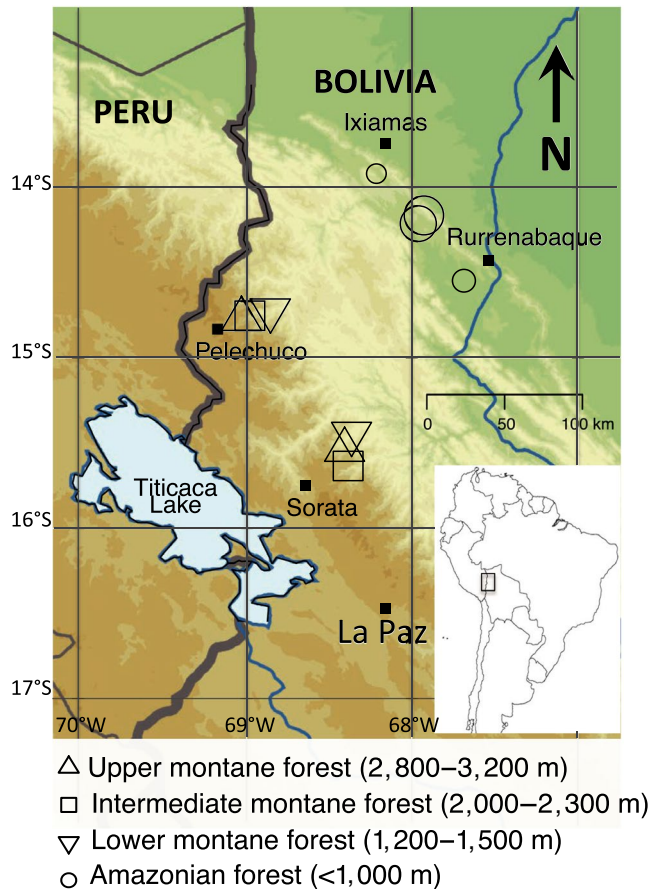
FIGURE 1 Study area in the Madidi region, Bolivia. The 90 plots are clustered among ten sites at four elevation bands: 36 were set among four Amazonian forest sites (<1,000 m elevation); 18 plots among two lower montane forest sites (1,200–1,500 m); 18 plots among two intermediate montane forest sites (2,000–2,300 m); and 18 plots among two upper montane forest sites (2,800–3,200 m). Sites are represented by different symbols, their sizes proportional to the number of plots at each locality. [Colour figure can be viewed at wileyonlinelibrary.com]

2.2 | Environmental data

A composite sample of the uppermost soil layer (0–15 cm below the litter layer) was collected for each plot by mixing soil from five sub-samples within the plot. Soil samples were air-dried and sieved (to <2 mm). Soil pH was measured in a 1:2.5 suspension of soil in deionized water by volume. Total C, N and S contents were determined by combustion (CHNS-932, LECO). Plant-available macronutrients (Ca, Mg, K, P), micronutrients (Fe, Mn, Co, Ni, Cu, Zn) and Al contents were determined by extraction using the Mehlich 3 method (Mehlich, 1984), and analysed through an inductively coupled plasma spectrometer (ICP, Elan 6000 Perkin-Elmer).

Data for precipitation-based variables were obtained from the Tropical Rainfall Measuring Mission database (Mulligan, 2006) and data for temperature-based variables from WorldClim (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005: http://www.worldclim.org/bioclim). From the ASTER Global Digital Elevation Map v. 2 (http://

asterweb.jpl.nasa.gov/gdem.asp) we estimated topographic variables for each plot: elevation, slope, and eastness and northness [as sin(aspect) and cosin(aspect), respectively].

