Commonness patterns and the size of the species pool along a tropical elevational gradient: insights using a new quantitative tool

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The goal of this study was a quantitative assessment of two-dimensional commonness in the lowland, dry, and montane tropical forests of the Madidi region (Bolivia). This region spans a large elevational and environmental gradient, with great diversity differences among sites. We aimed to correlate commonness patterns at different scales with elevation and with the size of the species pool. We also developed 1) a measure of ecological commonness and 2) a criterion to separate common from uncommon species; both based on the *h* index of academic productivity. With this approach, we calculated the 1) mean commonness of all species of the community; 2) proportion of common species of the community; and 3) mean commonness of the common species. The results showed that the commonness patterns in the Madidi region are strongly linked to the size of the species pool, independently of the environmental heterogeneity involved and the type of forest and spatial scale considered. Although these factors do not affect the general quality of the community, they do influence differences in commonness among species. Overall, we identified strong support for the oligarchy hypothesis, regardless of the strength of the pattern, and conclude that a quantitative approach to commonness could lead to great insights into community structure.

Variations in species commonness and in the number of species across regions are central subjects of community ecology. Although the term 'commonness' has different uses, here it refers only to a two-dimensional property of species that combines both local abundance and spatial distribution (Davidar et al. 2008, Kristiansen et al. 2009, Pitman et al. 2013); i.e. common species are those with high local abundance and broad spatial distribution, and uncommon species are those with low local abundance or narrow spatial distribution (Fig. 1). Within this context, little is known about commonness patterns in tropical forests and the causes for the observed differences between regions or along environmental gradients (Pitman et al. 2001, 2013, Macía and Svenning 2005).

Knowledge about common species is central to the understanding of ecosystems. Although common species are only a limited subset of the community, they account for the majority of individuals, biomass, and energy flows (Vázquez and Gaston 2004, Gaston 2010). Moreover, common species determine the spatial patterns of species distribution and biodiversity gradients even above that expected for their abundance (Lennon et al. 2003, Vázquez and Gaston 2004, Sizling et al. 2009, Pérez-Quesada and Brazeiro 2013). The two-dimensional approach to commonness is of great

practical importance because it could shed light on the mapping of vast unvisited areas and large-scale planning of ecosystems management (Pitman et al. 2001, 2013, Gaston and Fuller 2008).

The delimitation and characterization of common species have received much attention in the context of the oligarchy hypothesis, which suggests that Amazonian forests are dominated by a set of common species (i.e. abundant and frequent species) (Pitman et al. 2001). This pattern is assumed to result from the ecological superiority of those dominant species, which seem to be qualitatively different species from the rest, and form a limited and definable set. Even though the hypothesis was proposed to describe terra firme Amazonian forests, many authors have found the same situation in other tropical communities in the Neotropics (Brewer and Webb 2002, Bridgewater et al. 2004, Svenning et al. 2004, Macía and Svenning 2005, Macía 2008, 2011, Norden et al. 2009, Williams et al. 2010), Asian Paleotropics (Paoli et al. 2006, Keppel et al. 2011), and African Paleotropics (Eilu et al. 2004, Jabot and Chave 2011). Pitman et al. (2001, 2013) predicted the pattern to be stronger at the local and intermediate scales and within relatively homogeneous habitats, but why it is such a generalized observation in many types of forests remains largely unclear.

With respect to the relationship between species commonness and the size of the species pool, many groups have reported that species richness and species dominance are negatively correlated (Bazzaz 1975, Huston 1979, Armesto and Pickett 1985, Hubbell 2001, He and Legendre 2002, Hurlbert 2004, Dornelas et al. 2011). Because the same number of individuals is allocated across more species, there will be fewer individuals per species. Therefore, we expect the size of the species pool to relate negatively with species average abundance and, consequently, with its average commonness. Pitman et al. (2001) followed the same reasoning to argue that the quantitative differences between tropical and strongly oligarchic temperate forests are only a consequence of the greater diversity in the tropics but that the overall pattern is qualitatively the same. This scenario would imply that the degree of dominance of common species is negatively related to the size of the species pool while the proportion of common species is independent of it.

