**ORIGINAL
ARTICLE**

Oligarchic patterns in tropical forests: role of the spatial extent, environmental heterogeneity and diversity

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ABSTRACT

Aim Oligarchic patterns can vary from weak (i.e. little difference between rare and common species) to strong (i.e. a set of dominant species is immediately evident). Our aim was to understand the relationships between the strength of the oligarchic patterns, diversities (alpha, beta and gamma), and five potential causes (elevational variability, soil heterogeneity, elevation, soil conditions and geographical extent).

Location The Amazon–Andes transition in the Madidi region (Bolivia).

Methods We established 398 plots of 0.1 ha each, containing 121,183 individual woody plants belonging to 2390 species. Then we defined 500 sub-regions (= unique overlapping subsets of 50 plots from the pool of 398 plots) so they varied in extent from 220 to 17,700 km^2 within the study area. We employed two independent path analyses to relate environmental characteristics and geographical extent of sub-regions to (1) oligarchic strength and (2) alpha, beta and gamma diversities. We used generalized linear models to relate diversities to different measures of oligarchic strength.

Results Oligarchies at larger extents were weaker, a trend strongly driven by the pure effect of area and, secondarily, by environmental heterogeneity. Oligarchies at higher elevations were weaker than expected, and oligarchies in acidic and nutrients-poor soils were not stronger than those in less stressful soils. Trends in oligarchic strength were inversely correlated with those of gamma and beta diversity: weaker oligarchies were found in species-rich and heterogeneous communities.

Main conclusions Environmental heterogeneity and low landscape connectivity limit the strength of the oligarchic pattern. Although diversities (particularly beta diversity) and oligarchic strength are closely related, they are somewhat differently driven by external factors. In particular, oligarchic strength is more sensitive to spatial extent and less sensitive to environmental heterogeneity than beta diversity. Finally, the study of oligarchic patterns should consider *a priori* expectations based on species richness and turnover.

Keywords
commonness, elevational gradient, Madidi, rarity, soil heterogeneity, species spatial distribution, species turnover, tropical rain forest

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INTRODUCTION

How rare species can coexist and persist within communities has for a long time been a prominent research question in ecology, particularly regarding tropical forests (Wright, 2002). However, more attention to commonness patterns

and common species has increasingly been paid after Pitman *et al.* (1999, 2001) reported that Amazonian forests are predominantly composed by a limited set of abundant and frequent species ('oligarchs' or 'oligarchic species') that account for the majority of the individuals at any scale within relative large areas. Oligarchic patterns include two

dimensions of commonness (local abundances and frequencies) and apply only if a group of sites or samples is considered. Therefore, the study of oligarchic patterns differs from the study of species abundance distribution in taking into account the distribution of individuals among different samples, and from the study of species incidence distribution in taking into account the species' abundances. On the other hand, it differs from the study of beta diversity patterns in focusing on the individuals' identity instead of the species' identity: high species turnover is fully compatible with the presence of oligarchic patterns, and *vice versa* (Pitman *et al.*, 2001, 2013). Despite the theoretical and practical importance of this 'oligarchy hypothesis' (see Pitman *et al.*, 2013 for an extensive review), its links with environmental gradients and geographical scale are still not well understood. Specifically, recent studies indicate that oligarchic patterns can vary in strength along a continuum, from absent or very weak (i.e. impossible to define a set of oligarchic species) to strong oligarchic patterns (i.e. a set of dominant species is immediately evident), but the causes of such differences remain untested (Pitman *et al.*, 2013; Ter Steege *et al.*, 2013; Arellano *et al.*, 2014b).

Researchers employing data sets covering very substantial environmental heterogeneity (e.g., different precipitation, flooding regimes or geological substrates) are unlikely to find a strong oligarchic pattern (Tuomisto *et al.*, 2003; Pitman *et al.*, 2008; Réjou-Méchain *et al.*, 2008; Toledo *et al.*, 2011, 2012; but see Ter Steege *et al.*, 2013), supporting the idea of niche-based oligarchic patterns (Pitman *et al.*, 2013). *A priori*, elevation could be a major determinant of oligarchs' identity. The original oligarchy hypothesis was constrained to Amazonian forests below 500 m; at a given elevation, edaphic heterogeneity would define the intensity of the oligarchic pattern (Pitman *et al.*, 2001, 2013). To our knowledge, no study has examined whether regional-scale oligarchies are the result of regional-scale patches of relatively homogeneous environmental conditions, which we will test through the following hypotheses:

Hypothesis 1: Oligarchic species are common only within particular elevational ranges. *Prediction*: oligarchic patterns will be weaker in regions encompassing greater elevational variability.

Hypothesis 2: When similar elevations are considered, the edaphic heterogeneity determines the oligarchic strength, at any spatial extent. *Prediction*: oligarchic patterns will be stronger within relatively homogeneous soil conditions.

Apart from the effects of environmental heterogeneity, oligarchic strength seems to be greater within particularly stressful conditions, such as dry (Pennington *et al.*, 2009; Arellano *et al.*, 2014b), white-sand (Fine *et al.*, 2010) and swamp forests (Macía, 2011; Pitman *et al.*, 2014). Strong dominance patterns could be caused by fewer species successfully adapted to such specific conditions, stronger competition, more frequent disturbance, or because rare species are more prone to local extinction due to isolation from other patches of these relatively fragmented habitats

(Hubbell, 1979; Pennington *et al.*, 2009). Similar considerations could be made for forests at higher elevations, where temperature conditions are increasingly harsh and habitats show lower connectivity (Wiens, 2004; Kozak & Wiens, 2006; Graham & Fine, 2008). We will address these issues through two additional hypotheses:

Hypothesis 3: Low landscape connectivity and stressful thermal conditions increase the strength of the oligarchic patterns. *Prediction*: tropical montane forests at higher elevations will show stronger oligarchic patterns.

