



Niche breadth of oligarchic species in Amazonian and Andean rain forests

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Keywords

Climatic niche; Commonness; Edaphic niche; Environmental heterogeneity; *h* index; Niche breadth hypothesis; Oligarchy hypothesis; Rarity; Species dominance; Tropical rain forests

Nomenclature

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Abstract

Aim: To test the niche breadth hypothesis (NBH), which states that dominant species have broader environmental tolerances than rare species, focusing on oligarchic species distributions (1) along the gradients of edaphic and climatic individual variables, and (2) within the *n*-dimensional environmental frame defined by all edaphic and climatic variability.

Location: Amazonian and Andean tropical rain forests along a ca. 3000 m elevation gradient, covering an area of 200 × 200 km in northwestern Bolivia.

Methods: All woody plants with a DBH ≥ 2.5 cm were measured in 98 0.1-ha plots. We analysed 18 chemical properties of the soils in each plot. Climatic and topographic variables were obtained from available open-access databases. Three measures were calculated for each of the species found at each forest type: (1) regional-scale dominance based on frequency and local abundance, (2) niche breadth along each of the environmental variables, and (3) total niche size within the whole environment.

Results: Oligarchic species showed broader niche breadths than the other species that constituted the community assembly in both Amazonian and Andean rain forests. The niche breadth of any species tended to be positively correlated with its degree of dominance. The Amazonian forest showed a stronger oligarchic pattern than the Andean forest, and the Amazonian common species showed larger niches overall. However, this pattern differed for some particular variables: Amazonian oligarchies had narrower niches along the variables related to organic matter and most climatic variables, whereas Andean oligarchies had narrower niches along several micronutrient factors and temperature variables.

Conclusions: The results provide strong empirical support for the NBH in tropical rain forests. However, different patterns of dominance were found in the two habitats: oligarchic species ranged from narrow-niched species to very broad generalist species. Broad-niched oligarchic species have also been reported in other regions, suggesting an important role of niche size linking commonness at different scales. Oligarchic species exhibit relatively narrow niches with respect to soil factors if measured along wide gradients, regardless of the forest type studied. In contrast, the opposite pattern was found for many climatic variables, indicating higher sensitivity to climate in Amazonia compared to the Andes. Despite these differences, Amazonia has much larger total niche sizes for its common species than the Andes overall.

Introduction

Understanding how common plant species are distributed across the landscape is crucial for the management, conservation and comprehension of any tropical forest

ecosystem (Gaston & Fuller 2008; Gaston 2010; Pitman et al. 2013). In particular, the skeleton of tropical forest communities is constituted of a low proportion of the forest's large diversity because a limited number of abundant and frequent species account for the majority of

individuals within relatively large areas (Pitman et al. 2001; Macía & Svenning 2005). This idea is the core of the so-called 'oligarchy hypothesis', which has recently been revisited (Pitman et al. 2013). Following the conclusions of this paper, few empirical studies have examined the causes for this type of pattern, and it is still not clear why some species have such a level of dominance over large expanses. To address these issues, a major focus has been on the habitat specificity or the niche size of species, historically one of the major concerns of ecological research (e.g. Hutchinson 1957; Levins 1968; Ashton 1969; Rosenzweig 1981). Despite the significant advances reported during recent decades, the role of species niche size in the community assembly of tropical forests is still minimally understood. The major mechanistic hypothesis linking niche size and large-scale commonness is the niche breadth hypothesis (NBH), which, in its most general form, states that common species have broader niches than rare species (Brown 1984). It implies that two general types of species can be recognized: (1) species with broader environmental tolerances that would be able to attain higher local densities in some regions and could colonize new areas, attaining higher regional abundance; and (2) species with specific environmental requirements that are unlikely to find optimal conditions to colonize new areas anywhere and, therefore, would be locally restricted and scarce overall (Brown 1984).

The NBH is often cited in the literature on tropical forest dominance (e.g. Pitman et al. 1999, 2001, 2013; Ruokolainen & Vormisto 2000; Davidar et al. 2008; Kristiansen et al. 2009, 2012). However, according to Pitman et al. (2013), the NBH has not been properly tested, nor has the extent of species niches been rigorously quantified. To properly test the NBH, there must be some distinction between the resource distribution and the species distribution, as well as the integration of these two distributions in the measurement of species niches. Many niche metrics give the same weight to rare and common resources and, therefore, cannot discriminate the species with strong shifts in resource preferences from those using resources in proportion to their occurrence in the environment (Feinsinger et al. 1981; Smith 1982; Devictor et al. 2010). Hence, these metrics would not reflect the species' requirements because they constitute a mixture of both species characteristics and landscape characteristics.