The literature on two-dimensional commonness offers significant insights into community structure. However, the categorical approach employed so far (Fig. 1a) limits potential comparisons between different sets of taxa or different regions (Rabinowitz 1981, Rabinowitz et al. 1986, Ricklefs 2000). In contrast, here we propose to quantify commonness of species of a given community in a continuous way (Fig. 1b). This new approach does not allow distinction of different forms of rarity but greatly facilitates shifting from species-level to community-level questions about commonness.

To our knowledge, this study represents the first attempt to quantify and compare commonness patterns among lowland, dry, and montane tropical forests. We explored the relationships between commonness and the size of the species pool across different scales. First, we analyzed the variation of species commonness patterns with elevation and the size of the species pool at local scales (10×10 km). Second, we quantified commonness characteristics at larger scales, i.e. a) within large landscape units defined by the type of forest, and b) for the whole Madidi region (200×200 km),

which encompasses huge environmental variation. Finally, we tested whether the new methodological approach used here to quantify commonness in plant communities matches with the perspective on commonness of the oligarchy hypothesis (Pitman et al. 2001, 2013).

Methods

Study region and floristic data

During the last 12 yr, we carried out extensive standardized floristic inventories in the Madidi region, located on the eastern slopes of the Bolivian Andes, between latitude $-12.43°$ and $-15.72°$ and longitude $-69.48°$ and $-66.66°$. It includes mature forests from the Amazon to the forest limit, ca 4000 m. We inventoried ca 122 000 plant individuals through the establishment of 407 plots of 0.1 ha (20×50 m), with a minimum inter-plot distance of 250 m. The study region contains many vegetation types (Navarro et al. 2004, Fuentes 2005), but for the present study the plots were classified into three broad forest types: 1) lowland forests (include Amazonian and pre-Andean terra firme forests); 2) semideciduous Andean forests ('dry forests' in the following), characterized by lack of precipitation for 4–5 months yr^{-1} due to local rain shadow, with a prevalence of deciduous species (ranging from 650 to 1350 m in elevation); and 3) wet montane forests ('montane forests' in the following; includes different montane, Andean, sub-Andean, Yungas and ceja de monte formations). The assignment of plots to vegetation types was done in the field following the physiognomic and floristic indicators summarized by Navarro et al. (2004) and Fuentes (2005), who described in detail the vegetation types in the Madidi National Park and surrounding areas. Although almost exactly a threshold of 1000 m in elevation defines the limit between lowland and montane forests, four plots between 1000 and 1100 m were assigned to lowland forests, according to local environmental and floristic characteristics, and two plots between 900 and 1000 m were assigned to montane forests. Overall, 95 plots were inventoried in lowland forests, 82 in dry forests, and 230 in montane forests. These plots were dispersed over an area of roughly 110×110 km in lowland forests, 35×35 km in dry forests, and 130×130 km in montane forests.

Plots were installed to avoid big gaps or recent human disturbance. At each plot, we inventoried all woody plant individuals with a diameter equal or greater to 2.5 cm at 130 cm above ground. All species were collected at least once, except for a few well-known species like *Iriartea deltoidea* and *Socratea exorrhiza*. All individuals were identified to a valid species name or assigned to a morphospecies. Extensive taxonomic work was conducted during 2010 at the Herbario Nacional de Bolivia to ensure that all species and morphospecies names were standardized across all plots. Less than 3.5% of individuals were excluded from the analysis because they were sterile specimens that could not be assigned to a reliable morphospecies. All plot characteristics, floristic inventories, and voucher specimens are available to query in the TROPICOS database ($<$ www.tropicos.org/PlotSearch.aspx?projectid $=$ 20 $>$).
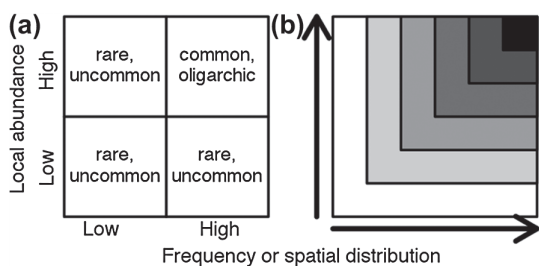

Figure 1. Categorical and quantitative approaches to two-dimensional commonness: (a) classification of species according to their local abundances and frequencies (Rabinowitz 1981, Rabinowitz et al. 1986); and (b) quantitative approach to the same concept of commonness (present study); darker greys indicate greater commonness. Two-dimensional commonness differs from uni-dimensional commonness in combining simultaneously two criteria: common species are those that combine high local abundances with high frequency. Therefore, from this point of view, frequent but locally scarce species are not considered common, neither locally abundant but infrequent species.