Hypothesis 4: Harsh soil conditions affect the strength of the oligarchic pattern. *Prediction*: nutrients-poor or highly acidic soils will show stronger oligarchic patterns than nutrient-rich and less stressful edaphic environments.

Previous rejections of the oligarchy hypothesis at geographical extents of $> 10,000$ km^2 (Tuomisto *et al.*, 2003; Réjou-Méchain *et al.*, 2008; Toledo *et al.*, 2011, 2012) could be also explained by spatially aggregated oligarchs as a result of dispersal limitation. This would cause the oligarchic pattern to be weaker at larger extents regardless of changes in environmental conditions. Previous findings suggest that spatial processes would occupy a secondary role in shaping oligarchicity in tropical forests. First, great overlap exists in the composition of oligarchies in different regions up to thousands of kilometres apart, as long as environmental conditions remain relatively similar (Pitman *et al.*, 2001; Macía & Svenning, 2005; Ter Steege *et al.*, 2013). Second, continental-scale differences within Amazonian forests can be relatively small and comparable to regional-scale variation in the composition of oligarchies associated with soil types (Honorio Coronado *et al.*, 2009). Finally, oligarchic trees are frequently tall species with strong dispersal abilities (Ruokolainen & Vormisto, 2000; Pitman *et al.*, 2001; Davidar *et al.*, 2008; Kristiansen *et al.*, 2009), and oligarchic shrubs or lianas may also show high dispersal potential. Here, we will test this idea directly:

Hypothesis 5: Dispersal-based processes unrelated to the environmental conditions affect oligarchic patterns. *Prediction*: oligarchic patterns at large spatial extents will be weaker than at small spatial extents.

On the other hand, the relationship between oligarchic patterns and other aspects of community structure has not been studied. Beta diversity (in a broad sense) was ephemerally related to oligarchic patterns through the 'uniformity hypothesis': the idea that floristic similarity among sites should be uniformly high (e.g. Tuomisto *et al.*, 2003; Toledo *et al.*, 2011). However, from a theoretical point of view, strong oligarchic patterns and high floristic heterogeneity are fully compatible: two samples of an oligarchic community could share only a tiny proportion of species, but these few shared species could represent most of the individuals (Pitman *et al.*, 2001). We will test for the relationship between beta diversity and oligarchic strength through the following hypothesis:

Hypothesis 6: Beta diversity is negatively correlated with the strength of the oligarchic pattern. *Prediction*: regions with more homogeneous composition will show stronger oligarchic patterns.

Species richness was considered in the interpretation of oligarchic patterns when presenting the hypothesis (e.g. Pitman *et al.*, 2001), but little developed elsewhere (Arellano *et al.*, 2014a). When comparing tropical and temperate forests qualitatively, Pitman *et al.* (2001) wrote:

> The difference [between both forests] is that rather than a few common species, tropical forests have dozens. And because tropical forests are so diverse, common trees there are not as abundant in absolute terms or as immediately obvious as common trees in temperate forests.

We will test this idea with the following hypothesis:

> Hypothesis 7: For a fixed number of individuals, the number of species correlates with the average species abundance (including the average abundance of oligarchic species). *Predictions*: oligarchic patterns will be weaker in regions with many species at local and/or regional scale.

Finally, to further understand the commonalities between oligarchic strength and the three diversities (alpha, beta, gamma), we will evaluate not only the statistical connection among them, but also the potential underlying external causes. To do so, we will evaluate the relative importance of all external predictors (elevational variability, edaphic heterogeneity, elevation, soil conditions and spatial extent) on the patterns of alpha, beta and gamma diversities as well.

METHODS

Study region and floristic data

We established 398 temporary plots (20 m × 50 m = 0.1 ha) across the Madidi region in the eastern slopes of the Bolivian Andes (latitudes −12.43° to −15.72°, longitudes −69.48° to −66.66°; www.mobot.org/madidi). Plots were located in multiple types of mature forests from 250 to c. 4000 m.a.s.l., avoiding large gaps or recent human disturbances. The mean distance between a plot and its nearest neighbour was 584 m (SD = 942 m). We inventoried all woody plants within the plots with a diameter at 130 cm from the rooting point ≥ 2.5 cm. We collected 15,909 voucher specimens and assigned them to 2390 species or standardized morphospecies. Individuals that could not be assigned to a species or morphospecies (1.67%) were excluded from the analyses; the final data set comprised 121,183 individuals. All data are available for consultation in Tropicos® (http://tropicos.org/PlotSearch.aspx?projectid=20), a data portal maintained by the Missouri Botanical Garden. Data availability and terms of use are specified in the *Ethical Code, Data Sharing and Publication Policy* of the Madidi Project, (http://www.mobot.org/MOBOT/Research/madidi/pdf/EthicalCode.pdf).

Sub-regions selection

Oligarchicity is an emergent property of a set of local communities, thus our unit of study was sub-regions within our overall study area, and not individual plots. We defined 'sub-region' as a unique subset of 50 plots from the pool of 398 plots. Among all the possible combinations of 50 plots, we selected 500 combinations so that different extents were represented in similar frequencies. The exact algorithm to construct sub-regions, along with the R code needed to implement it, can be consulted in the Supplementary Material of Arellano *et al.* (2015a). In the resulting sub-regions, the area of the minimum convex polygon containing the 50 plots varied from relatively local (220 km^2) to regional scales (17,700 km^2). The mean overlap between two sub-regions was 6.7 plots (13.42% of the plots), 99.75% of the pairs of sub-regions shared fewer than 25 of their plots, and 81.67% fewer than ten of their plots.