The oligarchy hypothesis was proposed for *terra firme* Amazonian trees, but the results of many papers that corroborated the hypothesis indicate that it could be a much more general ecological hypothesis (see Pitman et al. (2013) for examples of papers on different vegetation types, geographic areas, life forms and taxa). However, it is unknown how this hypothesis can be applied

to different habitats whose mechanisms and processes differ greatly. The present paper focuses on Amazonian and Andean tropical rain forests, which represent two species-rich tropical ecosystems with contrasting biotic and abiotic conditions (Hoom et al. 2010; Herzog et al. 2012; Cavers & Dick 2013). One marked difference between the two habitats is the more pronounced environmental heterogeneity of the Andean forest, which is characterized by a strong elevational gradient and rapid shifts in edaphic and micro-environmental variables at any elevation (e.g. Gentry 1995; Webster & Churchill 1995; Vitousek 1998; Gerold 2008). It is noteworthy that the oligarchy hypothesis harbours the idea that the oligarchic pattern is weak within highly heterogeneous conditions, particularly edaphic heterogeneity (Pitman et al. 2001, 2013). Three predictions emerge from this pattern. (1) Because oligarchic species are generalists, but only to a certain limit when conditions are highly variable, we expect that different sets of oligarchic species would dominate in each of the conditions. (2) In the climatically highly heterogeneous Andean conditions, we expect weaker oligarchies with relatively narrower niches than in the lowlands, whereas we expect Amazonian oligarchies to be more dominant and relatively broad-niched because the climatic conditions of these forests are relatively more homogeneous. This may, or may not, apply also for the edaphic conditions, since Amazonian soils could also present a pattern of significant variability (e.g. Phillips et al. 2003; Higgins et al. 2011). (3) The relevant niche dimensions for which the environmental heterogeneity is expected to have an effect over the strength of the oligarchic pattern are assumed to be edaphic in Amazonian rain forests at ~10 000-km² scale, according to Pitman et al. (2001), but could be different in the contrasting Andean rain forests.

The present study focused on Amazonian and Andean tropical montane rain forests within a 200 × 200 km area in northwestern Bolivia. We tested the NBH and associated predictions in both forest types with two large and fully comparable data sets, comprised of woody plant data and environmental data, particularly edaphic data. We aimed to answer the following five questions: (1) are the niche breadths of oligarchic species broader than the niche breadths of the other species that constitute a given community assembly; (2) does the NBH apply to a broad suite of environmental variables or only to a specific set of variables; (3) which are the most significant environmental factors for the different Amazonian and Andean rain forests; (4) are Amazonian oligarchies stronger than Andean oligarchies; and if so, (5) is this difference associated with relatively broader niches of Amazonian oligarchic species compared to the niche breadths of oligarchic Andean species?

Methods

Study area and sampling design

Fieldwork was carried out in two regions of northwestern tropical rain forests of Bolivia ~120 km apart, within or close to the Madidi National Park (Fig. 1). In Amazonian rain forests, we inventoried 44 plots distributed in five sites below 1000 m a.s.l., within an area of 30 × 100 km (Macía 2008). In Andean rain forests, we inventoried 54 plots in six sites between 1200 and 3100 m a.s.l. that focused on three elevational ranges: lower montane forest at 1200–1500 m, intermediate montane forest at 2000–2300 m and upper montane forest at 2800–3100 m (Arellano & Macía 2014). Montane plots were established within an area of 40 × 120 km. All studied localities were 1–4 days away from the nearest village, and only accessible on foot, except one in the lowlands that was accessible by motorboat.

We studied old-growth mature tropical rain forest that had sporadic pockets of disturbance from landslides in the montane areas but no recent sign of human perturbation in either Amazonian or Andean habitats. Plot locations within a site were selected to document all environmental variation existing in a site, but all plots were internally homogeneous forests. We avoided secondary forests,

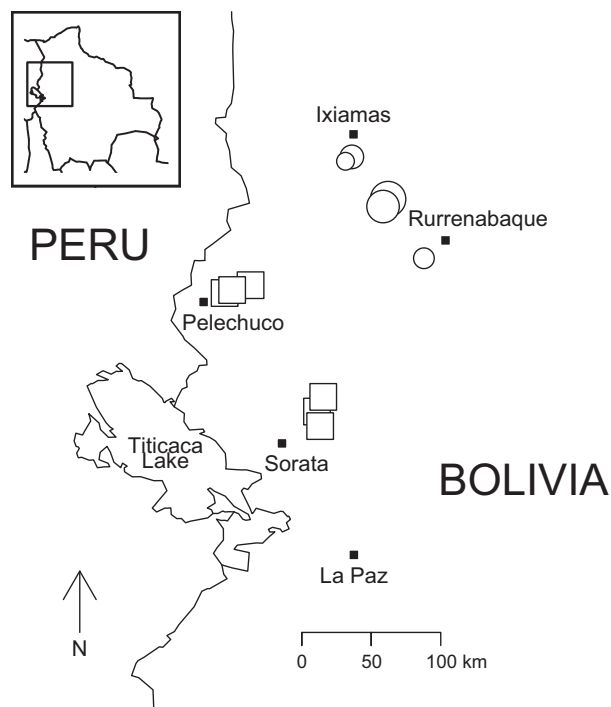


Fig. 1. Location of the 11 inventoried sites in northwestern Bolivia. Circles represent Amazonian forest sites, and squares represent Andean forest sites. The size of the symbols is proportional to the number of plots.

identified by the high abundance of *Cecropia* trees, bambuoids or vines and a lack of large trees. All forests received >2000 mm annual mean precipitation, and dry periods were 3–4 mo·yr⁻¹ in Amazonia and 2–3 mo in the Andes (Ribera 1992; Navarro et al. 2004; Hijmans et al. 2005). The mean annual temperature varied from 26 °C at the lowest elevations to 10 °C at the highest elevations. Both Amazonian and Andean soils were acidic (mean pH per site <5.5), with some plots of Amazonian rain forests having higher pH values (Macía et al. 2007). Amazonian soils were relatively sandy (>50%) and had less than 15% organic matter in the top layer, whereas Andean soils were highly organic, with 35–70% organic matter in the top layer at the three elevation ranges (Macía et al. 2007; Schawe et al. 2007).