Voucher specimens are kept in the LPB and MO herbaria (acronyms according to Thiers 2012).

Characterization of species commonness

We calculated species commonness based on a modified version of the h index, a widely known bibliometric tool to measure academic performance (Hirsch 2005). We assigned to each species a commonness proportional h index (h_p) when it was present in h_p percentage of plots with h_p percentage or more of the individuals in each of those plots. For example, a species with $h_p = 10\%$ is present in 10% of the plots and represents 10% or more of the individuals in those plots. The value of this index is not limited by sampling effort and varies within the interval 0–100%. This index cannot be obtained by using a single formula because it is the solution to the equation $h_p = f(h_p)$, where f could be any monotonically decreasing function. In practice, however, h_p is very easily obtained from the observed sequence of abundance values of the species (see Supplementary material Appendix 1 for the simple R code for its calculation). Because h_p measures properties in two dimensions with a single number, this index facilitates the integration of species-based information into the community level to explore commonness patterns, which is the focus of the present paper. Three community metrics are taken into account: 1) mean commonness of all species of the community; 2) proportion of common species of the community; 3) mean commonness of the common species, which is a measure of the strength of dominance shown by the common species.

Mean commonness at the local scale: measurement and determinants

To study the patterns at the local scale, we divided the study area with a regular grid of 10×10 km cells. Any cell containing five or more plots was considered a sampling unit. The elevation of a sampling unit was calculated as the mean elevation of the plots included. We calculated the mean h_p of all the species within a sampling unit.

To estimate the size of the species pool (S), defined as the total number of species within a sampling unit, we used the bootstrap estimator (Gotelli and Colwell 2010):

$$S = S_O + \Sigma \, (1 - p_i)^N$$

where S_O is the number of observed species within the sampling unit, p_i is the proportion of plots of a sampling unit where the species i is present, and N is the number of plots inventoried in the sampling unit.

To explain the observed pattern of mean commonness at the local scale, we conducted two simple linear regressions between the estimated size of the species pool and elevation as explanatory variables, and the mean h_p of the species of a sampling unit as the response variable. To assess the effect of one explanatory variable while controlling for the effect of the other, we conducted partial linear regressions. The statistical significance was estimated with a Monte Carlo test after 999 random permutations (Legendre 2008).

Delimitation of the set of common species

To obtain the group of common species in a community, we plotted a proportional commonness-rank curve to summarize the commonness profile of a community, ranking all species by their h_p indexes and, secondarily, by abundance (Fig. 2). The axes were scaled from 0 to 1 because we were interested in the shape of the curve less so in the absolute values (i.e. the number of species or the commonness attained by the most common species). With a quantitative measure of commonness, common species are defined as those above a given threshold of commonness, which separates them from the rest. We defined that threshold as the h index of the proportional commonness-rank curve. Graphically, this is interpreted as the point where the diagonal ($y = x$) crosses the proportional commonness-rank curve (Fig. 2). Given that this new coefficient is an h index of h_p indexes, we use the notation h_h. Unlike h_p, which measures attributes of the species, h_h measures a property of the community. For example, a community with $h_h = 0.10$ means that 10% of the observed species present h_p indexes above the 10th percentile. As in the case of h_p, this index cannot be obtained by using a single formula but is easily obtained from the observed sequence of h_p values of the species (Supplementary material Appendix 1). We propose the h_h criterion because it describes a characteristic of the community that does not depend on the number of species, i.e. it responds to the steepness of a curve but not to the number of points that constitute such curve (Fig. 2). Moreover, it is expressed formally as a proportion of species and therefore
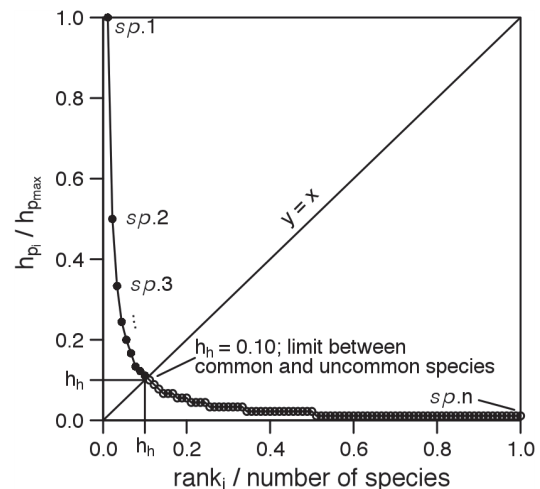