Relationships between external factors and community structure

We used two independent partial least squares path models (PLS-PM) to measure the strength of the relationships between the set of explanatory factors (elevational variability, edaphic heterogeneity, elevation, soil conditions and spatial extent) and different aspects of community structure: (1) oligarchic strength (Model A in Fig. 1); and (2) alpha, beta and gamma diversities (Model B in Fig. 1). PLS-PM allow the study of complex networks of relationships where variables can be modelled as response and predictor variables simultaneously. For example, soil conditions perform as predictors of oligarchic strength and simultaneously as response variables influenced by elevation. In addition, the PLS-PM allow us to infer the importance of abstract or conceptual variables that are not measured directly (latent variables). These latent variables summarize the joint effect of a set of measured variables (indicators) that function as proxies for the latent variables of interest (Grace, 2006). For example, 'maximum height' and 'diameter at 130 cm' would be two indicators that could be blended during PLS-PM to create the latent variable 'tree size'. The relationships between latent variables and ecological hypotheses of interest, and the relationships between blocks of indicators and their corresponding latent variables, are both fitted simultaneously when performing PLS-PM. The method is detailed in Grace (2006) and Sánchez (2013). The indicators of each of the latent variables were obtained as follows:

Indicators of elevational variability

The elevational variability was characterized by the standard deviation, and absolute and interquartile ranges of the elevation of the plots of a sub-region.

Indicators of soil heterogeneity

The soil heterogeneity was characterized by the standard deviation, absolute and interquartile range of each of the measured soil variables (pH, C, N, Ca, Mg, K, sand, silt and clay) for the plots of a sub-region. Details for the field soil

Model A

Model B

Figure 1 Fitted PLS-PM models representing the cause-effect relationships hypothesized to occur within our study region in the Amazon-Andes transition. Model A: determinants of oligarchic strength ('O. S.'); arrows pointing directly to the oligarchic strength (H1–H5) represent our research hypotheses 1–5 as posed in the Introduction. Model B: determinants of alpha, beta and gamma diversities. In both models 'Δ Elevation' and 'Δ Soil' refer to the latent variables 'elevational variability' and 'edaphic heterogeneity', respectively, and 'Extent' refers to the geographical extent. The width of each arrow is directly proportional to the absolute value of the standardized effect size, a measure of the strength of the relationship. Black arrows represent positive relationships, white arrows negative.
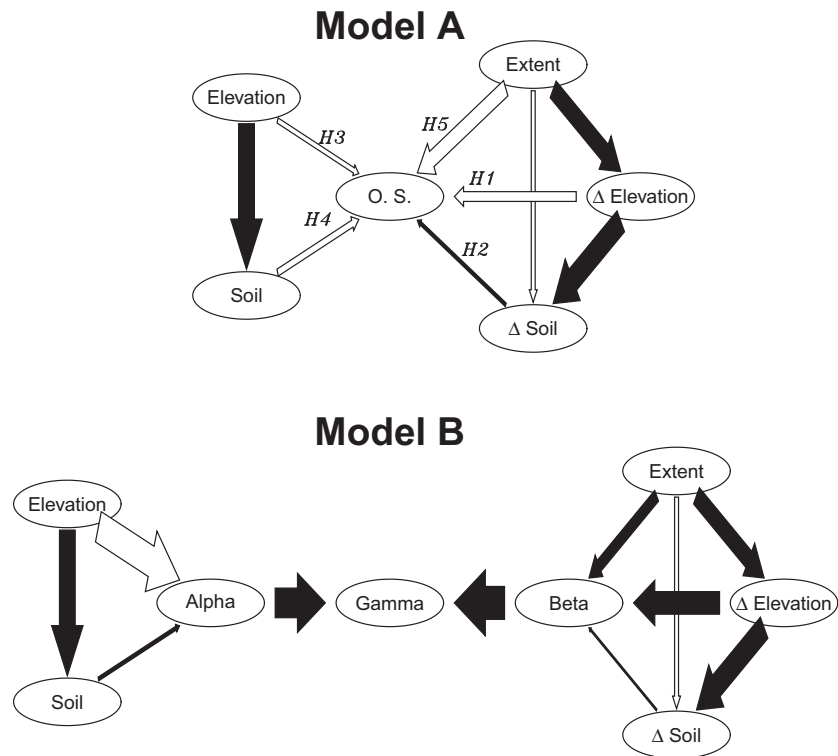
sampling and laboratory analyses are included in Appendix S1 in Supporting Information.

Indicators of elevation

The elevation was characterized by the mean and median of the elevation of the plots of a sub-region.

Indicators of soil

The soil conditions were characterized as the mean and median, for each measured soil variable, of the plots of a sub-region.

Indicators of spatial extent

The spatial extent was characterized by the mean pairwise inter-plot distance, median pairwise inter-plot distance, maximum pairwise inter-plot distance, and area of the minimum convex polygon containing the plots of a sub-region.

Indicators of alpha, beta and gamma diversities

Alpha diversity was quantified by the mean and median species richness of the plots of a sub-region, gamma diversity as total species richness of a sub-region, and beta diversity as true beta diversity (beta = gamma/mean alpha; Tuomisto, 2010).