2.3 | Measurement of co-dominance patterns

We used the *F* index of co-dominance as a metric of compositional difference between two communities. This index is the probability of finding two conspecifics of any species when taking one individual from each of two different locations (i.e., samples), *j* and *k*:

$$F_{jk} = \sum_{i=1}^{S} \frac{n_{ij}n_{ik}}{N_j N_k}$$

where n_{ij} is the abundance of species *i* in plot *j*, n_{ik} is the abundance of species *i* in plot *k*, N_j is the number of individuals in plot *j*, etc., and *S* is the total number of species. In a strict sense, *F* does not capture species' turnover as much as patterns of species' co-dominance: its value is large only when the two compared communities share the same suite of abundant species and low if otherwise, regardless of species overlap.

2.4 | Implementation of Inference to the Best Explanation

Similar analyses of the relative role of neutral and niche mechanisms have traditionally relied on linear models, partitioning the variation in the response variable into (a) variation explained exclusively by space (~dispersal, a neutral process), (b) variation exclusively explained by the environment or environmental differences (~niche processes), (c) variation explained by both, and (d) unexplained variation. We used an alternative approach to partitioning of variation based on abductive reasoning. Abductive reasoning or Inference to the Best Explanation (IBE) is one of the three forms of logical inference, along with deduction and induction (Campos, 2011; Lipton, 2003). Unlike traditional variation partitioning, IBE allows assessment of different hypotheses, without making them compete directly, by ranking explanations from more to less parsimonious and testing them sequentially. Firstly, raw data are analysed using a model for the most parsimonious hypothesis. Subsequently, the second most parsimonious hypothesis is tested on the residuals of the previous model, and so on. IBE favours simpler models over complex ones. The main advantage of IBE is that one can formulate various models of arbitrary shape and complexity.

During the modelling process, we assumed neutral processes to be the most parsimonious explanation of patterns of distance decay on species' co-dominance. In Hubbell's (2006) words, "obtaining acceptable fits from neutral models shifts the burden of proof to those who would assert that more complex theory is required to explain nature". Consequently, preferential attribution to neutral processes was based on considerations about parsimony alone and not on any a priori expectation regarding the relative importance of the different processes, despite the a priori

expectation being that niche processes are more important than neutral processes (Adler, HilleRisLambers, & Levine, 2007; Gravel, Canham, Beaudet, & Messier, 2006; Pitman et al., 2001). IBE thus functions as a stringent test on our prior hypotheses, more so than favouring confirmatory bias.

2.5 | The most parsimonious hypothesis: co-dominance patterns expected by neutral processes

Early versions of the neutral theory (Hubbell, 1979, 1997) modelled composition of local communities only in relation to the "omnipresent" source pool of species, disregarding the greater connectedness between nearby communities. Chave and Leigh (2002) developed a version of the neutral model for a very large forest where seeds disperse only a limited distance from their parents, and modelled co-dominance as a function of the distance r between samples j and k:

$$F(r) \approx \frac{1}{2\rho\pi\sigma^2 + \ln\left(\frac{1}{\nu}\right)} 2K_0\left(\frac{r\sqrt{2\nu}}{\sigma}\right)$$

where K_0 is the zero-th order modified Bessel function of the second kind, ρ is the density of individuals, ν is the speciation rate, and σ is the root mean square of the dispersal distance (the mean distance between a seed and its parent tree). In this model, ρ is constant for a given forest type, while ν and σ are the only free parameters. This model of decay has been successfully applied to a variety of systems, including tropical forests (Chave & Leigh, 2002; Condit et al., 2002; Gilbert & Lechowicz, 2004).

We fitted the neutral models of decay by minimizing the sum of the squared residuals using the method "nlminb" in the *optimx* function ("optimx" package) in the R statistical program (version 3.2.2; R Core Team, 2015). Estimates of both parameters (ν and σ) were obtained by jack-knife resampling (i.e., fitting many models per forest type, leaving out one plot each time), so that the mean of the resulting distribution represented the final estimation for both parameters, and the 0.025 and 0.0975 quantiles the corresponding 95% confidence intervals (CIs). Estimated parameters of two forest types are significantly different when their CIs do not overlap.

2.6 | Analysis of the residuals from the neutral model against environmental variables

To examine the relationship between the residuals of the neutral model (the variation of F between communities not explained by neutral processes) and environmental variables, we used Random Forest models (Cutler et al., 2007), fitted with the "randomForest" R package. This method combines many regression trees built from a bootstrap sample of response variables. In comparison with linear methods, Random Forests are non-parametric; thus they
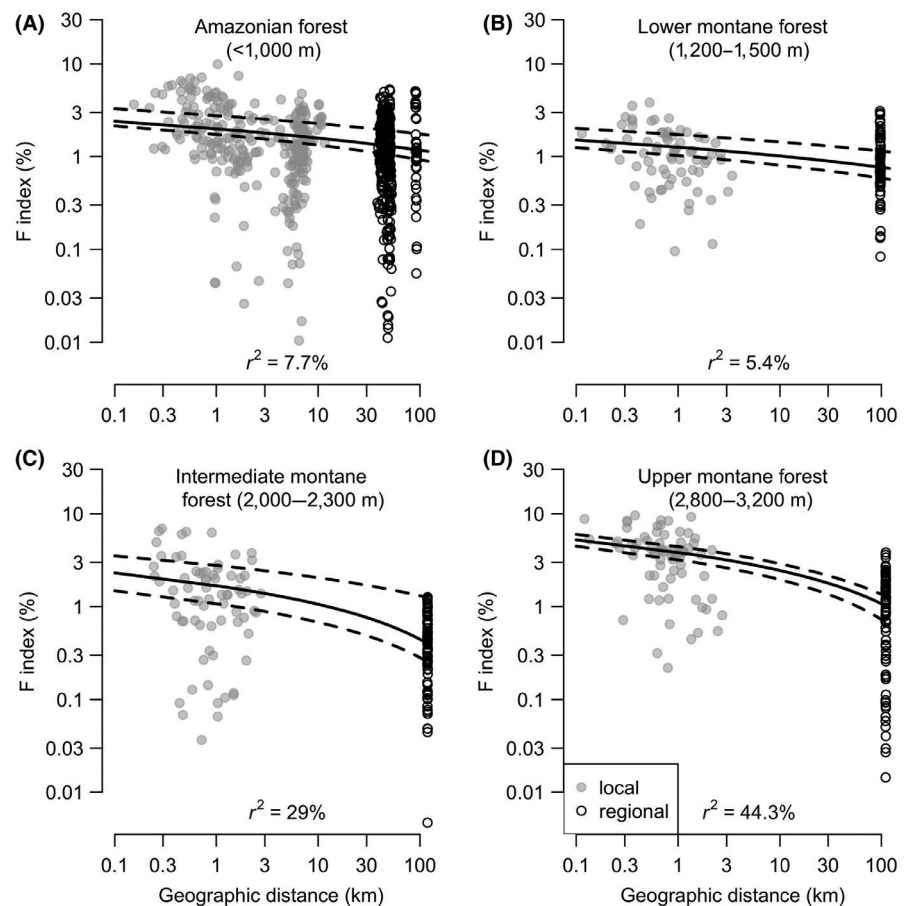

FIGURE 2 Distance decay by forest type. (a) Amazonian forest (<1,000 m elevation), (b) lower montane forest (1,200–1,500 m), (c) intermediate montane forest (2,000–2,300 m) and (d) upper montane forest (2,800–3,200 m). Solid lines represent the fitted neutral model. Dashed lines represent 95% confidence intervals. These models are fitted to the entire collection of samples, although different symbols are used to highlight the two scales considered in the entire study. Solid gray and open black dots refer to local and regional extents, respectively

TABLE 1 Percentages of variance in F index of co-dominance between pairs of plots explained by two models implemented consecutively. $r^2_{neutral}$ refers to percentage of the variance explained by spatial distance. r^2_{niche} refers to the percentage of the residuals from the neutral model explained by a Random Forest model based on environmental variables. $^{contr}r^2_{niche}$ refers to the explained variation in co-dominance (raw F index). The total explained variation is $r^2_{niche} + {^{contr}r^2_{niche}}$

	Amazonian forest (<1,000 m elev.)		Lower montane forest (1,200–1,500 m)		Intermediate montane forest (2,000–2,300 m)		Upper montane forest (2,800–3,200 m)	
	Local (<12 km)	Regional (>38 km)	Local (<12 km)	Regional (>38 km)	Local (<12 km)	Regional (>38 km)	Local (<12 km)	Regional (>38 km)
$r^2_{neutral}$ (%)	16.1	0.2	14.2	3.5	11.0	5.3	17.1	1.6
r^2_{niche} (%)	36.5	34.5	33.3	32.6	20.7	22.5	43.6	50.5
$^{contr}r^2_{niche}$ (%)	30.7	34.4	28.6	31.5	18.4	21.4	36.1	49.7
Total ($r^2_{neutral} + {^{contr}r^2_{niche}}$) (%)	46.7	34.6	42.8	35.0	29.4	26.6	53.2	51.3

allow for complex interactions between variables while being less prone to over-fitting.

We built two Random Forest models for each forest type (elevational band), one at the local scale (defined as pairs of plots <12 km apart in our dataset) and one at the regional scale (pairs of plots 38–120 km apart). As predictor variables, we included the Euclidean pairwise distances of the environmental variables between plots. A preliminary analysis showed high correlation (Pearson's $|r| > 0.70$) between some variables. To avoid redundancy we chose only one of the correlated variables as a surrogate for the rest (Appendix S2, segregated by extent and forest type). The goodness-of-fit of each model was measured with two metrics. First, the squared Pearson's r ($r^2_{neutral}$ and r^2_{niche}, respectively) between observations and expectations, which measure the ability of the predictors to explain the response variable directly included in the model (i.e., F in the case of the neutral model, but residual F for Random Forest models). Second, the contributed r^2 ($^{contr}r^2$) for each model measures the ability of the predictors to explain the original response variable (F), as $^{contr}r^2_{neutral} = r^2_{neutral}$ and $^{contr}r^2_{niche} = (1 - {^{contr}r^2_{neutral}}) \times r^2_{niche}$. These were used to estimate the relative importance of the neutral and niche processes.

3 | RESULTS

3.1 | Relationship between co-dominance (F index) and geographic distances

The magnitude of change in tree species composition as a function of distance increased with elevation (Figure 2). The predictive ability of the neutral model differed between forest types. It was negligible in Amazonian forests and lower montane forests ($r^2_{neutral} = 7.7\%$ and 5.4%, respectively), but moderate in the intermediate and upper montane forests ($r^2_{neutral} = 29.0\%$ and 44.3%, respectively). In all cases, the fit of the model was better at the local extent than at the regional extent (Table 1). Dispersal potential (the distance parameter in the neutral model, σ) in the montane forests decreased with elevation, being 81.9 m, 51.4 m and 33.8 m in lower, intermediate and upper montane forests, respectively (Table 2). The dispersal potential found in the Amazonian forest ($\sigma = 63.5$ m), however, was smaller than in the lower montane forest ($\sigma = 81.9$ m).

3.2 | Relationship between residual F index and environmental differences

The variation in the residuals of the neutral model was relatively well explained by environmental variables included in Random Forests models in all cases; r^2_{niche} ranged between 20.7% and 43.6% at the local extent, and between 22.5% and 50.5% at the regional extent (see Table 1). Regardless of geographical extent, lowest and highest r^2_{niche} values were observed at intermediate and upper forests, respectively (Table 1). The contributed r^2 from the niche hypothesis ($^{contr}r^2_{niche}$) was always greater than that from the neutral model ($^{contr}r^2_{neutral}$) regardless of extent or forest type. Also, $^{contr}r^2_{niche}$ was greater at the local than regional extent among plots within elevation bands (Table 1). The relative weight of the niche variables

TABLE 2 Fitted parameters of the neutral model of distance decay in floristic similarity for forest types at elevation bands in the Madidi region, Bolivia

Forest type	Parameter	Estimated	Lower and upper boundaries of the 95% confidence interval	
Amazonian (<1,000 m elev.)	Speciation rate (ν)	4.8e−13	3.66e−14	7.02e−12
	Dispersal (σ) (m)	63.5[b]	56.1	64.0
Lower montane (1,200–1,500 m)	Speciation rate (ν)	2.9e−13	4.29e−15	2.29e−12
	Dispersal (σ) (m)	81.9[c]	75.7	87.1
Intermediate montane (2,000–2,300 m)	Speciation rate (ν)	6.7e−09	3.83e−11	1.09e−08
	Dispersal (σ) (m)	51.4[b]	47.0	64.3
Upper montane (2,800–3,200 m)	Speciation rate (ν)	2.2e−09	1.19e−09	6.29e−09
	Dispersal (σ) (m)	33.8[a]	31.8	35.7

Based on the 95% confidence intervals we found some significant differences in dispersal potential σ, indicated by superscripts.

($^{contr}r^2_{niche}$) at both geographical extents was highest in upper montane forests, followed by Amazonian forests and lower forests, while it was lowest in intermediate montane forests (Table 1).

The relative importance of individual environmental variables, measured as the increase of node purity in the Random Forest models, varied greatly between forest types and spatial scales (Figure 3; Appendix S3 contains the numerical values with standard deviations). Climate (including elevation) and topographic variables were most important in the Amazonian forest, with the exceptions of precipitation of coldest quarter of the year (Bio19) and northness, which were of moderate relevance in explaining the residual co-dominance in the upper montane forest. Among soil properties, pH was the most important variable in every forest type. Overall, environmental variables were more important locally than regionally in all forest types (Figure 3).

4 | DISCUSSION

Speciation and seed dispersal alone cannot explain variation in tree species' co-dominance in our study area, despite the preferential attribution we gave to neutral processes. This finding supports the idea that tropical forests, particularly at the regional extent, are more similar in terms of co-dominance than anticipated under Hubbell's neutral models (Terborgh, Foster, & Percy, 1995; Pitman, Terborgh, Silman, & Núñez, 1999; Pitman et al., 2001). Furthermore, our results showed that the changes in co-dominance that the neutral model could not explain were strongly correlated with environmental variables, indicating that environmental differences were, overall, more important than neutral processes for all four forest types at both local and regional extents.

4.1 | Dispersal in the Amazon–Andes transition

We found that the distance decay pattern became steeper with elevation along the entire gradient. In the Andes, an elevation increase of 800 m resulted in 30–35% reduction in dispersal potential (σ) within lower, intermediate and upper montane forests. This

finding is consistent with expected increases in frequency and also effectiveness of dispersal barriers in higher-elevation montane ecosystems (Arellano, Umaña et al., 2016; Ghalambor et al., 2006), a pattern observed elsewhere (Bjorholm, Svenning, Skov, & Balslev, 2008; Condit et al., 2002).

However, we noted that among lower-elevation forest types, dispersal potential was unexpectedly lower in the rather flat Amazonian forest than in the moderately steep lower montane forest. One possible explanation is that dispersal kernels at lower elevations are limited by larger seed size rather than by topographic barriers, counteracting the greater landscape connectivity. A study conducted by Hillyer and Silman (2010) in a neighbouring region reported average seed masses of 0.35 g for Amazonian lowland species, while average seed masses dropped to <0.15 g for species above 2,000 m in the Andes. This is consistent with the general correlation between temperature or net primary productivity and seed mass observed at large scales, including the Amazon (Malhado et al., 2015). We ran our dataset against the Royal Botanic Gardens Kew (2008) Seed Information Database and verified that our flora does contain taxa with smaller seeds at higher elevations. Arguably, a greater prevalence of heavy-seeded tree taxa (on average) in the Amazonian flora, with reduced seed rain ranges, may result in a limited dispersal potential compared to lower montane forests.

4.2 | Niche processes affecting the distance decay in co-dominance

The combination of comprehensive soil analyses and a highly flexible modelling approach resulted in the high predictive power attributed to the niche hypothesis (as suggested by Jones et al., 2008; Chang, Zelený, Li, Chiu, & Hsieh, 2013). Our results confirm that niche-based processes are more important than neutral processes in structuring tropical plant communities from local to regional scales, even within narrowly defined elevational bands. This finding is consistent with the existing literature on drivers of compositional change, including both co-dominance patterns (Arellano et al., 2015; Pitman et al., 2001, 2013) and patterns of beta diversity (Jones et al., 2008; Macía,
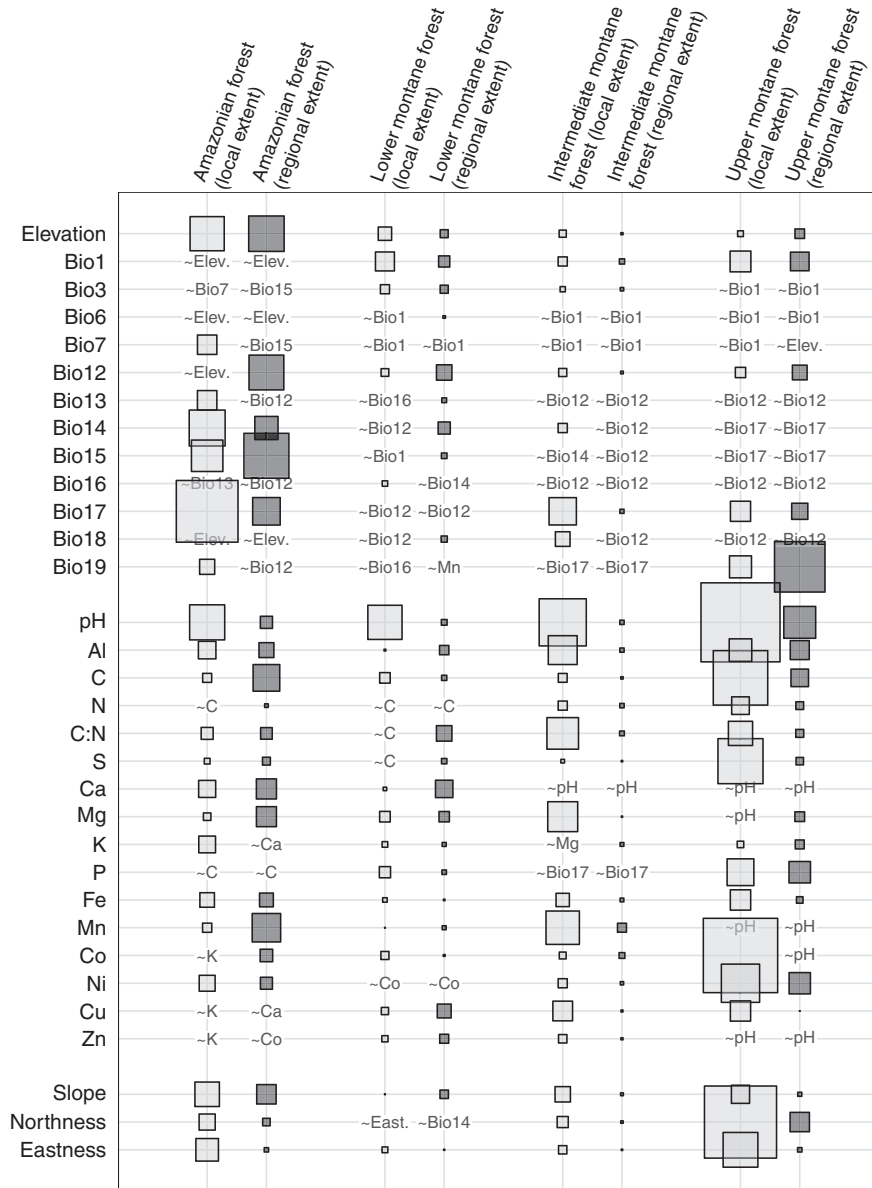
FIGURE 3 Importance of variables in Random Forest models that predict residuals from a neutral model of distance decay in forests at four elevation bands (Amazonian forest, <1,000 m elevation; Lower montane forest, 1,200–1,500 m; Intermediate montane forest, 2,000–2,300 m; Upper montane forest, 2,800–3,200 m) and two extents (local and regional, <12 km and 38–120 km apart, respectively) in Amazonian and montane forests in the Madidi region (Bolivia). Importance of variable is displayed by a square with size proportional to the increase in node purity (INP) in the corresponding Random Forest model. Variables are grouped as bioclimate (included elevation), soil chemistry, and topography. Variables excluded because they were highly correlated ($|r| > 0.70$) with others are replaced with their best correlated variable, displayed as "~representative". Appendix S3 contains the numerical results, with standard deviations. Climatic variables are labelled according to WorldClim database (Hijmans et al., 2005) schema: Bio1 = annual mean temperature (all temperatures in °C × 10); Bio2 = mean diurnal range [mean of monthly (maximum temperature−minimum temperature)]; Bio3 = isothermality [(Bio2/Bio7) × 100]; Bio4 = temperature seasonality (standard deviation × 100); Bio5 = maximum temperature of warmest month; Bio6 = minimum temperature of coldest month; Bio7 = temperature annual range (Bio5 − Bio6); Bio8 = mean temperature of wettest quarter; Bio9 = mean temperature of driest quarter; Bio10 = mean temperature of warmest quarter; Bio11 = mean temperature of coldest quarter; Bio12 = annual precipitation (all precipitations in mm); Bio13 = precipitation of wettest month; Bio14 = precipitation of driest month; Bio15 = precipitation seasonality (coefficient of variation); Bio16 = precipitation of wettest quarter; Bio17 = precipitation of driest quarter; Bio18 = precipitation of warmest quarter; Bio19 = precipitation of coldest quarter

Ruokolainen, Tuomisto, Quisbert, & Cala, 2007; Myers et al., 2013; Phillips et al., 2003).

Previous studies in the tropics have demonstrated the importance of temperature and precipitation-based variables on floristic variations (Blach-Overgaard, Svenning, Dransfield, Greve, & Balslev, 2010; Sesnie, Finegan, Gessler, & Ramos, 2009). Our results not only support the role of temperature and precipitation, but also highlight the role of climate specialization in shaping patterns of species' local

abundances, especially at elevations below 1,500 m. At higher elevations, most climate variables were of lesser importance. It is possible that climate generalists (i.e., species with abundances that barely change between different climates) make up the bulk of high-elevation tropical plant communities (Ghalambor et al., 2006; Stevens, 1992).

Soil differences were also important in determining levels of co-dominance that diverged from those expected by neutral processes. In the studied area, pH was clearly the most important soil variable. Similar correlations between soil acidity and composition have been reported from other montane and lowland forests (Homeier et al., 2012; Jones et al., 2008; Pyke, Condit, Aguilar, & Lao, 2001). Small variations in Al toxicity (closely related to soil acidity) had a large effect on the floristic composition of Amazonian forests but, quite surprisingly, not on any of the montane forests. Perhaps Al toxicity entirely bars particular species (Andersen, Turner, & Dalling, 2010; Jones et al., 2008), while it does not substantially affect the abundance of tolerant species. Amazonian forests may be more responsive to Al than any of the montane forest types, where 37–43% of individuals belonged to families with many and/or strong Al-hyperaccumulators (in comparison to 13% of the individuals in the Amazonian forest: Jansen, Broadley, Robbrecht, & Smets, 2002).

Variables associated with organic matter (C, C:N) are important in most tropical forests (Andersen et al., 2010; Duque et al., 2002; Homeier et al., 2012; Jones et al., 2008; Phillips et al., 2003), but in our study they were not so for Amazonian forest. By contrast, our results for base cations (Mg, K, Ca) show that they are the most important in Amazonian forests, with at least one of the cations being among the most relevant edaphic variables at either the local or regional extent in all forest types. The association of floristic composition with these cations has been widely reported in the Amazon (Duque et al., 2002; Macía et al., 2007; Phillips et al., 2003; Toledo et al., 2012; Tuomisto & Ruokolainen, 1994), as well as in montane forests at various elevations (Andersen et al., 2010; Homeier et al., 2012). Other potential drivers of compositional changes, like P (Duque et al., 2002; Jones et al., 2008), Fe (Macía et al., 2007) and some micronutrients, were rather poor predictors of co-dominance patterns across all forest types.

4.3 | Changes with elevation and geographical extent

Regarding the effect of the geographical extent (local and regional scales) on the importance of the environment in determining floristic co-dominance patterns, we found that $^{contr}r^2_{niche}$ was greater in all forests at the regional extent. Similarly, previous studies suggest that longer environmental gradients result in more niche-structured communities (Kristiansen et al., 2012; Pansonato et al., 2013), though others have found either the opposite pattern or no scale-dependency (Arellano, Tello et al., 2016). This discrepancy may be related to the selection of different predictors at different scales (e.g., large-scale studies frequently focus on climate, while small-scale studies tend to incorporate more soil variables; Duque et al., 2002; Jones et al., 2008; Chang et al., 2013).

We expected that more heterogeneous landscapes at higher elevations would result in a greater accumulation of specialists (Hutter et al., 2013; Kozak & Wiens, 2010; Qian & Ricklefs, 2012), and consequently a greater correlation between distance decay and niche differences, which would shape a clear elevational trend in co-dominance. However, our results did not support this expectation, perhaps due to the limited number of plots per forest type. At least for the environmental variables and the spatial extents considered, we found that landscape heterogeneity does not necessarily increase with elevation (as for Arellano, Umaña et al., 2016). It is also possible that greater environmental heterogeneity was counterbalanced by an increase in the dominance of generalist species (Ghalambor et al., 2006; Stevens, 1992), blurring the gradient in the intensity of plant–environment associations with elevation.

Taken together, our results reinforce the idea that deterministic processes are more important than neutral processes in driving floristic differentiation in tropical rain forests at both local and regional extents (Adler et al., 2007; Gravel et al., 2006; Pitman et al., 2001). Dispersal limitation was stronger in intermediate and upper montane forests than in any other forest type, as was the importance of environment in driving co-dominance patterns. The Amazonian forest was more niche-structured, while also being more dispersal-limited than the lower montane forest, probably due to the greater abundance of species with heavier, less dispersible seeds.

AUTHOR CONTRIBUTIONS

LNT and IGC conceived the hypotheses and designed the study. GA, MJM and VC collected the data. LNT, GA and IP analysed the data. LNT, GA, IGC and IP wrote the manuscript, MJM and VC discussed the results and contributed to the writing.

DATA ACCESSIBILITY

Data are stored in the Tropicos® database hosted at the Missouri Botanical Garden (http://www.tropicos.org/PlotSearch.aspx?projectxml:id=20), as part of The Madidi Project (https://madidiproject.weebly.com/).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Number of plots, individuals and taxa, and environmental variables in our study of Amazonian and Andean forest across ten sites in the Madidi region, Northwestern Bolivia

Appendix S2. Correlations between environmental distances for the four forest types studied in the Madidi region, Bolivia, in an Excel file

Appendix S3. Importance of variables in Random Forest models that predict residuals from a neutral model of distance decay. The table provides the numerical results for Figure 3, with standard deviations