Floristic data collection

We established six to 12 plots of 0.1 ha (20 × 50 m) in each of the 11 inventoried sites, with a minimum inter-plot distance of 500 m in Amazonian rain forests and 250 m in Andean rain forests, giving a total of 98 plots. At each plot, all woody plants with stems rooting within the plot limits and with a DBH (measured at 130 cm from the ground) ≥2.5 cm were measured. All measured individuals were identified or assigned a morphospecies name, and each was collected at least once in the sites. The full set of vouchers was deposited at the Herbario Nacional de Bolivia, and almost a full set of duplicates was deposited in the Missouri Botanical Garden. Less than 5% of the individuals were excluded in the analysis because they were sterile specimens that could not be assigned to a reliable morphospecies name. All data are available for query at the TROPICOS database (<http://www.tropicos.org/PlotSearch.aspx?projectid=20>).

Environmental data collection

At each plot, we obtained a compound sample of superficial soil (0–15 cm below the litter layer) from the mixture of five subsamples collected in the centre of five subplots disposed in zig-zag fashion. Soil samples were air dried and passed through a 2-mm sieve. Soil pH was determined in deionized water and in 1 M KCl solutions, with a soil/solution ratio of 1:2.5. Total C, N and S were determined in a LECO CHNS-932 elemental analyzer. Organic C was determined with the Walkley and Black wet digestion method (Walkley & Black 1974). Extractable Al, Ca, Co, Cu, Fe, K, Mg, Mn, Na, Ni, P and Zn content was measured with Melnich-3 extractions (Mehlich 1984) followed by determination using inductively coupled plasma-mass spectrometry (ICP-MS) in an Elan 6000 Perkin-Elmer spectrometer.

Climatic data, as represented in all data of 19 bioclimatic variables stored in the WorldClim database, were downloaded for the study area (Hijmans et al. 2005). We computed the elevation, slope, eastness and northness aspects from the ASTER Global Digital Elevation Map v 2, a digital elevation model with 30-m resolution (<http://asterweb.jpl.nasa.gov/gdem.asp>). A summary of the environmental conditions of each forest type can be found in Appendix S1.

Data analysis

Quantification of commonness and delimitation of oligarchic species

We calculated species commonness based on a modified version of the h index, a widely known bibliometric tool for measuring academic performance (Hirsch 2005), following Arellano et al. (2014). We assigned to each species a commonness proportional h index (h_p) when it was present in h_p per cent of plots and accounted for h_p per cent or more of the individuals in each of those plots. For example, a species with $h_p = 5\%$ means that the species is present in 5% of the plots and accounts for 5% or more of the individuals of those plots. This metric simultaneously combines local abundance and landscape frequency, the two-dimensional framework to which the oligarchy hypothesis refers. To separate oligarchic species from the other species, we first ranked species by their h_p index and second by their total abundance. Each species i was assigned a relative rank ($=\text{rank}_i/\text{number of species}$) and a relative h_p ($=h_{pi}/\text{maximum } h_p$). The number of oligarchic species was the i for which the relative h_{pi} equals the relative rank_i . Given that this new coefficient is in fact an h index of h_p indices, we use the notation h_h . Unlike h_p , which measures attributes of the species, h_h measures a property of the community. As in the case of h_p , the interpretation of h_h is as follows: a community with $h_h = 0.10$ signifies that 10% of the observed species present h_p indices above the 10th percentile. Low h_h indices correspond to communities dominated by a very limited set of species, whereas high h_h indices indicate fewer differences between species and, hence, relatively weaker oligarchies.

Niche breadth calculation

For each species i , we calculated the niche breadth (1) along each environmental variable k , separately, and (2) for the whole (multidimensional) environment. To do so, we extended the niche breadth measure of Smith (1982) to continuous variables. The niche breadth measure of Smith (1982) is based on the differential use of R different states of the resource k by a given species i and is calculated as follows (Eq. 1):

$$NB_{ik} = \sum_{j=1}^R \sqrt{p_j q_j} \quad (1)$$

where NB_{ik} is the niche breadth of the species i for the resource k , p_j is the proportion of the resource state j available for use (among the R different resource states of k), and q_j is the proportion of times that the species i is observed to use the resource state j . Contrary to other niche breadth measures, Smith's approach takes into account the differential distribution of R different states of the resource k , (not all resource states are equally common). Therefore, it discriminates the species with strong shifts in resource preferences from those using resources in proportion to their occurrence in the environment. The values close to 1 indicate that the species is insensitive to the state of the resource k . The values close to 0 correspond to those species that appear only in very specific and rare states of k .

To spread from a discrete suite of R states of a given resource to a continuous measure of the resource distribution, we estimated the probability density function of each environmental variable k by applying a Gaussian kernel to the observed distribution of values of k . This is an estimate of how common or rare are the different values of the variable k , and is denoted as $f(k)$. Similarly, and with the same kernel parameters, we estimated the probability density function of the occurrence of the species i along the environmental variable k . This is a continuous estimate of the distribution of the species i along the environmental variable k , and is denoted as $g(i_k)$. Finally, we calculated the niche breadth of species i for the environmental variable k (NB_{ik}) as the overlap between $f(k)$ and $g(i_k)$ (Eq. 2):

$$NB_{ik} = \int_{\min(k)}^{\max(k)} \sqrt{f(k)g(i_k)} \quad (2)$$

This measure takes values between 0 and 1. The values close to 1 indicate that the species is insensitive to the environmental conditions. The values close to 0 correspond to those species that appear only in very specific and rare conditions. NB_k is an estimate of the niche breadth of a given species along one environmental axis; it is an univariate measure of niche breadth, and thus was calculated separately for each species and each environmental variable considered.