Figure 2. Example of a proportional commonness-rank curve and delimitation of common species of a community with the h_h criterion. The x-axis represents the proportional rank of a given species, ranked by h_p index. Because it is proportional, it varies within the range [0, 1], instead of [1, number of species]. The y-axis represents the ratio between the h_p index of a species and the h_p of the most common species. Because it is proportional, it varies within the range [0, 1] instead of [0, maximum h_p]. The point where the diagonal crosses the proportional commonness-rank curve is its h index (h_h), which is used in the present study as the threshold between common and uncommon species. The represented example community has $h_h = 0.10$: 10% of the species are qualified as common.

it is comparable among communities that differ in their number of species.

Patterns of common species at the local scale

We delimited the set of common species within 10×10 km sampling units following the h_h criterion. Then we counted the number of common species and divided that by the size of the species pool to find the proportion of common species in the estimated size of the species pool. To know how common the common species were, we calculated their mean h_p.

To identify potential determinants of patterns of common species, we conducted four simple linear regressions, one for each combination of one response variable (proportion of common species and mean h_p of common species) with one explanatory variable (estimated size of the species pool and elevation). Finally, to explore the effect of one explanatory variable while controlling for the effect of the other, we conducted four partial linear regressions, one for each combination of one response variable with one explanatory variable. The statistical significance of the partial regressions was estimated with a Monte Carlo test after 999 random permutations (Legendre 2008).

Comparison between forest types and characterization of the region

To explore possible differences between lowland, dry, and montane tropical forests, we characterized each forest type on the basis of the mean h_p of their species, proportion of common species, and the mean h_p of its common species, following the same calculations as described above for the local-scale analysis. To characterize the whole Madidi region (200×200 km), all plots were considered together and all calculations repeated.

Comparison between h_h criterion and Pitman et al. (2001, 2013) perspective on commonness

We compared our h_h value to the original oligarchy concept by extracting all the plots below 500 m elevation and delimiting the set of common species to be compared with those of Pitman et al. (2001, 2013). All of the calculations and analyses were done with R (R Development Core Team). The level of significance for all analyses was 0.05.

Results

Commonness at the local scale

The mean commonness of all species of the community at the local scale (10×10 km) ranged from 0 to 2.55% (mean $h_p = 0.58\%$). It increased significantly with elevation (adjusted $R^2 = 0.23$; p = 0.002), even when the effect of the species pool was partialled out ($R^2 = 0.12$; p = 0.041) (Table 1). It was also negatively related with the size of the species pool (adjusted $R^2 = 0.19$; p = 0.006); however, when the effect of the elevation was partialled out such relationship was not statistically significant ($R^2 = 0.08$; p = 0.106).

The proportion of common species in the sampling units ranged from 0 to 21.0% of the species pool (mean $h_h = 5.14\%$) and was not related with pool size (adjusted $R^2 = 0.03$; p = 0.183), even when the effect of the elevation was partialled out ($R^2 = 0.01$; p = 0.632) (Table 1). We found a slight increase in the proportion of common species with elevation (adjusted $R^2 = 0.11$; p = 0.031), but it did not remain statistically significant when the effect of the size of the species pool was partialled out ($R^2 = 0.09$; p = 0.087).

The mean commonness of the common species varied between 4.62 and 20.0% (mean $h_p = 11.26\%$). It was negatively related with the size of the species pool (adjusted $R^2 = 0.20$; p = 0.007), even when the effect of the elevation was partialled out ($R^2 = 0.19$; p = 0.014) (Table 1). In contrast, it was not significantly related with the elevation (adjusted $R^2 = 0.01$; p = 0.263), even when the effect of the size of the species pool was partialled out ($R^2 < 0.01$; p = 0.991).