Indicators of the strength of the oligarchic pattern

This was a pure latent response variable within our most important model (Model A; Fig. 1). It was characterized by

three indicators: (1) The h_h index, which measures the proportion of species that are 'common', meaning simultaneously abundant at the local level and widespread across a given area. To calculate h_h, we first characterized each species of a sub-region by its h two-dimensional commonness index: a species with $h = 5\%$ has at least 5% of the individuals in at least 5% of the samples (Arellano *et al.*, 2014b). Then, we ranked species by their h indexes and secondly by their total abundance. Each species i was assigned a relative rank (= $rank_i$/number of species) and a relative h (= h_i/maximum h). The number of common species was the i for which the relative h_i equals the relative $rank_i$, and h_h the proportion of common species so-defined. As larger h_h values (proportionally larger sets of common species) indicate weaker oligarchic patterns, we employed $1 - h_h$ instead of h_h to measure strength of the oligarchic pattern instead of its weakness. (2) Spearman's rank correlation rho between mean abundance and frequency of species. Given that the oligarchy hypothesis predicts strong correlations between both aspects (Pitman *et al.*, 2013), this statistic can be considered a proxy for the oligarchic strength within a given sub-region. (3) The F index of co-dominance (Leigh *et al.*, 1993), by calculating the probability that two individuals randomly selected from two different samples will belong to the same species, which equals:

$$F = \sum_{i=1}^{s} \frac{x_{ij} x_{ik}}{N_j N_k}$$

where x_{ij} is the abundance of the species i in the plot j, x_{ik} is the abundance of the species i in the plot k, N_j is the total number of individuals in the plot j, N_k is the total number

of individuals in the plot k, and S is the total number of species. The F index equals unity if all the individuals in the two plots belong to the same species, and equals zero if the plots do not share any species, but otherwise it can vary fully independently of the floristic dissimilarity between pairs of plots (Chao *et al.*, 2005; Jurasinski *et al.*, 2009; Tuomisto, 2010). The value of the indicator at a given sub-region was calculated as the mean of all pairwise comparisons among the 50 plots of the sub-region.

The indicators are expected to be highly redundant measures of the same variable, but in some cases do not correlate well with the latent variable they are supposed to measure. We excluded all indicators with loadings < 0.70 from both models. These were: all indicators related to sand, clay and Mg contents; mean and median K; mean Ca; standard deviations, ranges and interquartile ranges of silt, pH and C; and interquartile range of K (28 out of 61 indicators). Finally, the assumption of PLS-PM that relationships between variables are linear was considered too stringent; consequently, all indicators were substituted by their ranks in the analyses.

Each of the causal relationships evaluated received an observed coefficient when fitting the PLS-PM models, which is the standard coefficient of a partial linear regression. To control for the bias caused by the repeated inclusion of some plots into different sub-regions, each observed coefficient was compared against 999 expected coefficients calculated through 999 permutations of the blocks of indicators and keeping the allocation of plots to sub-regions constant. The unbiased importance of each predictor in each model was then characterized by its standard effect size (SES), calculated as:

$$\text{SES} = \frac{\text{observed coefficient} - \text{mean (null coefficients)}}{\text{sd (null coefficients)}}.$$

We will refer to SES of the paths in Models A and B as SES_A and SES_B respectively.

Relationships between different aspects of community structure (hypotheses 6 and 7)

We tested for dependence between diversities (alpha, beta and gamma), and oligarchic strength using generalized linear models (GLM) to fit indicators of oligarchic strength as functions of the indicators of the different diversities independently. We fitted three models for each pairwise comparison: (1) with the intercept only; (2) with the intercept and the linear term; and (3) with the intercept, the linear term and the quadratic term. In each case, we compared the three models with the corrected Akaike information criterion (AICc), keeping the simplest model differing less than two AICc units from the lowest AICc value of the three models. These GLM models test for statistical dependence between variables: we did not assume functional relationship between variables and the results were not interpreted as if reflecting causality.

All calculations and analyses were performed with R 3.1.1. (R Core Team, 2014). The PLS-PM was done using *plspm* package (Sánchez, 2013; Sánchez *et al.*, 2013). The R code

employed to calculate the h_h index was taken from Appendix 1 of Arellano *et al.* (2014b).

RESULTS

Relationships among external factors

The results of both PLS-PM models reflected the expected relationships between environmental and geographical variables in the Amazon–Andes gradient overall (Fig. 1). Higher elevations were associated with more organic soils ($\text{SES}_A = 16.18$ and $\text{SES}_B = 15.49$) characterized by higher levels of N and C, lower levels of pH, silt and Ca (Table 1). Larger sub-regions tended to encompass substantially greater elevational variability ($\text{SES}_A = 10.46$, $\text{SES}_B = 10.68$), and this variability increased the edaphic heterogeneity (i.e. variation in C, N and K; Table 1) ($\text{SES}_A = 13.47$, $\text{SES}_B = 13.26$). However, larger sub-regions showed slightly more homogeneous soils than expected for the elevational variability included ($\text{SES}_A = -3.76$, $\text{SES}_B = -3.72$).

Relationships between external factors and oligarchic strength (hypotheses 1–5)

We found partial support for our expectations regarding drivers of oligarchic strength (Model A; Fig. 1). Elevational heterogeneity *per se* decreased oligarchic strength ($\text{SES}_A = -5.09$), as expected by hypothesis 1. However, the edaphic heterogeneity effect on the oligarchic strength was negligible and positive ($\text{SES}_A = 1.94$), indicating no support for hypothesis 2. We also found no support for the hypotheses predicting stronger oligarchic patterns in relatively hostile environments (hypotheses 3 and 4): forests at higher elevations showed weaker oligarchic patterns ($\text{SES}_A = -2.96$), and oligarchies were weaker in the more acidic soils with lower contents of Ca ($\text{SES}_A = -4.00$). Finally, we found weaker oligarchic patterns at larger spatial extents (Fig. 2a–c), a trend strongly driven by the pure effect of the spatial extent ($\text{SES}_A = -9.35$) in clear support for hypothesis 5.

Relationships between external factors and alpha, beta and gamma diversities

The results of our PLS-PM model including the three diversities (Model B; Fig. 1) reflected lower alpha diversity at higher elevations ($\text{SES}_B = -17.85$). Within a given elevation, more organic soils tended to contain more species, although this effect was substantially weaker than that of elevation and did not overcome it ($\text{SES}_B = 2.02$). We found also that larger sub-regions tended to encompass more compositional units (higher beta diversity) (Fig. 2e). The effect of spatial extent on beta diversity was largely mediated by the effect of the elevational variability ($\text{SES}_B = 12.25$), although extent *per se* also influenced beta diversity ($\text{SES}_B = 7.18$). These results indicated a prevalent role of niche-based processes determining the number of compositional units in the study area,

Table 1 Mean correlations (loadings) between latent variables (conceptual, constructed, imaginary variables) and their indicators (measured variables that act as proxies for the latent variables). Only indicators with absolute loading values > 0.70 were retained in each model. 'Model A' includes oligarchic strength, but not diversities. 'Model B' includes diversities, but not oligarchic strength. Both are represented in Fig. 1. 'MCP' refers to the minimum convex polygon encompassing the 50 plots of each sub-region.

Latent variable	Indicator	Model A	Model B
Extent	Inter-plot distance (mean)	0.98	0.98
	Area of the MCP	0.97	0.97
	Inter-plot distance (median)	0.96	0.96
	Inter-plot distance (maximum)	0.95	0.95
Elevational variability	Elevation (standard deviation)	0.96	0.96
	Elevation (range)	0.87	0.87
	Elevation (interquartile range)	0.79	0.79
Soil heterogeneity	C (standard deviation)	0.95	0.95
	N (standard deviation)	0.93	0.93
	K (standard deviation)	0.86	0.86
	C (interquartile range)	0.86	0.86
	N (interquartile range)	0.85	0.85
	C (range)	0.84	0.84
	N (range)	0.81	0.81
	K (range)	0.73	0.73
Soil	N (mean)	0.92	0.93
	C (mean)	0.92	0.93
	C (median)	0.89	0.91
	Silt (mean)	−0.86	−0.87
	pH (median)	−0.87	−0.85
	N (median)	0.83	0.86
	pH (mean)	−0.84	−0.81
	Silt (median)	−0.81	−0.82
	Ca (median)	−0.78	−0.74
Elevation	Elevation (mean)	0.99	0.99
	Elevation (median)	0.99	0.99
Alpha diversity	Number of species (mean)	–	0.99
	Number of species (median)	–	0.99
Beta diversity	Number of compositional units	–	1
Gamma diversity	Number of species	–	1
Oligarchic strength	F index	0.86	–
	Spearman's rho	0.84	–
	$1 - h_h$ index	0.75	–

followed in importance by dispersal processes. Remarkably, edaphic heterogeneity added almost nothing to the effect of spatial extent and elevational variability on beta diversity ($SES_B = 1.08$), indicating a negligible importance of soils in determining species turnover above the effect of the other factors. Finally, both alpha and beta diversities greatly affected the gamma diversity ($SES_B = 15.89$ and $SES_B = 16.88$ respectively) as expected, given the mathematical relationships between them. Finally, alpha diversity was independent of the extent of the sub-region (Fig. 2d) whereas the gamma diversity of sub-regions of different extent mimicked the species accumulation curve for the whole study area (Fig. 2f).

Relationships among different aspects of community structure (hypotheses 6 and 7)

The results of the different GLM analyses showed that the different indicators of oligarchic strength are not independent of community-level trends of alpha, beta and gamma diversity. However, such relationships were neither linear nor monotonic in half of the cases (Fig. 3).

Beta diversity was clearly and negatively correlated with the strength of the oligarchic pattern. In particular, the number of compositional units was tightly and linearly correlated with the Spearman's rho of the abundance versus frequency relationship of the species within each sub-region (Fig. 3g). In fact, the fitted GLM suggests that abundances and frequencies of species will be almost perfectly correlated if only one compositional unit is considered (predicted rho > 0.997). The F index was negatively correlated with beta diversity, although sub-regions with ≥ 18 compositional units did not show differences in their F values (Fig. 3k). The indicator of oligarchic strength based on the h_h index showed low resolution and high variability among sub-regions, but the same overall trend (Fig. 3c).

Gamma diversity of sub-regions showed very similar relationships with the three indicators of oligarchic strength than those of beta diversity. Overall, oligarchic patterns were weaker in sub-regions with more species than those in sub-regions with fewer species, regardless of the indicator considered (Fig. 3d,h,l). In contrast, alpha diversity displayed a different trend. Specifically, both species-poor (< 45 species/plot) and species-rich (> 65 species/plot) sub-regions showed relatively strong oligarchic patterns, whereas sub-regions with intermediate alpha diversity (c. 50–60 species/plot) showed the weakest oligarchic patterns observed (Fig. 3a,e,i).

DISCUSSION

The results of Model B and the changes of diversities with extent (Fig. 2d–f) reflected well-known relationships between external factors and diversity variables in the Amazon–Andes gradient. Regarding oligarchic strength, it is limited by environmental heterogeneity (as expected), but also very notably by spatial extent and landscape connectivity (Model A). Although diversities (particularly beta diversity) and oligarchic strength are closely related, they respond somewhat differently to external factors. These relationships between external factors and oligarchic strength, as well as differences and similarities between oligarchic strength and the three diversities, are discussed in more detail below.

Oligarchic strength within regions of different geographical extents

Larger sub-regions showed weaker oligarchic patterns, as predicted, a trend caused by the increase in elevational variability, but more importantly by geographical extent *per se*. Thus, dispersal limitation alone could cause important
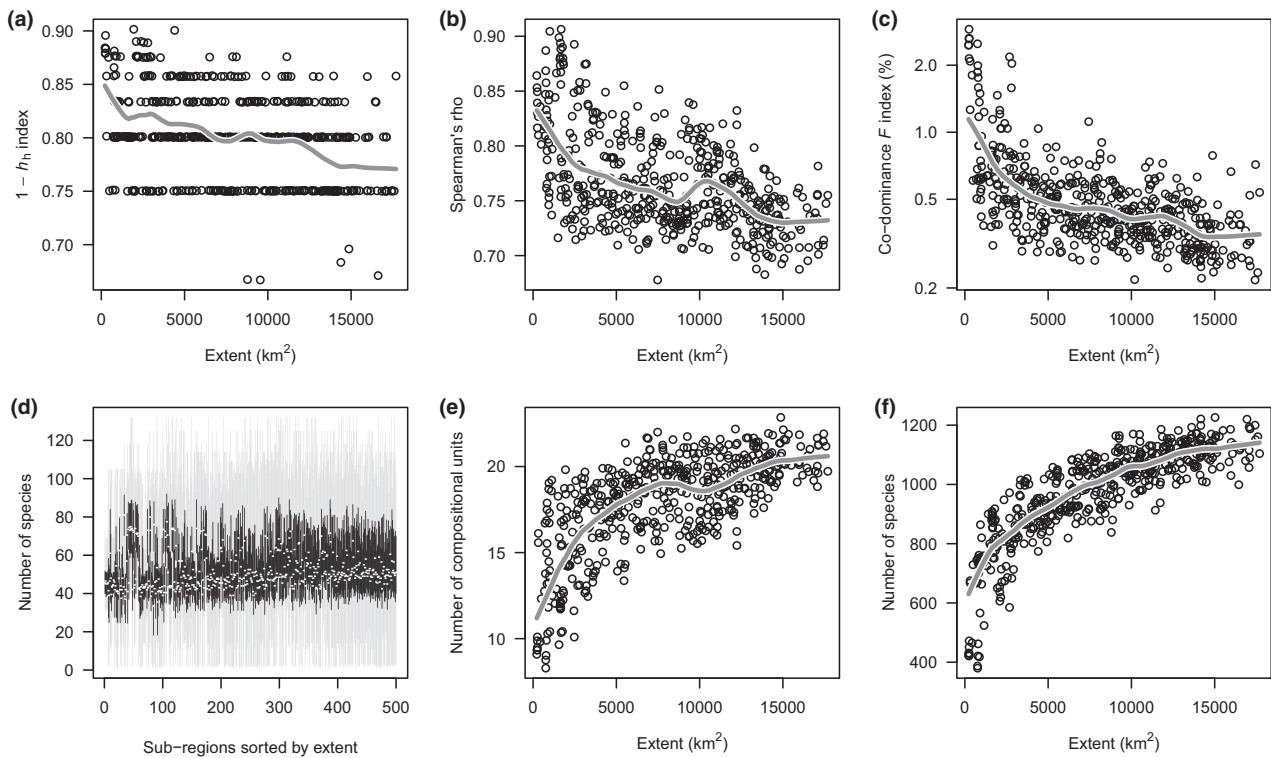
Figure 2 Changes across geographical extents in oligarchic and diversity-related community structure features. The upper three pannels show changes in the strength of the oligarchic pattern, measured as $1-h_h$ index (a), Spearman's rho (b) and the co-dominance F index (c). The three pannels in the bottom row show changes in the three measurements of diversity: alpha diversity (d), beta diversity (e) and gamma diversity (f). Lowess lines are fitted to all variables except in panel (d), where the alpha diversity of the sub-regions is represented by 500 very narrow boxplots (thin grey lines cover the range of alpha diversity values within each sub-region, black lines encompass the interquartile range, and the white points represent the median values).

spatial aggregation of oligarchic species in spite of their hypothesized strong dispersal abilities (Ruokolainen & Vormisto, 2000; Pitman *et al.*, 2001; Davidar *et al.*, 2008; Kristiansen *et al.*, 2009; Arellano *et al.*, 2015b). This is in agreement with findings of Ter Steege *et al.* (2013), who found that even the most widespread hyper-dominant species in the Amazonia tended to be common only within particular regions, regardless of the environmental changes involved. On the other hand, our results indicate that there is a significant turnover of the oligarchic species caused by environmental changes, supporting the idea that environmental homogeneity is required by oligarchic species to be distributed over very large expanses (Pitman *et al.*, 2001; Macía & Svenning, 2005; Honorio Coronado *et al.*, 2009).

Interestingly, the strength of the oligarchic pattern seems to be more sensitive to the spatial extent *per se* and less sensitive to environmental changes than beta diversity (Model A versus Model B). This supports the idea that common species shaping oligarchic patterns have broader niches than uncommon species that form the bulk of the community and shape beta diversity patterns (Brown, 1984; Arellano *et al.*, 2014a). Although both phenomena are related, oligarchic strength and beta diversity are theoretically two different things and thus it is not surprising that they respond

differently to external factors such as environmental heterogeneity and dispersal limitation.

Oligarchic strength versus elevation

The oligarchic pattern was weaker at higher elevations, providing no support for the idea of stronger oligarchies in more extreme edaphic conditions or harsh environments. This trend could be explained by an important effect of local isolation on the strength of oligarchic patterns, mediated by stronger dispersal limitation of the species at higher elevations (Wiens, 2004; Kozak & Wiens, 2006; Graham & Fine, 2008). This is congruent with the results discussed above (i.e., oligarchies more sensitive to space *per se* than to environment) and previous studies on Andean forests, which reported that local abundances of widespread species differ greatly from one place to another (Arellano & Macía, 2014). Furthermore, oligarchic patterns at the 100 km scale in upper montane forests in Madidi are weaker than those reported for lowland Amazonian forests at distances of 1400 km (Pitman *et al.*, 2001) and 1900 km (Macía & Svenning, 2005).

Alternatively, if we assume oligarchs to be late-successional species that are successfully adapted to their environmental conditions, long-term stability of a given community would be
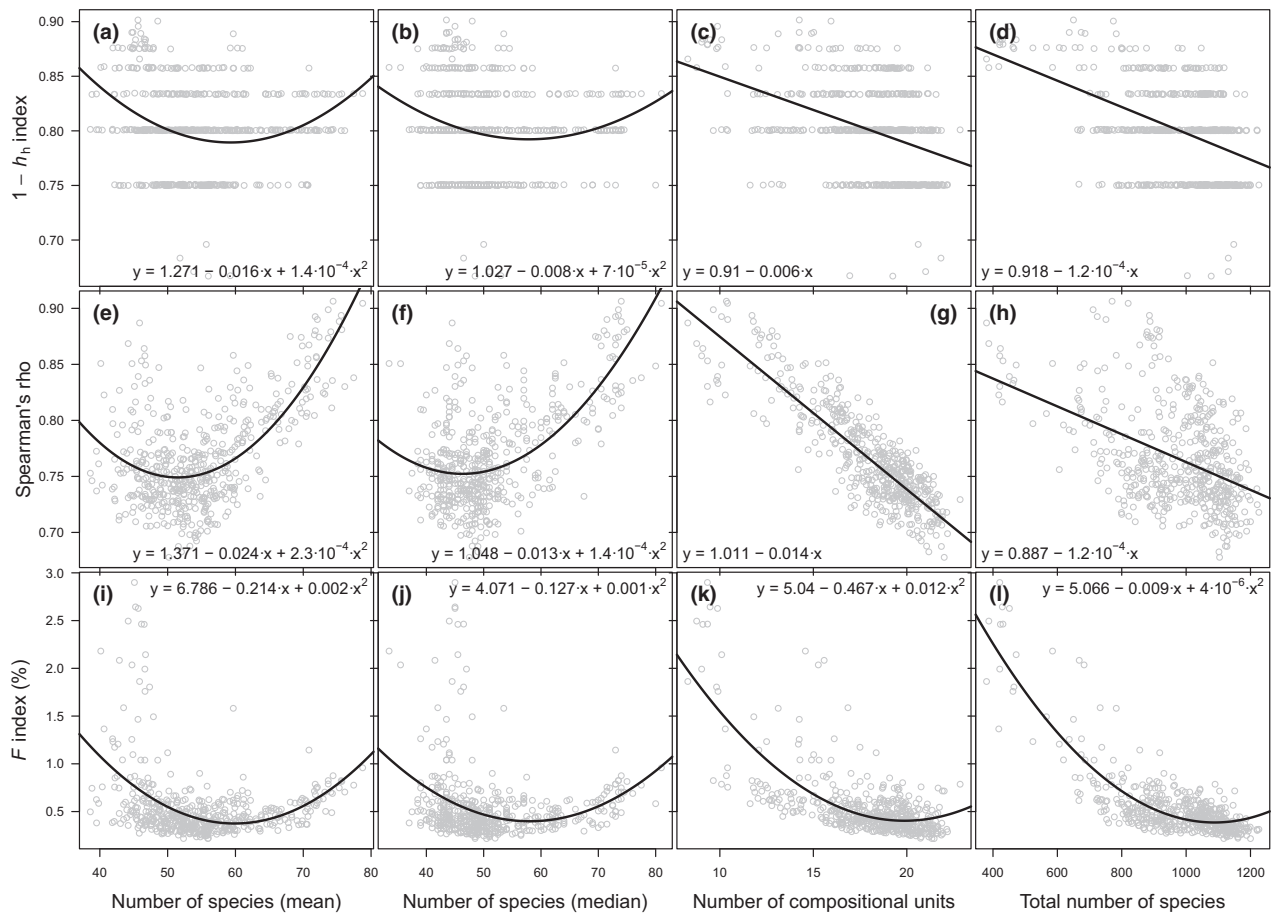
Figure 3 Results of the generalized linear models relating different indicators of alpha, beta and gamma diversities (x axes) with the three indicators of oligarchic strength (y axes). In each panel, each grey point represents a sub-region ($N = 500$). The equations indicate the shape of the relationships by expressing y as a function of x. The x variable in panels (a), (e) and (i) is the mean number of species per plot in a sub-region; in panels (b), (f) and (j) is the median number of species per plot in a sub-region; in panels (c), (g) and (k) is the true beta diversity; and in panels (d), (h) and (l) is the gamma diversity. The y variable in panels (a), (b), (c) and (d) is $1 - h_h$ index, a measure of oligarchic strength based on the proportion of common species; in panels (e), (f), (g) and (h) it is the Spearman's rho of the correlation between local abundance and frequency of the species within a sub-region; in panels (i), (j), (k) and (l) it is the F index of co-dominance.

needed to create strong oligarchic patterns. Possibly, Andean forests lack such long-term stability due to steep terrain and frequent landslides. If such disturbances create opportunities for more pioneer or opportunistic species, the deterministic oligarchic pattern would be blurred or weakened by an increasing importance of stochasticity at greater elevations.

It is particularly intriguing that sub-regions at higher elevations show weaker oligarchic patterns given the strong effect of elevation on alpha diversity and the observed trend of species-poor sub-regions to show stronger oligarchic patterns. From that point of view, one should expect to find strong oligarchies at higher elevations. It is possible that oligarchic strength, being an emergent property of a group of samples, is affected predominantly by processes happening at the landscape scale (such as meta-population dynamics or legacies of ancient human occupation) than of local processes at the plot scale. This could explain also the non-monotonic relationship between alpha diversity and oli-

garchic strength, while beta diversity, gamma diversity and oligarchic strength are all closely and monotonically related.

Oligarchic strength versus alpha, beta and gamma diversities

The strength of the oligarchic pattern and the overall floristic heterogeneity go hand in hand: regions with greater floristic turnover show weaker oligarchic patterns, as expected by our hypothesis 6. Although this is not a particularly surprising result, it indicates that some previous perspectives on the study of oligarchicity could require further re-thinking. Although they could be independent in theory and regarding underlying causes (as discussed above), our results emphasize the dependence of oligarchic patterns on uniformity/heterogeneity patterns of the whole community. Such dependence is of critical importance from both theoretical and practical perspectives for at least two reasons. First, it indicates that strong

biotic interactions may determine the importance and identity of oligarchic species (Legendre *et al.*, 2005; Tuomisto & Ruokolainen, 2006), or an important effect of oligarchic species in the composition of the non-oligarchic accompanying species (Gaston, 2010). Second, it indicates that oligarchic species, although being the subset of species most likely to be shared among different regions, tend to be associated with particular floristic compositions and hence could serve as indicators of vegetation types at least at regional scales. Therefore, if common species (easy to sample) change along a given region, we can expect uncommon species (difficult to sample) to change as well. Conversely, if common species do not change, we should expect uncommon species not to change, even if we cannot sample them properly and they are absent from our inventories. The validity of this hypothesis should be directly measured based on intensive and detailed floristic inventories, but its significance for the estimation of uncommon taxa distributions can hardly be overstated.

Regarding the results for alpha and gamma diversities, these provide mixed support for our hypothesis 7. On the one hand, the regional number of species co-varies with the strength of the oligarchic pattern, perhaps through changes in the average abundances of species. On the other hand, local species diversity does not correlate negatively with oligarchic strength along the whole evaluated gradient of diversity. Thus, a simple cause-effect relationship between species richness and species dominance seems implausible in spite of previous suggestions (Bazzaz, 1975; Huston, 1979; Pitman *et al.*, 2001; Dornelas *et al.*, 2011; Arellano *et al.*, 2014b), at least when a wide array of habitats is considered. In particular, many sub-regions with mean and median alpha diversity of > 70 species/plot showed relatively strong oligarchic patterns, especially when compared with the sub-regions of intermediate local richness. These sub-regions tended to include many Amazonian plots below 800 m in elevation, indicating that Amazonian forests show stronger oligarchic patterns than expected given their high alpha diversity. It is possible that the vast expanses of Amazonian forest near the study region function as a continuous source of propagules of common species, while such a mass-effect is negligible in the case of forests at higher elevations in the studied area. Alternatively, such mass-effect could provide many rare species from the Amazonian forests, so our results would need to be interpreted as Amazonian forests having higher alpha diversity than the expected for their oligarchic strength. In any case, oligarchic or alpha diversity patterns of Amazonian forests seem to respond to somewhat different processes than those determining the community structure of forests at higher elevations.

Diversity patterns as null expectations for oligarchic patterns

Any study on dominance/oligarchic patterns (and probably those of rarity) should explicitly consider diversity encompassed at alpha and gamma levels, as well as the species turn-

over included (as done by Pitman *et al.*, 2013). Different regions can have half of their respective individuals belonging to a single species, but the significance of this phenomenon would differ depending on the number of species contained. Also, different regions may share a limited suite of common species, but this is not the same if they share *only* those species, as when they are floristically alike overall. While some nominally oligarchic patterns are expected under the assumption that common taxa follow the same rules as the rest of the taxa (e.g neutral dynamics *sensu* Hubbell, 2001), others represent intriguing deviations from the effects of general forces shaping distributional patterns at different scales. For example, two random Amazonian plots in any region of western Amazonia, with floristic compositions drawn from very different pools of species, are likely to contain >10% of the individuals belonging to the palm *Iriartea deltoidea*. Such dominance deviates from the expectations of other theories that have obtained a great amount of empirical support (Hubbell, 2001; Pitman *et al.*, 2001), and that is what makes this species and other oligarchs particularly interesting taxa.

CONCLUSIONS

Oligarchic strength appears to be closely coupled with general trends of regional species richness and turnover, although responding differently to external factors. As the interesting patterns pertaining to oligarchies reside essentially in how they deviate from baseline expectations, such baseline expectations should be included in the study of oligarchic patterns. Finally, how to quantify different aspects of species-level and community-level oligarchic properties, and how to develop more precise predictions, are still important unanswered questions in the development of a powerful oligarchicity theory.

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SUPPORTING INFORMATION

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

Appendix S1 Soil sampling and analyses.

BIOSKETCH

G. Arellano is a community ecologist focused on the study of commonness/rarity patterns, community assembly and beta diversity determinants. He is part of the Madidi Project, a long-term study in the Bolivian Andes aiming to document the flora of the Madidi region, study the structure and dynamics of plant communities and generate infrastructure and capacity that advances the careers of Bolivian students and researchers (www.mobot.org/madidi/).

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