To estimate an overall niche breadth of a species, we obtained a measure of total niche size (NB_{iT}) for each species i . To do that, we repeated all the previously mentioned calculations but used the orthogonal axes from a principal components analysis (PCA) instead of the original environmental variables. This PCA describes an n -dimensional hypervolume in which the dimensions are resources along

which the organisms interact with the environment, hence representing the Hutchinsonian realized niche (Hutchinson 1957; Devictor et al. 2010). For our purposes, the main advantage of the PCA is that it summarizes the whole environmental variability into independent orthogonal axes. This allows quantifying the environmental hypervolume occupied by a given species by calculating the product of all niche breadths along all possible orthogonal directions (Eq. 3):

$$NB_{iT} = \prod_{k=1}^n NB_{ik} \quad (3)$$

where NB_{iT} is the total niche breadth of the species i , NB_{ik} is the niche breadth of the species i along the PCA axis k , and n is the number of PCA axes. With this measure, each species is characterized by a total niche breadth NB_{iT} , an estimate of the hypervolume occupied by that species within the whole multidimensional environment.

Oligarchy and niche breadth

At each forest type, we analysed the relationship between h_p indices of species and their total niche size NB_T with Pearson correlations. We repeated the analysis for each environmental variable k by comparing h_p with NB_k . To compare the niche breadth of oligarchic vs non-oligarchic species we performed Kolmogorov–Smirnov tests for NB_T and NB_k along each of the environmental variables. We applied the Bonferroni correction for multiple comparisons to minimize the false discovery rate.

Amazonian vs Andean oligarchies

To determine if the homogeneous Amazonian rain forests harbour stronger oligarchies than the Andean rain forests, we (1) compared their h_h indices and (2) compared the h_p indices of each forests' oligarchic species with Mann–Whitney U -tests. To determine if the niche breadths of Amazonian oligarchic species are broader than the niche breadths of Andean oligarchic species, we (1) compared the NB_T indices of each forests' oligarchic species with Mann–Whitney U -tests, and (2) repeated this analysis for NB_k along each environmental variable k individually, applying a Bonferroni correction. Finally, to check the assumption that there are more heterogeneous environmental conditions in Andean rain forests than in Amazonian forests we calculated the coefficient of variation (CV) for each variable k in both forest types.

All calculations and analyses were performed for each forest type separately using R 2.15.1 GUI 1.52 (R Foundation for Statistical Computing, Vienna, AT, US). The level of significance for all analyses was 0.05.

Results

Floristic data

A total of 31 519 individuals belonging to 1518 species of trees and lianas ≥ 2.5 cm DBH were recorded in 98 0.1-ha plots. In the Amazonian region, 808 species were found in 44 plots (12 642 individuals), whereas in the Andean region 877 species were found in 54 plots (18 876 individuals).

Oligarchy and niche breadth

We found a positive and significant correlation between the total niche size and dominance of Amazonian species (Pearson $r = 0.57$, $P < 0.001$) and Andean species ($r = 0.53$, $P < 0.001$; Fig. 2). We found the same trend for most of the environmental variables, except BIO4 and BIO15 (temperature seasonality and precipitation seasonality, respectively), although often with weaker correlations in the case of climatic variables and in the Andean rain forests (Table 1). For both forest types, the relationship between species dominance and the niche breadth measure along every edaphic variable was always positive and statistically highly significant.

The total niche of oligarchic species was significantly larger than the total niche of non-oligarchic species, both in Amazonian rain forests (Kolmogorov–Smirnov $D = 0.68$, $P < 0.001$) and in Andean rain forests ($D = 0.73$, $P < 0.001$). When compared with the niche breadths along each of the environmental variables, we found that the niches of oligarchic species were systematically larger than the niches of the non-oligarchic species (Table 2). The only exceptions were in Andean rain forests along elevational gradients and seven climatic variables (BIO1, BIO5, BIO6, BIO8–BIO11: annual mean temperature, maximum temperature of warmest month, minimum temperature of coldest month, and mean temperatures of the wettest, driest, warmest and coldest quarters, respectively), for which the differences were not statistically significant. In the case of Amazonian forests, all environmental variables were statistically significant.

Amazonian vs Andean oligarchies

In Amazonian rain forests, we identified 115 oligarchic species out of 808 ($h_h = 0.14$), of which *Rinorea viridifolia* ($h_p = 15.91\%$), *Iriartea deltoidea* and *Rinorea apiculata* (both $h_p = 11.36\%$) showed the highest dominance (Fig. 2). In Andean rain forests, we identified 175 oligarchic species out of 877 ($h_h = 0.20$), of which *Clusia sphaerocarpa* ($h_p = 9.26\%$), *Myrsine coriacea* and *Psychotria carthagenensis* (both $h_p = 7.41\%$) showed the highest dominance.