Commonness at larger scales

The three broad forest types showed contrasting characteristics of commonness patterns and differences in the size of the species pool (Table 2). The montane forest had the largest species pool (1975 species), followed by the lowland forest (1232 species), whereas the dry forest had the smallest species pool (457 species). Lowland and montane forests showed very similar mean commonness of species (mean h_p 0.76 and 0.80% respectively), but the dry forest was almost double that value (mean $h_p = 1.47\%$). The montane forest had the lowest commonness of common species (mean h_p of common species = 2.58%), followed by the lowland forests (mean h_p of common species = 2.92%), while the common species of the dry forest showed the strongest dominance of any forest type (mean h_p of common species = 5.26%).

Table 1. Results of the simple and partial linear regressions between the size of the species pool and elevation using the h_p index for the three commonness metrics studied. Values are standardized coefficients in the regression. Significant results are shown in bold ($**p < 0.01$; $*p < 0.05$).

	Mean h_p of all species	Proportion of common species	Mean h_p of common species
Size of the species pool	**−0.46** ($R^2_{adj} = 0.19$)**	−0.23 ($R^2_{adj} = 0.03$)	**−0.46** ($R^2_{adj} = 0.20$)**
Elevation	**0.51** ($R^2_{adj} = 0.23$)**	**0.37* ($R^2_{adj} = 0.11$)**	0.20 ($R^2_{adj} = 0.01$)
Size of the species pool; elevation partialled out	−0.30 ($R^2 = 0.08$)	−0.10 ($R^2 = 0.01$)	**−0.46* ($R^2 = 0.19$)**
Elevation; size of the species pool partialled out	**0.38* ($R^2 = 0.12$)**	0.33 ($R^2 = 0.09$)	0.002 ($R^2 < 0.01$)

Table 2. Community structure parameters for the lowland, dry, and montane forests and the whole Madidi region; h_p was the commonness index used.

Forest types	Mean h_p of all species (%)	Proportion of common species (%)	Mean h_p of common species (%)	Estimated number of species	Mean elevation (m)
Lowland	0.76	11.77	2.92	1232	498
Dry	1.47	11.81	5.26	457	940
Montane	0.80	12.66	2.58	1975	2052
All	0.69	13.92	2.07	2831	1465

In contrast, the proportion of common species (h_h) was similar among the three forest types (12–13%).

When the whole Madidi region was considered, the mean commonness and the commonness of the common species were lower than for the three forest types separately, but the proportion of common species was similar ($h_h = 14\%$) (Table 2).

At the larger scale, the species were less common but more equally common (Fig. 3). This pattern was associated with a greater proportion of common species (greater h_h) but with less difference in commonness (in h_p) between common and uncommon species.

Delimitation of the set of common species below 500 m

The subset of all plots below 500 m is a similar system to the Ecuadorean and Peruvian Amazonian forest where Pitman et al. (2001, 2013) developed the original oligarchy hypothesis. While they applied their expert criteria to separate oligarchic species from the rest, we applied the h_h criterion. We found a total of 122 common species (12.41% of the estimated species pool) below 500 m in 66 0.1-ha plots in the Madidi region (Supplementary material
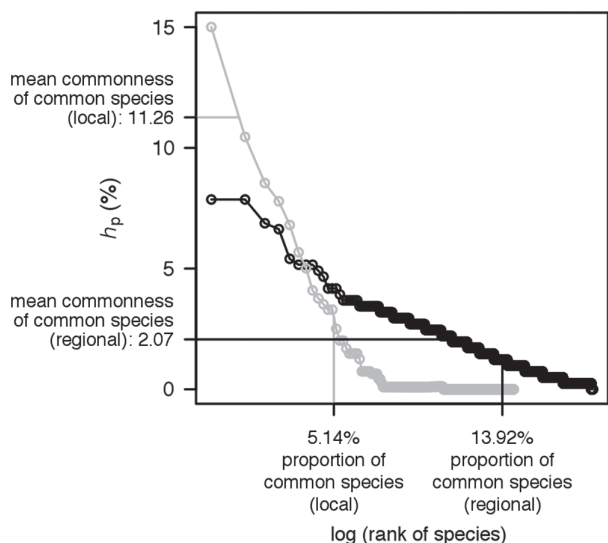

Figure 3. Across-scale comparison of the distribution of commonness between the whole Madidi region (in black) and mean values of 10 × 10 km sites within the region (in grey). The highlighted values correspond to the delimitation and characterization of the set of common species at local and regional scales.

Appendix 2). Of these species, 108 were trees, and 14 were lianas. The selected species ranged from 2 species that were present in 10.61% of the plots as at least 10.61% of the individuals (*Iriartea deltoidea* and *Rinorea viridifolia*) to 47 species present in 1.52% of the plots as 1.52% of the individuals or more. The most common liana species was *Hebanthe occidentalis* ($h_p = 3.03\%$).

Discussion

Our goal was to perform a quantitative assessment of two-dimensional commonness along an extensive tropical elevational gradient. We also aimed to compare two spatial scales and different types of forests.

Commonness at local scales showed a clear elevational pattern with species being more common, on average, at higher elevations. There was also a negative relationship between the number of species and the degree of species dominance at local scales. These results agree with those of many previous researchers and are logically grounded in the allocation of the same amount of individuals across a different number of species, which affects the mean abundance and, consequently, mean commonness (Hubbell 2001, He and Legendre 2002, Hurlbert 2004, Dornelas et al. 2011). The same logic of the size of the species pool applies to the alpha-diversity, even within those sampling units with relatively similar plots and, therefore, relatively small pool of species. That means that, regardless of the size of the species pool, the species within sampling units with high alpha-diversity will tend to present a lower proportion of individuals within each plot, and therefore their commonness (as measured by h_p) will decrease in average. If the elevation and alpha-diversity are correlated within our study region (a general pattern found in most Andean regions for different taxa; Kessler et al. 2001, Krömer et al. 2005, Kessler 2009, Karger et al. 2011, Kluge and Kessler 2011, Laurance et al. 2011, Palin et al. 2011), this could explain the relationship between elevation and mean commonness that the size of the species pool does not explain.

The elevational pattern has no real parallel when the three forest types are considered at larger scales by elevation. Although the differences between lowland and montane forests were expected for the elevational ranges considered, the dry forest did not show intermediate characteristics as would be expected according to its elevation. In contrast, the size of the species pool seemed to be a more robust predictor of the differences between types of forest, particularly within the dry forest, with fewer but much more common species than the other two forest types. Some authors reporting the same pattern in other dry forests have suggested different ecological determinants of this stronger dominance, such as stronger competition, more frequent disturbance, or the presence of rare species more prone to local extinction due to isolation from other dry areas (Hubbell 1979, Pennington et al. 2009). All of these mechanisms could influence the commonness patterns by modifying the size of the species pool. Moreover, our results for lowland and montane forests suggest that the mechanisms shaping species commonness differences between sites are the same as those shaping continuous diversity changes

along the elevational gradient (Karger et al. 2011, Kluge and Kessler 2011, Kraft et al. 2011, Sanders and Rahbek 2012). These results, added to those obtained at the local scale, suggest that the degree of dominance of species, far from being determined solely by local processes such as successful adaptation to local environmental conditions, could be largely driven by the evolutionary and historical processes that shape the species pool within a given area (Lessard et al. 2012b).

While the degree of species dominance seems to be largely driven by the species pool, we found presence of a dominant set of common species, i.e.: the so-called 'oligarchic pattern' sensu Pitman et al. (2001, 2013), at all scales and types of forest with independence of the size of the species pool. The consistency of the oligarchic pattern at the large scales studied (types of forest and whole Madidi region) is noteworthy. In all cases, a limited and definable set of common species accounted for 11–14% of the species pool. These figures, which are h_h values, are strikingly similar to those underlying the original concept of oligarchy (10% in Yasuní and 15% in Manu). Moreover, other works directly addressing oligarchy with subjective expert criteria offer similar proportion of common species, with 119 oligarchic species out of 1087 (11%) reported in Yasuní (Macía 2011), 94 oligarchic species out of 877 (11%) reported in lowland Madidi (Macía 2008), 121 oligarchic species out of ca 1000 (12%) in Brazilian cerrado (Bridgewater et al. 2004) and 38 oligarchic species out of 311 (12%) in liana communities in Yasuní (Burnham 2002). Other researchers report contrasting results, ranging from 30% of common species (Eilu et al. 2004) to only one or few species, usually *Iriartea deltoidea* and *Socratea exorrhiza* in the Amazonia, and homologous dominant species in other tropical forests (Paoli et al. 2006, Norden et al. 2009, Jabot and Chave 2011). Unfortunately, comparisons with all these results are very limited because of the inherent subjectivity of the categorical or merely descriptive approaches to commonness (Ricklefs 2000). In general, our results coupled with those of others suggest a general dominance pattern at these scales; however, given the mentioned limitations, we do not intend to extrapolate beyond the comparison with the original oligarchy hypothesis.

The consistency of the oligarchic pattern at both scales is surprising because we analyzed data sets that were very different in number of species (< 500 to > 2500), elevational ranges (< 300 to ca 4000 m), and environmental heterogeneity (from relatively homogeneous patches within the same forest type to the huge environmental variation covered by the whole Madidi region). At first sight, this consistency does not support the assumption of oligarchies present only at limited environmental heterogeneity (Pitman et al. 2001, 2013), and hence contrasts with the conclusions of previous researchers who rejected the oligarchy hypothesis based on datasets covering great environmental heterogeneity (Tuomisto et al. 2003, Réjou-Méchain et al. 2008, Toledo et al. 2011, 2012). We acknowledge that the environmental heterogeneity covered by the whole Madidi region has an effect on the strength of the oligarchic pattern, probably weaker than any of the more homogeneous 10 × 10 km areas considered at the

local scale (Fig. 3). However, the method employed here does not require addressing oligarchy with an all-or-nothing view, and allows quantifying oligarchic patterns that are not obvious under more subjective approaches. Overall, our results clearly indicate the existence of a definable set of dominant species under very different conditions and, at least, from the local to regional scale. Further study would be required of the patterns of oligarchic co-occurrence to distinguish a combination of habitat-characteristic oligarchies from the presence of true large-scale generalist oligarchies.

Overall, it is very unlikely that our conclusions are biased by the method employed. The strong similarities between our quantitative approach applied to forests below 500 m in the Bolivian Amazon and the expert criteria of Pitman et al. applied to forests in the Ecuadorean and Peruvian Amazon indicate that our method fits very well with the original concept of oligarchy. Similarities include the amount of species qualified as common in Madidi (12% of the estimated species pool vs 10–15%) and the identities of these species, with 45 of our Madidi common species below 500 m shared as common in Yasuní or Manu or both, while Yasuní and Manu shared 42 of their regional sets of common species (Supplementary material Appendix 2; Pitman et al. 2013). The type of individuals that we included in our inventory and that Pitman et al. did not (lianas, shrubs, and treelets) explains some minor differences. For example, we found several oligarchic *Piper* and Melastomataceae species, as well as several oligarchic liana species. Unfortunately, no comparable studies have addressed the dominance of treelets or shrubs in the Neotropics. However, our method seems to perform well for lianas, since 5/14 of our oligarchic liana species are also reported as oligarchic in Yasuní (*Combretum laxum*, *Uncaria guianensis*, *Petrea maynensis*) (Burnham 2002, Macía 2011) or among the most dominant species in other forests in the Neotropics: *Dalbergia frutescens* (Pereira Villagra et al. 2013) and *Hippocratea volubilis* (Imbert et al. 2000, Rice et al. 2004). Finally, these results indicate not only that the same pattern can be found in different regions, but also evidence large-scale dominance of certain species across different regions in northwestern Amazonia, at least when similar habitats are considered, for both trees and lianas (Burnham 2002, 2004, Pitman et al. 2013).

We have found that the commonness patterns in the Madidi region are strongly linked to the size of the species pool, independently of the elevational variability involved and the type of forest and spatial scale considered. Remarkably, these factors affect the inter-species differences in commonness but not the general quality of the community. Although previous researchers have rejected the oligarchy hypothesis (Tuomisto et al. 2003, