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Untangling the importance of niche breadth and niche position as drivers of tree species abundance and occupancy across biogeographic regions

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Abstract

Aim: Ecological niches shape species commonness and rarity, yet, the relative importance of different niche mechanisms within and across ecosystems remains unresolved. We tested the influence of niche breadth (range of environmental conditions where species occur) and niche position (marginality of a species' environmental distribution relative to the mean environmental conditions of a region) on tree-species abundance and occupancy across three biogeographic regions.

Location: Argentinian Andes; Bolivian Amazon; Missouri Ozarks.

Time period: 2002–2010.

Major taxa studied: Trees.

Methods: We calculated abiotic-niche breadths and abiotic-niche positions using 16 climate, soil and topographic variables. For each region, we used model selection to test the relative influence of niche breadth and niche position on local abundance and occupancy in regional-scale networks of 0.1-ha forest plots. To account for species–environment associations caused by other mechanisms (e.g., dispersal), we used null models that randomized associations between species occurrences and environmental variables.

Results: We found strong support for the niche-position hypothesis. In all regions, species with higher local abundance and occupancy occurred in non-marginal environments. Observed relationships between occupancy and niche position also differed from random species–environment associations in all regions. Surprisingly, we found little support for the niche-breadth hypothesis. Observed relationships between both local abundance and niche breadth, and occupancy and niche breadth, did not differ from random species–environment associations.

Main conclusion: Niche position was more important than niche breadth in shaping species commonness and rarity across temperate, sub-tropical and tropical forests. In all forests, tree species with widespread geographic distributions were associated with environmental conditions commonly found throughout the region, suggesting that niche position has similar effects on species occupancy across contrasting biogeographic regions. Our findings imply that conservation efforts aimed at protecting

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populations of common and rare tree species should prioritize conservation of both common and rare habitats.

1 | INTRODUCTION

The mechanisms that determine species commonness and rarity have broad implications for community assembly and species coexistence (Chesson, 2000; Hubbell, 2001), conservation of rare species threatened by extinction due to small population sizes and/or geographic distributions (Hubbell, 2013), and ecosystem functioning (Mouillot et al., 2013). However, key gaps remain in our understanding of the mechanisms that determine species commonness and rarity at different spatial scales (Gaston, Blackburn, & Lawton, 1997). In many ecosystems, species that are abundant at local scales (high local abundance) often have widespread geographic distributions at regional scales (high occupancy), giving rise to positive relationships between local abundance and occupancy across species, a macroecological pattern known as the abundance-occupancy (Brown, 1984; Gaston et al., 2000). Although this relationship seems to be pervasive in nature (Gaston et al., 2000), the extent to which similar ecological mechanisms underlie these relationships across different ecosystems remains unresolved.

Two key mechanisms proposed to explain interspecific differences in local abundance and occupancy are niche breadth and niche position. The niche-breadth hypothesis predicts that local abundance (mean abundance of a species in sites where it occurs) and occupancy (number of sites in which a species occurs) are higher for species that maintain viable populations in a wide range of environmental conditions (i.e., large niche breadths) (Brown, 1984). For example, geographic range sizes are often larger for species with larger environmental tolerances and habitat breadths (Slatyer, Hirst, & Sexton, 2013). In contrast, the niche-position hypothesis predicts that local abundance and occupancy are higher for species that maintain viable populations in non-marginal environments with abiotic or biotic conditions that are relatively common in a region (Gaston et al., 1997; Hanski, Kouki, & Halkka, 1993; Venier & Fahrig, 2016). Species with non-marginal niche positions occur in sites with environments more similar to the mean environmental conditions of a region, whereas species with marginal niche positions occur in habitats with environments more dissimilar from the mean environmental conditions of a region (Gaston et al., 1997; Hanski et al., 1993). For instance, rank abundances of insects and their host plants are positively correlated, suggesting that common insect species occur on common host plants (Gaston et al., 1997). Therefore, a given species may have high local abundance and occupancy because it is a habitat or resource generalist (large niche breadth), specialized to environmental conditions that are common in a region (non-marginal niche

position), or a combination of both mechanisms (Sheth, Jiménez, & Angert, 2014).

Despite decades of interest in how niche breadth and niche position influence species abundance and occupancy, the relative importance of these mechanisms within and across ecosystems remains unresolved. Previous tests of the niche-breadth and niche-position hypotheses have yielded mixed results. Some studies found that both niche breadth and niche position strongly explained interspecific differences in local abundance and occupancy in a wide range of taxa including crustaceans, insects, birds and plants (Boulangeat, Lavergne, Van Es, Garraud, & Thuiller, 2012; Gaston & Spicer, 2001; Heino, 2005; Heino & Tolonen, 2018; Hurlbert & White, 2007; Pannek, Ewald, & Diekmann, 2013; Thompson, Gaston, & Band, 1999). In contrast, others found that niche breadth, but not niche position, explained interspecific differences in local fish abundance (Faulks, Svanbäck, Ragnarsson-Stabo, Eklöv, & Östman, 2015) and plant occupancy (Sheth et al., 2014). Other studies also found that niche position, but not niche breadth, explained differences in local abundance and occupancy of birds (Gregory & Gaston, 2000), aquatic macroinvertebrates and diatoms (Heino & Grönroos, 2014; Perez Rocha et al., 2018). To date, relatively few of these studies have focused on plants, leaving an important gap in our understanding of how niche breadth and position influence patterns of species abundance and occupancy across taxa.

Mixed empirical support for the niche-breadth and niche-position hypotheses may reflect methodological limitations and geographic gaps in previous studies. First, distributions of species across environmental gradients can be influenced by both dispersal and niche mechanisms (Pulliam, 2000). However, most studies that estimate niche breadth and niche position based on spatial associations between species distributions and the environment do not account for the potential influence of dispersal. Second, comparative studies testing the influence of niche breadth and niche position among low-diversity and high-diversity communities are rare. Most studies have focused on relatively low-diversity communities in temperate regions (Boulangeat et al., 2012; Faulks et al., 2015; Gaston & Spicer, 2001; Heino, 2005; Heino & Grönroos, 2014; Heino & Tolonen, 2018; Hurlbert & White, 2007; Pannek et al., 2013; Perez Rocha et al., 2018; Sheth et al., 2014; Thompson et al., 1999). In contrast, only a handful of studies have focused on high-diversity communities in the tropics (Arellano, Cala, & Macía, 2014; Kristiansen, Svenning, Grández, Salo, & Balslev, 2009), where dispersal limitation and stochastic processes have been suggested to override the importance of ecological niches in determining species abundances

(Chisholm & Pacala, 2011; Hubbell, 2001). These gaps limit our understanding of how niche mechanisms may contribute to general patterns of species abundance at continental to global scales.

We investigated the relative importance of niche breadth and niche position in determining local abundance and occupancy of tree species across temperate, sub-tropical and tropical forests. Specifically, we tested the hypotheses that local abundance and occupancy across woody plant species increase with niche breadth and decrease with niche position. Our study included regional-scale networks of 0.1-ha forest plots in three contrasting biogeographic regions (Table 1): temperate oak-hickory forest, Missouri Ozarks, USA (46 species); premontane sub-tropical forest, Argentinean Andes (63 species); lowland tropical forest, Bolivian Amazon (355 species). Our analyses proceeded in three steps. First, we measured abiotic-niche breadth and abiotic-niche position for each species in each region using 16 climate, soil and topographic variables. Second, we used linear regression and model selection to test the relative importance of niche breadth and niche position in determining local abundance and occupancy within each region. Third, to account for other processes that may influence observed patterns of niche breadth and niche position across environmental gradients (e.g., dispersal), we used a null model that removed associations between species occurrences and local environmental conditions within each region, while preserving both the observed mean local abundance and occupancy of each species and observed spatial structure of the environment in each region.

2 | MATERIAL AND METHODS

2.1 | Forest plot networks

Our study included regional forest-plot networks in three distinctive biogeographic regions: a high-diversity, lowland tropical forest in the Bolivian Amazon (Arellano, Cala, et al., 2014; Myers et al., 2013; Tello et al., 2015); a low- to intermediate-diversity, premontane subtropical forest in the Argentinian Andes (Blundo, González-Espinosa, & Malizia, 2016); and a low-diversity temperate (oak hickory) forest in the Missouri Ozarks, USA (Myers et al., 2013) (Table 1 and Supporting Information Table S1). In Bolivia, we included 42 0.1-ha

(20-m × 50-m) plots distributed among four localities in and around Madidi National Park: Chalalan (6 plots), Hondo (18), Quendeque (5) and Tuichi (13). In Missouri, we included 36 0.1-ha (20-m × 50-m) plots distributed among three state parks (Babler, Meramec, and Onondaga Caves State Park; 8 plots per park) and two field stations [Reis Biological Station (4 plots) and Tyson Research Center (8 plots)]. In Argentina, we included 14 0.1-ha (20-m × 50-m) subplots, each located within a separate 1-ha (20-m × 500-m) permanent plot in one of two localities: Jujuy (4 plots) and Salta (10). Each 1-ha permanent plot had seven to ten 0.1-ha subplots in which both soil and tree data were collected. We randomly chose one of these 0.1-ha subplots (hereafter plots) for our analyses. In each plot, we recorded all individuals of woody plant species (hereafter trees) with a diameter at breast (dbh) of ≥ 2.5 cm in Bolivia and Missouri and ≥ 10 cm dbh in Argentina. Given the difference in minimum dbh among the three regions, we performed two sets of analyses: (a) an analysis including all individuals ≥ 2.5 cm dbh in Bolivia and Missouri, and all individuals ≥ 10 cm dbh in Argentina; and (b) an analysis including only individuals ≥ 10 cm dbh in all three regions. The two analyses yielded similar results. For simplicity, we, therefore, present results from the analysis including all individuals and present summary results for the analysis including only individuals ≥ 10 cm dbh in the Supporting Information in Table S5.

In each region, forests plots were distributed across a range of environmental conditions and geographic distances (Table 1 and Supporting Information Table S2). In Bolivia and Missouri, we established plots outside of floodplains and areas with recent anthropogenic or natural disturbance (Myers et al., 2013). In Argentina, some plots had some selective logging and cattle transhumance (e.g., movement of livestock between lowlands and mountains) in the past (Blundo et al., 2016).

2.2 | Local species abundance and species occupancy

Mean local abundance and occupancy provide complementary measures of species commonness and rarity at different spatial scales (Bock & Ricklefs, 1983). In each region, we calculated mean local abundance (hereafter local abundance) as the mean number of

TABLE 1 Overview of forest-plot networks in three biogeographic regions

Region	No. of species ≥ 2.5 cm (≥10 cm)	No. of species excluding singletons ≥ 2.5 cm (≥10 cm)	No. of plots	Dominant forest type	Elev. (m)	Geographic distance (km)
Missouri Ozarks	46 (34)	38 (31)	36	Temperate oak-hickory	171–295	0.05–87
Argentinian Andes	(63)[*]	(51)[*]	14	Sub-tropical premontane	465–996	6–236
Bolivian Amazon	355 (154)	297 (119)	42	Tropical lowland	280–593	0.03–74

Note: Regions are arranged from lowest (top row) to highest (bottom row) species richness. Singleton = species represented by a single individual. Elevation = range of elevation among plots. Geographic distance = range of geographic distances among plots

[*]Minimum diameter at breast height (dbh) 10 cm.

individuals of a species in all plots that contained ≥ 2 individuals of that species. We calculated occupancy (hereafter occupancy) as the proportion of plots in a region that contained ≥ 1 individual of that species. We included species that occurred in a single plot as long as they had more than one individual present in that plot. Species with only one individual (singletons) were excluded to minimize potential bias due to under-sampling and because niche breadth cannot be calculated for singletons (explained below).

2.3 | Niche breadth and niche position

For each species in each region, we calculated abiotic-niche breadth and abiotic-niche position using 16 climate, soil and topographic variables (Supporting Information Table S2). In each plot, we used nine soil variables (sand, clay, pH, electrical conductivity, organic matter, P, Na, total N, K) and two topographic variables (elevation, slope) measured in all three regions; detailed descriptions of soil methods are provided in Myers et al. (2013), Arellano, Cala, et al. (2014) and Blundo et al. (2016). In brief, we measured soil variables in each plot from an air-dried, composite soil sample collected from a depth of 0–20 cm (Argentinean Andes), 0–30 cm (Bolivian Amazon) and 0–15 cm (Missouri Ozarks) and analysed at local soil laboratories. We calculated the elevation and slope of each plot using GIS (Bolivian Amazon) or in the field (Missouri Ozarks, Argentinean Andes). Our initial set of climate variables included 19 bioclimatic variables from WorldClim averaged from 1970 to 2000 at a $c.$ 1-km^2 resolution (Fick & Hijmans, 2017). However, because the Argentinean Andes had fewer plots (14) than the number of bioclimatic variables (19), we reduced the number of bioclimatic variables to five variables across all regions by selecting variables that were not strongly correlated in all regions (Spearman test, $r < .70$; Supporting Information Table S2). First, we standardized all environmental variables to z-scores (mean = 0, SD = 1) to control for differences in variances and measurement units. Standardization was done for each region separately to maintain the unique environmental variation of each region and test whether niche breadth and niche position explain changes in local abundance and occupancy within each region. Second, we performed separate principal components analyses (PCAs) for (a) soil and topographic variables combined (11 variables total; 9 soil, 2 topographic – Supporting Information Table S2) and used the first five principal components axes as predictor variables, which together explained 82–90% of the variation in soils and topography, and (b) climate variables (5 variables total – Supporting Information Table S2) and used the first two principal components axes as predictor variables, which together explained 84–91% of the variation in climate (Supporting Information Table S3).

We calculated the abiotic-niche breadth of each species in each region using a variation of Anderson's (2001) method (Supporting Information Table S4). First, we calculated the mean value of each environmental variable e across all forest plots occupied by all individual trees of species s in region r ($\overline{x_{s.e.r}}$). Second, we calculated the squared environmental distances between $\overline{x_{s.e.r}}$ and the

environmental value of the forest plot, in which the nth individual tree of species s occurs ($x_{s.e.r.n}$). The niche breadth of species s ($NB_{s.r}$) was calculated as the sum of this quantity (i.e., $\sum_{e=1}^{E} \left(x_{s.e.r.n} - \overline{x_{s.e.r}} \right)^2$) across all environmental variables. Third, to account for differences in the total number of individual trees among species ($N_{s.r}$), we calculated the species' mean niche breadth ($MNB_{s.r}$) by dividing $NB_{s.r}$ by $N_{s.r}$. Thus, the mean niche breadth of a species represents the mean squared environmental distance between individuals of the species and the mean environmental conditions of plots where the species was present. When all individuals of a species occurred in a single plot, such that the environmental values for each individual were the same as their centroid (i.e., $MNB_{s.r}$ = 0), we assigned the species the smallest value of mean niche breadth calculated in the region, and added this smallest mean niche-breadth value to each species' original mean niche breadth to maintain differences among species.

We calculated the abiotic-niche position of each species in each region following Sheth et al. (2014) (Supporting Information Table S4). First, we calculated the mean value for each environmental variable e across all forest plots in a region ($\overline{x_{e.r}}$). Second, we calculated the mean value of each environmental variable across all forest plots occupied by all individual trees of species s in region r ($\overline{x_{s.e.r}}$). Third, we calculated the niche position of each species ($NP_{s.r}$) as the mean sum of squared differences between $\overline{x_{s.e.r}}$ and $\overline{x_{e.r}}$, across all environmental variables. Thus, the niche position of a species represents the 'marginality' of a species' environmental distribution relative to the mean environmental conditions of a region (Sheth et al., 2014). Species with higher values of niche position occur in habitats with marginal environmental conditions, that is, environmental conditions that are relatively rare in a region. In contrast, species with lower values of niche position occur in habitats with non-marginal environmental conditions, that is, environmental conditions that relatively common in a region.

Advantages of these methods over others (e.g., convex hull polygons; outlying mean index) include: (a) niche breadth can be calculated for species with as few as two individuals; (b) niche breadth and niche position are calculated using mean sum of squared distances (equivalent to inter-point distances), which account for species abundance and outlying individuals in species' distributions; and (c) no reduction in dimensionality of environmental variables is necessary. Niche-breadth and niche-position values for each species are available in Supporting Information Table S6.

2.4 | Statistical and null-model analyses

To test the predicted relationships among local abundance and occupancy (response variables) and abiotic-niche breadth and abiotic-niche position (predictor variables), we used linear regression and model selection to compare relationships between each response variable and all three combinations of predictor variables (niche breadth only, niche position only, niche breadth and niche position together). We evaluated normality of model residuals using the Shapiro test and qqplot visualization using the 'MASS' package in

R. We improved normality of the data by $\log_{10}$ transforming predictor variables and local abundance, and logit transforming occupancy (Warton & Hui, 2011). We calculated the variance inflation factor (VIF) to assess potential effects of collinearity that may result when both variables are included in the same model. The VIFs in the Argentinean Andes, Missouri Ozarks and Bolivian Amazon were 1.72, 1.81 and 2.16, respectively, justifying the inclusion of both predictor variables in the same model (Burnham & Anderson, 2002). We then calculated the Akaike information criterion corrected for sample size (AICc) for each linear model using the 'car' package in R. Delta AICc (ΔAICc) and Akaike model weights (ωAICc) were calculated from AICc values to select the best model for local abundance and occupancy.

To account for other processes that may influence observed patterns of niche breadth and niche position across environmental gradients (e.g., dispersal), we used a null model that removed any associations between species occurrences and local environmental conditions. In each region, the null model preserved both the observed spatial structure of the environment (environmental conditions and geographic locations of each plot) and the observed local abundance and occupancy of each species. To remove associations between species occurrences and the environment, we randomized the occurrence of species across plots within each region. We could not randomize locations of individuals because (a) the geographic coordinates of individual trees within each 0.1-ha plot were not recorded, and (b) each 0.1-ha plot contained a single measurement for each environmental variable (i.e., environmental variation across different locations within each 0.1-ha plot was not measured). In each of 1,000 iterations of the null model, we calculated slopes of the relationships between each observed response variable (local abundance and occupancy) and the predictor variable(s) from the best-fit model in each region. To test our hypotheses, we calculated the proportion of null-expected slopes that were greater or less than the observed slopes. We considered the niche-breadth hypothesis supported if less than 5% of the null-expected slopes were greater than the observed slope (i.e., empirical relationship more positive than the null expectation), and the niche-position hypothesis supported if less than 5% of the null-expected slopes were less than the observed slope (i.e., empirical relationships more negative than the null expectation). We performed all analyses in R (R Core Team, 2018).

To further explore the potential effects of dispersal on species abundance and occupancy, we evaluated the influence of maximum plant height (*m*) on local abundance and occupancy using both simple linear-regression and multiple linear-regression models. We used maximum plant height as a proxy for dispersal distance because it is one of the best correlates of seed-dispersal distances across plant species, and maximizes the probability of estimating seed dispersal based on reproductive individuals (Thomson, Moles, Auld, & Kingsford, 2011). For each species in Argentina and Bolivia, we estimated maximum plant height in the field. For each species in Missouri, we obtained height at reproductive maturity from the United States Department of Agriculture PLANTS Database (http://

plants.usda.gov) or the Missouri Botanical Garden Plant Finder (https://www.missouribotanicalgarden.org/plantfinder/plantfindersearch.aspx). Since these regression analyses yielded insignificant or weak relationships, we present these results in the Supporting Information (Figures S5, S6 and Tables S5–S10) and highlight them briefly in the Discussion.

3 | RESULTS

3.1 | Local abundance and occupancy across biogeographic regions

Local abundance and occupancy were positively related in Missouri (R^2 = .19, *p* < .001) and Argentina (R^2 = .20, *p* < .001), but unrelated in Bolivia (R^2 = .01, *p* = .13) (Supporting Information Figure S1). Local abundance ranged from 1–46 in the Missouri Ozarks to 1–8 in the Argentinian Andes and Bolivian Amazon, where a local abundance of 1 means that the number of plots occupied by a species was equal to the total number of individuals of that species (e.g., two individuals in two plots). Occupancy (proportion of plots occupied) ranged from .03–1 in the Missouri Ozarks, .07–.79 in the Argentinean Andes and .02–.71 in the Bolivian Amazon.

3.2 | Relative importance of niche breadth and niche position as drivers of local abundance and occupancy

Local abundance and occupancy were significantly related to observed abiotic-niche breadths and abiotic-niche positions in all three regions. In Missouri and Argentina, occupancy was best explained by the model that included niche position alone, whereas in Bolivia occupancy was best explained by the model that included both niche breadth and position (Table 2 and Figure 1). In all regions, local abundance was best explained by the model that included both niche breadth and position, compared to models with either variable alone (Table 2, Figure 2 and Supporting Information Figure S2). Results were generally consistent when using individuals ≥ 10 cm dbh for Missouri and Bolivia; the only exception was for local abundance in Bolivia, where local abundance was best explained by niche position alone (Supporting Information Table S4).

As predicted by the niche-position hypothesis, local abundance and occupancy both decreased with niche position in all three regions (Table 2, Figure 1 and Supporting Information Figure S2). In other words, locally abundant or widespread species occurred in non-marginal environments with environmental conditions close to the mean environmental conditions in the region. These patterns were qualitatively similar using only individuals ≥ 10 cm dbh in all three regions (Supporting Information Table S5). Moreover, the observed relationship between occupancy and niche position differed significantly from random species–environment associations in all regions, whereas the observed relationship between local abundance and niche position only differed from random species–environment

TABLE 2 Results from model selection testing the relative importance of abiotic-niche breadth (NB) and abiotic-niche position (NP) as predictors of local tree-species abundance and occupancy in a temperate, sub-tropical and tropical forest

Areas	Predictors	Intercept	Parameter estimate (β) NB	NP	R^2	AICc	ΔAICc	ωAICc
Temperate oak-hickory forest, Missouri Ozarks, USA	Intercept	0.72				31.8	17.9	0
	Abundance ~ NB+NP	**1.32**	**−0.94**[**]	**−0.36**[***]	**0.45**[***]	**13.9**	**0**	**0.98**
	Abundance ~ NB	0.54	0.17		0.01	33.7	19.78	0
	Abundance ~ NP	0.50		−0.20[***]	0.28[***]	21.5	7.59	0.02
	Intercept	−0.89				155.9	66.55	0
	Occupancy ~ NB+NP	−2.41	−0.48	−1.82[***]	0.84[***]	91.5	2.11	0.26
	Occupancy ~ NB	−6.38	5.12[***]		0.41[***]	138.1	48.72	0
	Occupancy ~ NP	**−2.83**		**−1.74**[***]	**0.84**[***]	**89.4**	**0**	**0.74**
Sub-tropical premontane forest, Argentinian Andes	Intercept	0.37				7.1	42.77	0
	Abundance ~ NB+NP	**0.72**	**−0.45**[***]	**−0.38**[***]	**0.61**[***]	**−35.6**	**0**	**1**
	Abundance ~ NB	0.34	0.04		0.002	9.3	44.91	0
	Abundance ~ NP	0.33		−0.23[***]	0.39[***]	−15.7	19.89	0
	Intercept	−0.89				142.3	87.37	0
	Occupancy ~ NB+NP	−1.41	0.30	−1.18[***]	0.83[***]	55.1	0.24	0.47
	Occupancy ~ NB	−2.58	1.79[***]		0.43[***]	116.4	61.44	0
	Occupancy ~ NP	**−1.14**		**−1.28**[***]	**0.83**[***]	**54.9**	**0**	**0.53**
	Intercept	0.32				−271.3	40.19	0
Tropical lowland forest, Bolivian Amazon	**Abundance ~ NB+NP**	**0.36**	**−0.09**[***]	**−0.11**[***]	**.14**[***]	**−311.5**	**0**	**1**
	Abundance ~ NB	0.32	−0.02[*]		0.01	−272.9	38.58	0
	Abundance ~ NP	0.32		−0.04[***]	0.04[***]	−280.3	31.24	0
	Intercept	−2.76				762.1	557.67	0
	Occupancy ~ NB+NP	**−2.87**	**0.47**[***]	**−0.78**[***]	**0.85**[***]	**204.4**	**0**	**1**
	Occupancy ~ NB	−3.15	0.98[***]		0.64[***]	464.5	260.1	0
	Occupancy ~ NP	−2.64		−1.11[***]	0.77[***]	329.7	125.3	0

Note: Niche breadth and position were calculated using individuals ≥ 2.5 cm at diameter breast height (dbh) in Bolivia and Missouri, and individuals ≥ 10 cm dbh in Argentina. Best-fit models for each response variable are highlighted in bold. AICc = Akaike information criterion corrected for sample size; ΔAICc = delta AIC; ωAICc = Akaike model weights.

*p < .05.

**p < .01.

***p < .001.

associations in the Argentinian Andes (Figure 1 and Supporting Information Figure S4).

In contrast, we found little to no support for the niche-breadth hypothesis. As predicted by the niche-breadth hypothesis, occupancy increased with niche breadth in all three regions (Table 2 and Supporting Information Figure S3). However, local abundance decreased with niche breadth in all three regions (Table 2 and Figure 2), a pattern opposite to the prediction that locally abundant species should have broader abiotic niches. These patterns were qualitatively similar using only individuals ≥ 10 cm dbh in all three regions (Supporting Information Table S5). Moreover, observed relationships

between local abundance, occupancy, and niche breadth were no different than expected from random species–environment associations (Supporting Information Figure S4).

4 | DISCUSSION

Our results suggest that patterns of species commonness and rarity in temperate, sub-tropical and tropical forests are more strongly influenced by abiotic-niche position than by abiotic-niche breadth. In all three regions, occupancy decreased with niche position,
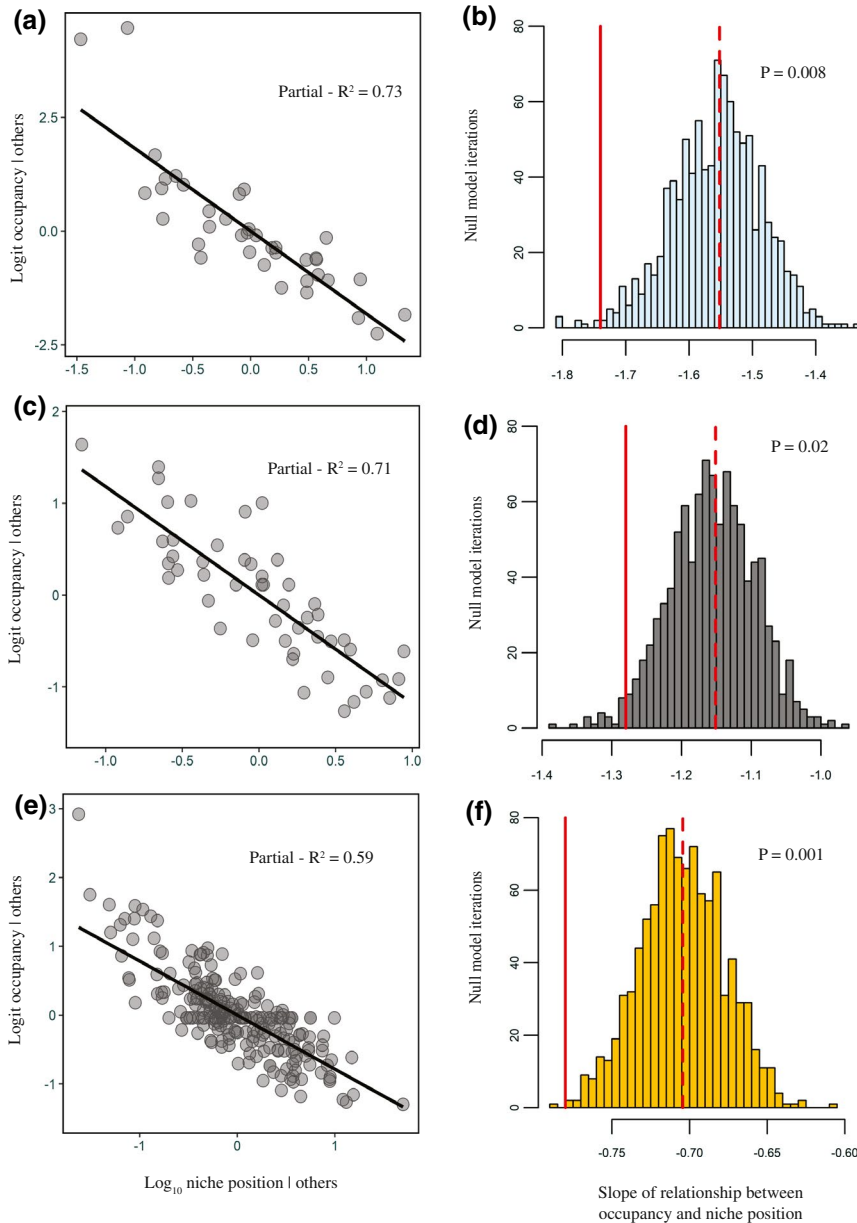
FIGURE 1 Relationships between occupancy and abiotic-niche position in a temperate, sub-tropical and tropical forest. Left column: partial-regression plots showing relationships between occupancy and abiotic-niche position after accounting for the influence of niche breadth in the (a) Missouri Ozarks (*n* = 38 species), (c) Argentinian Andes (*n* = 51 species) and (e) Bolivian Amazon (*n* = 297 species). Units on the *x* and *y* axes are standardized residual deviations indicating the independent effects after accounting for effects of other predictor variables. Right column: results from null-model analysis testing for non-random relationships between occupancy and abiotic-niche position in each region. Histograms show expected slopes (colour bars) from 1,000 iterations of a null model that preserved the observed local abundance and occupancy of each species, but removed associations between species occurrences and the abiotic environment. Dashed red lines show the mean expected slope from the null model. Solid red lines show the observed slopes from the best-fit models (Table 2). The observed relationship between occupancy and niche position was significantly more negative than expected from the null model in all three regions [Colour figure can be viewed at wileyonlinelibrary.com]

indicating that tree species with widespread geographic distributions (high occupancy) generally occur in non-marginal environments with environmental conditions that are relatively common in the region. Moreover, our null model revealed that these relationships were stronger than expected from random associations between species occurrences and the abiotic environment. Collectively, our results support the hypothesis that niche position is an important determinant of interspecific differences in occupancy across contrasting biogeographic regions.

Negative relationships between occupancy and niche position indicate that geographically widespread species tend to occur in non-marginal environments. This pattern may reflect at least two non-mutually exclusive mechanisms. First, species with widespread geographic distributions may occur in environments that are relatively common in the region due to high dispersal (Guo, Brown, Valone, & Kachman, 2000). Species with higher dispersal could

either colonize more sites with favourable environmental conditions, or maintain populations in sink habitats with unfavourable environmental conditions (Pulliam, 2000). Although dispersal likely contributes to patterns of occupancy and niche position observed in our study, our null-model analysis revealed that the occupancy–niche position relationship was stronger (more negative) than would be expected based solely on random associations between species occurrences and the abiotic environment (Figure 1). Additionally, our exploratory analyses of a dispersal-related trait (maximum plant height) indicated relatively weak relationships between occupancy and maximum height (Supporting Information Figures S5, S6 and Tables S7–S12).

Second, species with widespread geographic distributions may possess traits that allow them to maintain viable populations in non-marginal environments. Indirect support for this mechanism comes from studies showing systematic changes in tree community

FIGURE 2 Relationships between local abundance and abiotic-niche breadth in a temperate, sub-tropical and tropical forest. Left column: partial-regression plots showing relationships between local abundance and abiotic-niche breadth after accounting for the influence of niche position in the (a) Missouri Ozarks (*n* = 38 species), (c) Argentinian Andes (*n* = 51 species) and (e) Bolivian Amazon (*n* = 297 species). Units on the *x* and *y* axes are standardized residual deviations indicating the independent effects after accounting for effects of other predictor variables. Right column: results from null-model analysis testing for non-random relationships between local abundance and abiotic-niche breadth in each region. Histograms show expected slopes (colour bars) from 1,000 iterations of a null model that preserved the observed local abundance and occupancy of each species, but removed associations between species occurrences and the abiotic environment. Dashed red lines show the mean expected slope from the null model. Solid red lines show the observed slopes from the best-fit models (Table 2). The observed relationship between local abundance and niche breadth was not significantly different than expected from the null model in all three regions [Colour figure can be viewed at wileyonlinelibrary.com]
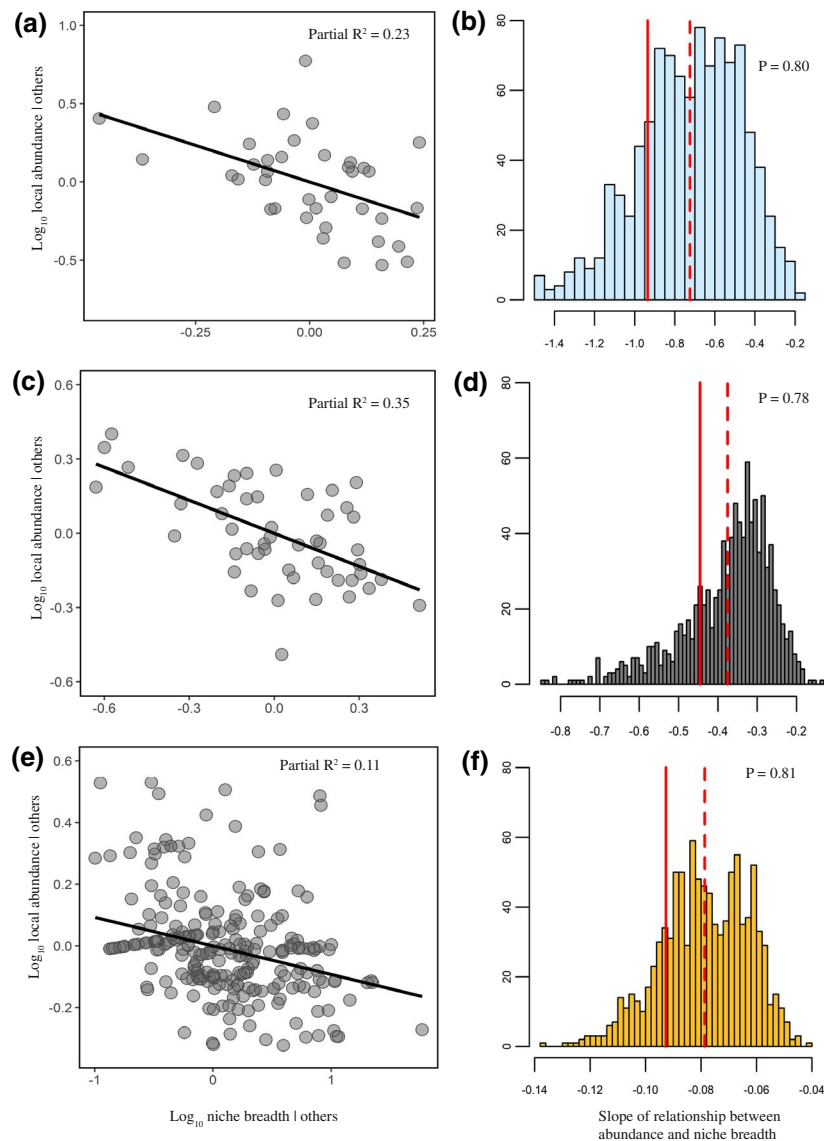
composition or species abundances across environmental gradients. In our study regions, for example, climate, soil and/or topographic variables have strong influences on tree species abundances (Arellano, Cayola, Loza, Torrez, & Macía, 2014; Arellano et al., 2017) and variation in species composition among habitats is unexplained by spatial variables alone (Blundo, Malizia, Blake, & Brown, 2012; Myers et al., 2013). In contrast, low-occupancy (rare) species may be associated with rare environmental conditions because they are habitat specialists (Harrison, Viers, Thorne, & Grace, 2008) or minimize competition with common species in those habitats (Lloyd, Lee, & Wilson, 2002). By explicitly comparing effects of the same climate, soil and topographic variables across regions, our study provides insights into how similar abiotic-niche mechanisms may underlie patterns of species occupancy across dissimilar biogeographic regions.

In contrast, we found that dissimilar mechanisms appear to underlie similar relationships between local abundance and abiotic-niche position across regions. As with occupancy, local abundance was negatively related to niche position in all three regions (Table 2 and Supporting Information Figure S2). However, our null-model

analysis revealed that the abundance–niche position relationship was more negative than expected by chance in Argentina, but not significantly different from the null expectation in Bolivia and Missouri (Supporting Information Figure S4). This result may reflect unmeasured abiotic and biotic variables that are part of a species *n*-dimensional niche (Hutchinson, 1959), differences in environmental heterogeneity among regions (Supporting Information Table S2) or differences between the spatial grain sizes at which we measured environmental variables and the spatial grain sizes of abiotic and biotic conditions that have the strongest influences on local abundances (Gaston et al., 1997). In particular, biotic interactions at small spatial scales (e.g., host–enemy interactions and resource competition) have been shown to strongly influence species abundance (Craine & Dybzinski, 2013; Klironomos, 2002; Mangan et al., 2010). In addition, relationships between local abundance and niche position may be stronger in regions with more heterogeneous environmental conditions where environmental filters can have stronger effects on species abundances. For example, forest plots in the Argentinian Andes spanned a larger range of elevations (*c.* 996 m) than plots in

the Bolivian Amazon (*c.* 593 m) and Missouri Ozarks (*c.* 295 m). In addition, plots in the Argentinian Andes are located across two mountain ranges, in which climate varies strongly among sites (Blundo et al., 2016) and included some early-successional forests comprised of tree species with functional traits related to resource acquisition in disturbed habitats (Blundo, Malizia, & González-Espinosa, 2015).

Our results provide little to no support for the niche-breadth hypothesis. In all three regions, relationships between occupancy and niche breadth (Supporting Information Figure S3) did not differ significantly from those expected from the null model (Supporting Information Figure S4). This result suggests that species with widespread geographic distributions are more likely to occur in a wider range of habitats due to random sampling effects (Lambdon, 2008). Differences in the importance of sampling effects may help explain why some studies find positive relationships between occupancy and niche breadth (Heino, 2005; Köckemann, Buschmann, & Leuschner, 2009; Pannek et al., 2013; Siqueira, Bini, Cianciaruso, Roque, & Trivinho-Strixino, 2009; Siqueira et al., 2012), while others find no relationship (Gaston et al., 1997; Gregory & Gaston, 2000; Moore, Schlichting, Bagchi, & Lammens, 2018; Perez Rocha et al., 2018). Interestingly, studies that find support for the niche-breadth hypothesis across plants have focused on the role of niche breadth in determining species range size, that is, abundance patterns at larger spatial scales where regional environmental factors may become more important. For instance, previous studies of trees in North America and Europe (Köckemann et al., 2009; Morin & Lechowicz, 2013) found that niche breadth quantified using climatic variables and a small number of soil variables had a positive influence on range size, but failed to explain local abundance (Köckemann et al., 2009). This suggests that abundance patterns at smaller spatial scales may be more strongly influenced by local environmental factors. In addition, we found that local abundance decreased with niche breadth in all three regions (Table 2 and Figure 2), a pattern opposite to the prediction that abundant species have broader abiotic niches. This result suggests that common species may be more specialized in their abiotic niches than rare species (smaller abiotic-niche breadths in common than rare species). Indeed, a recent study of intraspecific trait variation in tropical trees found that common species have lower intraspecific trait variation, suggesting greater habitat specialization than rare species (Umaña, Zhang, Cao, Lin, & Swenson, 2017). Studies involving reciprocal transplants of common and rare species across environmental gradients that mimic large and small abiotic-niche breadths can provide important insights into how local niche specialization influences patterns of species abundance.

Theory suggests that abiotic niches may have a weaker influence on species abundance and membership in higher-diversity communities. In these communities, abundances and distributions of large numbers of rare species may be constrained due to strong recruitment limitation (Hubbell et al., 1999; Hurtt & Pacala, 1995). As a consequence, most pairs of species may encounter and compete with one another infrequently (Hubbell & Foster, 1986), which may reduce selection for niche differentiation and cause random changes in species relative abundances (Hubbell, 2001). Consistent with this

idea, we found that the relationship between occupancy and abiotic niche position was strongest in the lowest- and intermediate-diversity regions (Missouri Ozarks, partial R^2 = .73; Argentinian Andes, partial R^2 = .71), and weakest in the highest-diversity region (Bolivian Amazon, partial R^2 = .59) (Figure 1). Previous studies in these forests also found similar effects of environmental variables on species composition, where environmental variables had a relatively stronger influence in Missouri than Bolivia (Myers et al., 2013), spatial variables had a relatively stronger influence in Bolivia than Missouri (Myers et al., 2013) and spatial variables had a stronger influence than environmental variables in Argentina (Blundo et al., 2016). Building on these findings, we suggest that future studies explore the hypothesis that abiotic niche breadth and niche position have relatively weaker effects on species commonness and rarity in biogeographic regions with higher species richness, greater dispersal or recruitment limitation (Hubbell et al., 1999; Hurtt & Pacala, 1995; Myers et al., 2013), more infrequent interactions among competitors (Hubbell & Foster, 1986; Myers & Harms, 2009) and more homogeneous environmental conditions (i.e., abiotic niche space; MacArthur, 1972).

In conclusion, our findings advance previous studies by testing whether relationships between species commonness and rarity, niche breadth, and niche position show consistent patterns across contrasting biogeographic regions. Previous tests of the niche-breadth and niche-position hypotheses have yielded mixed results, have largely focused on a single biogeographic region, and/or have not accounted for other processes (e.g., dispersal) that may influence species distributions across environment gradients. By explicitly testing the relative importance of niche breadth and niche position across three biogeographic regions using standardized environmental variables and a null model that accounts for random species–environment associations, we find that species with widespread geographic distributions consistently occur in regionally common (non-marginal) environments, whereas species with narrow geographic distributions occur in regionally rare (marginal) environments. These results suggest that similar abiotic-niche mechanisms may determine regional patterns of tree species commonness and rarity across temperate, sub-tropical and tropical forests. Our findings imply that conservation efforts aimed at protecting populations of common and rare tree species should prioritize conservation of both common and rare habitats.

DILYS M. VELA DÍAZ is a forest community ecologist interested in understanding mechanisms that shape patterns of biodiversity across scales in temperate and tropical ecosystems, and applying insights from niche theory to conservation of rare species.

DATA AVAILABILITY STATEMENT

The processed data for each species (mean local abundance, occupancy, niche breadth, niche position) are available in the Supporting Information. The raw data for each plot in Missouri are available at Dryad Digital Repository (https://datadryad.org/stash/share/hETDuBLFbvDLXK8GSJ6heUTvw7gu5ZUX2dRiZuL-ss4) (https://doi.org/10.5061/dryad.80gb5mknx). The raw data for each plot in Argentina are available at ForestPlots (http://www.forestplots.net/data-packages/Vela_Diaz_et_al_2020). The raw data for each plot in Bolivia are deposited at Tropicos (http://tropicos.org/PlotSearch.aspx?projectid=20).

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SUPPORTING INFORMATION

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