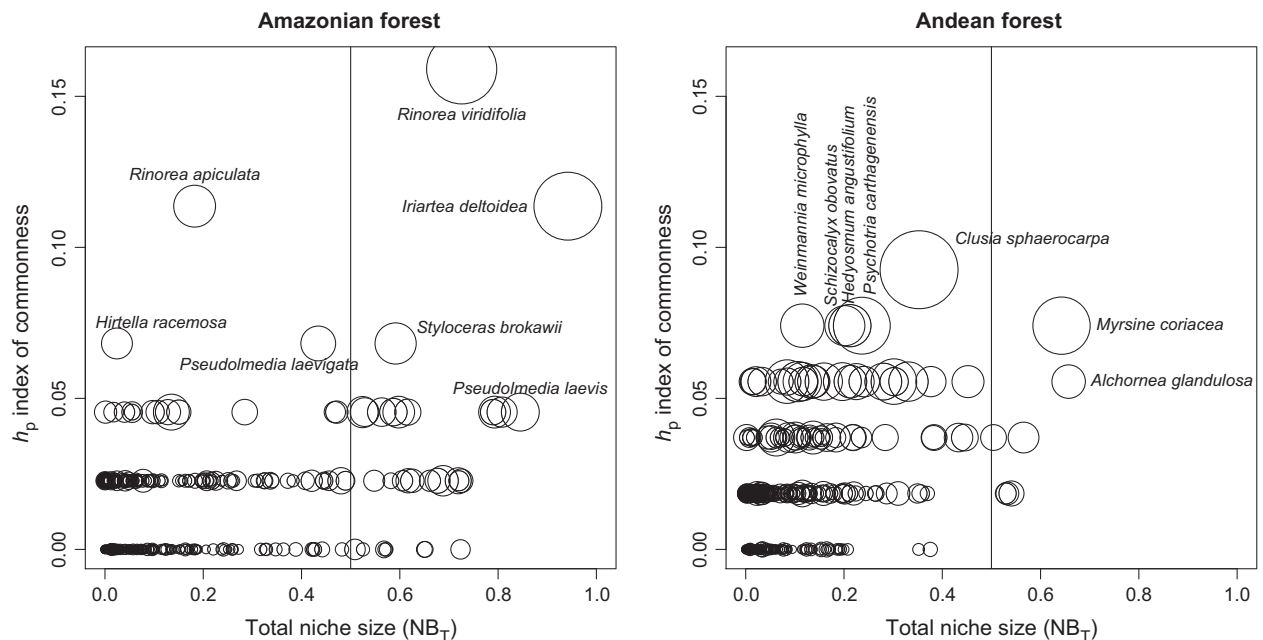


Fig. 2. Total niche size (NB_T) vs the h_p index of commonness combining local abundance and landscape frequency for all species recorded in 98 0.1-ha plots of Amazonian ($n = 808$) and Andean ($n = 877$) tropical rain forests in northwestern Bolivia. The vertical line indicates an arbitrary threshold between specialist and generalist species (0.5). The circle size is proportional to the total number of individuals in each type of forest.

The mean h_p index of commonness for Amazonian oligarchic species was 3.12%, whereas for Andean oligarchic species it was 2.98%. These differences were statistically highly significant (Mann–Whitney $U = 13397$, $P < 0.001$).

The average of the total niche size was twofold higher in Amazonian oligarchies (mean $NB_T = 0.26$) than in Andean oligarchies (mean $NB_T = 0.13$), and the difference was statistically highly significant (Mann–Whitney $U = 12823$, $P < 0.001$). When particular niche breadths were analysed along each of the environmental variables, Amazonian and Andean oligarchies did not show significant differences in their niche breadths along half of the environmental variables (Table 3). Concerning the climatic variables, Amazonian and Andean oligarchies differed significantly in their niche breadths along ten out of 19 climatic variables. Amazonian oligarchies showed significantly broader niches than Andean oligarchies for BIO1, BIO2 and BIO7 (annual mean temperature, mean diurnal range and annual temperature range, respectively). In turn, Andean oligarchies showed significantly broader niches than Amazonian oligarchies for BIO5, BIO11, BIO12, BIO14, BIO16, BIO17 and BIO19 (maximum temperature of warmest month, mean temperature of coldest quarter, annual precipitation, precipitation of driest month, and precipitation of wettest, driest and coldest quarters, respectively). Concerning the soil variables, Amazonian and Andean oligarchies differed significantly in their niche breadths along nine out of 18 edaphic

variables (Table 3). Amazonian oligarchies showed significantly broader niches than Andean oligarchies for some extractable elements (Co, Fe, Mn, Na) but significantly narrower niches along organic C, total C, total N, total S and extractable K content. Concerning topographic variables, Amazonian oligarchies showed statistically significant broader niches than Andean oligarchies along the northness aspect. The results for elevation, slope and eastness aspect were not statistically significant.

The coefficients of variation showed that Andean rain forests were more heterogeneous overall than Amazonian rain forests and particularly for the climatic and topographic variables, except for isothermality (BIO3) and slope (Table 3). Furthermore, Andean soils were more heterogeneous for the P, Ca, Fe, Co and especially Mn and Na extractable content. However, the Amazonian soils showed higher heterogeneity in pH, organic C, total C, total N, total S and extractable Al, Cu, K, Mg, Ni and Zn contents.

Discussion

The NBH considering total niche size

Oligarchic species have broader niche breadths than the other species that constitute the community assembly in Amazonian and Andean rain forests, and the niche breadth of any species tends to be positively correlated with its degree of dominance. The consistency of both

Table 1. Results of Pearson correlations between niche breadth measure along individual environmental variables and species dominance (h_p index) as recorded in 98 0.1-ha plots of Amazonian and Andean tropical rainforests in northwestern Bolivia. The bioclimatic codes follow Hijmans et al. (2005) (<http://www.worldclim.org/bioclim>).

Environmental variables	Pearson correlations for Amazonian rain forests	Pearson correlations for Andean rain forests
Elevation	0.14*	-0.082
Slope	0.27***	0.331***
Northness aspect	0.31***	0.384***
Eastness aspect	0.31***	0.427***
pH (H ₂ O)	0.17***	0.260***
pH (KCl)	0.17***	0.218***
Organic C	0.22***	0.163***
Total C	0.20***	0.195***
Total N	0.23***	0.248***
Total S	0.21***	0.263***
Extractable Al	0.20***	0.347***
Extractable Ca	0.23***	0.259***
Extractable Co	0.25***	0.278***
Extractable Cu	0.27***	0.383***
Extractable Fe	0.21***	0.331***
Extractable K	0.21***	0.208***
Extractable Mg	0.27***	0.290***
Extractable Mn	0.25***	0.300***
Extractable Na	0.26***	0.230***
Extractable Ni	0.29***	0.297***
Extractable P	0.27***	0.232***
Extractable Zn	0.28***	0.249***
BIO1	0.14**	-0.056
BIO2	0.15***	0.125*
BIO3	0.14**	0.231***
BIO4	0.10	0.031
BIO5	0.14**	-0.049
BIO6	0.12*	-0.046
BIO7	0.17***	0.177***
BIO8	0.14**	-0.061
BIO9	0.14**	-0.056
BIO10	0.13*	-0.062
BIO11	0.14**	-0.05
BIO12	0.15**	0.131**
BIO13	0.16**	0.287***
BIO14	0.13*	-0.016
BIO15	0.08	-0.006
BIO16	0.15**	0.245***
BIO17	0.16**	-0.013
BIO18	0.13*	0.028
BIO19	0.16***	-0.039

The significance was assessed using Bonferroni-corrected P -values: *** P < 0.001; ** P < 0.01; * P < 0.05.

results supports the NBH in tropical rain forests. This is in agreement with studies indicating that common species tend to be present at two or more habitat types (Pitman et al. 1999; Macía & Svenning 2005) and that widespread species show broad environmental tolerances (Davidar

Table 2. Results of Kolmogorov–Smirnov tests comparing the niche breadth measure along individual environmental variables of oligarchic vs non-oligarchic species as recorded in 98 0.1-ha plots of Amazonian and Andean tropical rainforests in northwestern Bolivia. In all the significant cases, the niche breadths of oligarchic species were greater than the niche breadth of non-oligarchic species. The bioclimatic codes follow the codes of Hijmans et al. (2005) (<http://www.worldclim.org/bioclim>).

Environmental variables	Kolmogorov–Smirnov tests for Amazonian rain forests	Kolmogorov–Smirnov tests for Andean rain forests
Elevation	0.26***	0.130
Slope	0.47***	0.530***
Northness aspect	0.57***	0.464***
Eastness aspect	0.58***	0.642***
pH (H ₂ O)	0.31***	0.271***
pH (KCl)	0.29***	0.345***
Organic C	0.35***	0.368***
Total C	0.30***	0.407***
Total N	0.40***	0.504***
Total S	0.39***	0.518***
Extractable Al	0.35***	0.462***
Extractable Ca	0.42***	0.473***
Extractable Co	0.48***	0.536***
Extractable Cu	0.43***	0.619***
Extractable Fe	0.50***	0.542***
Extractable K	0.27***	0.428***
Extractable Mg	0.42***	0.532***
Extractable Mn	0.49***	0.495***
Extractable Na	0.53***	0.295***
Extractable Ni	0.48***	0.536***
Extractable P	0.46***	0.466***
Extractable Zn	0.38***	0.511***
BIO1	0.26***	0.123
BIO2	0.37***	0.248***
BIO3	0.44***	0.370***
BIO4	0.21*	0.283***
BIO5	0.26***	0.135
BIO6	0.26***	0.106
BIO7	0.42***	0.237***
BIO8	0.25***	0.123
BIO9	0.25***	0.125
BIO10	0.26***	0.123
BIO11	0.26***	0.123
BIO12	0.25**	0.321***
BIO13	0.25***	0.345***
BIO14	0.31***	0.208***
BIO15	0.25***	0.278***
BIO16	0.22**	0.405***
BIO17	0.29***	0.245***
BIO18	0.31***	0.293***
BIO19	0.27***	0.202**

The significance was assessed using Bonferroni-corrected P -values: *** P < 0.001; ** P < 0.01; * P < 0.05.

et al. 2008; Slatyer et al. 2013). However, this is in contrast with other Amazonian studies that were more focused on a family or genus, which found that broad tolerance to topographical or edaphic gradients did not affect

Table 3. Results of Mann–Whitney *U* tests comparing the niche breadth measure along individual environmental variables of Amazonian and Andean oligarchic species as recorded in 98 0.1-ha plots in northwestern Bolivia. A measure of environmental heterogeneity for each variable and forest type is also presented. The bioclimatic codes follow the codes of Hijmans et al. (2005) (<http://www.worldclim.org/bioclim>).

Environmental variables (<i>k</i>)	Comparison of niche breadth (NB _{<i>k</i>})	Mann–Whitney tests	Environmental heterogeneity (CV _{<i>k</i>}) [†]		
			Amazonian	vs	Andean
Elevation	n.s.	9130	789 m	<	1974 m
Slope	n.s.	8859	0.57	>	0.33
Northness aspect	Amazonian > Andean	12987**	4.54	<	7.43
Eastness aspect	n.s.	12041	18.13	<	161.43
pH (H ₂ O)	n.s.	10032	0.21	>	0.15
pH (KCl)	n.s.	9672	0.247	<	0.253
Organic C	Andean > Amazonian	4689***	1.05	>	0.38
Total C	Andean > Amazonian	3800***	1.07	>	0.37
Total N	Andean > Amazonian	2575***	0.83	>	0.31
Total S	Andean > Amazonian	1081***	0.76	>	0.34
Extractable Al	n.s.	9732	0.76	>	0.30
Extractable Ca	n.s.	11888	1.18	<	1.59
Extractable Co	Amazonian > Andean	12651**	0.82	<	1.48
Extractable Cu	n.s.	8968	0.54	>	0.49
Extractable Fe	Amazonian > Andean	7640*	0.38	<	0.46
Extractable K	Andean > Amazonian	5397***	0.67	>	0.54
Extractable Mg	n.s.	11787	0.89	>	0.81
Extractable Mn	Amazonian > Andean	12607*	0.79	<	1.61
Extractable Na	Amazonian > Andean	14384***	0.33	<	1.26
Extractable Ni	n.s.	10497	0.88	>	0.54
Extractable P	n.s.	10461	0.72	<	1.00
Extractable Zn	n.s.	8463	1.29	>	0.74
BIO1	Amazonian > Andean	7783*	0.04	<	0.16
BIO2	Amazonian > Andean	15376***	0.02	<	0.10
BIO3	n.s.	11656	0.02	>	0.01
BIO4	n.s.	8728	0.087	<	0.089
BIO5	Andean > Amazonian	7171**	0.04	<	0.09
BIO6	n.s.	8314	0.05	<	0.42
BIO7	Amazonian > Andean	15905***	0.04	<	0.10
BIO8	n.s.	8230	0.04	<	0.16
BIO9	n.s.	8074	0.05	<	0.17
BIO10	n.s.	8230	0.04	<	0.15
BIO11	Andean > Amazonian	7213**	0.04	<	0.17
BIO12	Andean > Amazonian	4465***	0.03	<	0.18
BIO13	n.s.	8550	0.03	<	0.10
BIO14	Andean > Amazonian	5903***	0.07	<	0.48
BIO15	n.s.	8412	0.03	<	0.13
BIO16	Andean > Amazonian	5531***	0.03	<	0.12
BIO17	Andean > Amazonian	6017***	0.09	<	0.39
BIO18	n.s.	8253	0.15	<	0.21
BIO19	Andean > Amazonian	7679*	0.09	<	0.34

The significance was assessed using Bonferroni-corrected *P*-values: ****P* < 0.001; ***P* < 0.01; **P* < 0.05; n.s.: not significant. [†]All values are coefficients of variation except those for the elevation, which are ranges.

the local abundances of palms (Kristiansen et al. 2009) or understorey plants, such as Melastomataceae, Pteridophyta (Tuomisto et al. 2003) and *Psychotria* species (Kinupp & Magnusson 2005). That these latter studies found no support for the NBH may be explained by the fact that these typically understorey plants or low-stature trees tend to have a narrower ecological tolerance and stronger turnover compared to larger species, likely because of their

more limited dispersal abilities (Ruokolainen & Vormisto 2000; Duque et al. 2002; Chust et al. 2006; Davidar et al. 2008).

The finding that most species, even many oligarchic species, show total niche sizes <0.5 is in agreement with previous studies, which found that floristic differences were equally well explained for common and rare species through edaphic differences (Tuomisto et al. 2003;

Ruokolainen et al. 2007). Even if common species dominate the forest in some circumstances, they are not necessarily indifferent to environmental heterogeneity (Phillips et al. 2003; Kristiansen et al. 2012). In fact, different patterns can be recognized among oligarchic species, and most of them represent a mixture of narrow-niched dominant species (e.g. *Hirtella racemosa* and *Rinorea apiculata* in Amazonia or *Weinmannia microphylla* and *Schizocalyx obovatus* in the Andes) and very broad generalists (e.g. *Iriartea deltoidea* and *Pseudolmedia laevis* in Amazonia or *Myrsine coriacea* and *Alchornea glandulosa* in the Andes) occupying different habitats. This is congruent with previous studies, as several authors have reported that both types of species constitute the regional oligarchies (Pitman et al. 2001, 2013; Paoli et al. 2006; Macía 2008, 2011; Honorio Coronado et al. 2009).

The existence of abundant and widespread environmental specialists or narrow-niched species could be explained if the resource on which they are specialized is abundant and widespread in the study region. This pattern is known as the resource availability hypothesis (RAH; Gaston 1994; Gaston et al. 1997) and is fully compatible with the NBH. Remarkably, the narrow-niched oligarchic species seem to be more specific for the region, whereas the broad-niched oligarchic species found here are very often reported in the cited studies for northwestern Amazonia, among many other studies (e.g. Duque et al. 2002, 2009; Valencia et al. 2004; Toledo et al. 2012). For example, the most broad-niched species among the 1518 species studied here is the palm *I. deltoidea*, possibly the oligarchic species most consistently reported in different regions in northwestern Amazonia.

Therefore, broad-niched oligarchic species could constitute the common set of oligarchs between different Amazonian regions at a very large or continental scale, following the NBH (Pitman et al. 2001, 2013; Macía & Svenning 2005), whereas more specialized oligarchic species would be predominantly present at scales in the order of $\leq 10\,000\text{ km}^2$, following the RAH. The comparison of these two alternative hypotheses, and the study of the spatial scale at which they may apply most, deserve further attention. However, the fact that our broad-niched dominant species are also reported as dominant in other places is in agreement with a positive relationship between niche breadth and geographical range, a general ecological pattern (Slatyer et al. 2013). Hence, it is clear that niche size plays a significant role in the consistency of commonness patterns across scales, linking local abundance, landscape frequency and geographic range size, as hypothesized by Brown (1984). Unfortunately, such conclusions cannot be directly applied to the Andean rain forests, given the absence of previous works addressing oligarchy in this ecoregion.

The NBH considering particular environmental variables

The broader edaphic niches of oligarchic species and the significant correlations between dominance and niche breadth along all edaphic variables reinforce the idea that the tolerance to different soil conditions is an important driver of large-scale dominance, as suggested for Amazonian rain forests (Pitman et al. 2001), but can be applied to Andean rain forests as well. However, the results are not as conclusive for the climatic variables (included elevation) in the Andean forest, where the niche breadth of oligarchic species seems to be similar to that of the rest of the species. This could be explained by rare species showing relatively broad climatic niches inherited from the relatively climatic generalist taxa that are assumed to have colonized the Andes during its uplift (Ricklefs & Cox 1972; Frey et al. 2007). Such niche conservatism for the climatic niche dimensions could be more intense than for the edaphic dimensions, along which adaptations usually occur between close-related taxa (Wright 2002; Fine et al. 2005; Kembel & Hubbell 2006; Paoli et al. 2006; Wiens et al. 2010; Hardy et al. 2012). However, the causes underlying this lack of differences between common and rare species with respect to climatic factors in the Andes deserve further research.

Amazonian vs Andean rain forests

Amazonian rain forests showed stronger and much more generalist oligarchic species than Andean rain forests when the total niche size was considered. This could be explained by a larger environmental homogeneity in Amazonia overall, which is congruent with previous works that reported weak or absent oligarchic species under heterogeneous environmental conditions (Tuomisto et al. 2003; Pitman et al. 2008; Réjou-Méchain et al. 2008; Toledo et al. 2011, 2012). As expected, a similar pattern was found for several edaphic variables (Co, Fe, Mn and Na), for which Amazonian rain forests are more homogeneous and Amazonian oligarchic species present broader niches than Andean oligarchs. However, contrary to our expectation, we found that Amazonian soils are more heterogeneous than Andean soils with respect to those variables in relation to the organic matter content (organic C, total C, N, S and extractable K), with narrower niches of Amazonian oligarchic species along these variables. This is most likely caused by the relatively highly organic soils of many plots inventoried in the upper limit of the Amazonian rain forests, which also contain a different set of oligarchic species than those oligarchs present on lower plots with five to ten times less organic matter. The inclusion of such a source of edaphic and floristic heterogeneity within the Amazonian data set

is a potential caveat to extrapolate our results to other Amazonian rain forests of more homogeneous conditions (e.g. Pitman et al. 1999, 2001). Nevertheless, it holds that oligarchic species present relatively narrow niches on soil factors if measured along wide gradients, regardless of the forest type studied.

Concerning the climatic results, the Andean rain forests show a much more heterogeneous climate than the Amazonian rain forests, as expected for the larger elevation gradient covered. However, and contrary to expectation, Andean oligarchs do not show systematically narrower climatic niches than Amazonian oligarchic species. In fact, this only occurs for the annual mean temperature (BIO1) and two thermic variables for which the niche breadth is of rather difficult interpretation: mean diurnal range (BIO2) and temperature annual range (BIO7). For seven other climatic variables (BIO5, BIO11, BIO12, BIO14, BIO16, BIO17 and BIO19), of which five are related to precipitation, the Amazonian oligarchs show narrower niches than the Andean oligarchs, even when measured along a narrower range of conditions. This implies that Andean oligarchic species show a thermic (elevational) zonation along a very wide gradient, which is compatible with a lower sensitivity to climatic conditions than Amazonian oligarchs. As mentioned above, previous authors have proposed that montane floras could be largely composed of climatic generalists (Stevens 1992; Ghalambor et al. 2006; Frey et al. 2007; Laurance et al. 2011), but the mechanisms involved require further research.

Finally, given that common species constitute the assemblage of forest communities, represent a high number of individuals and are involved in large numbers of biotic interactions (Gaston & Fuller 2008; Gaston 2010), further studies should be focused on understanding the distribution patterns of these species in different forest types and analysing their responses to different environmental variables; the results could shed light on the management and conservation of tropical rain forests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Environmental conditions of Amazonian and Andean rain forests in the Madidi Region (north-western Bolivia).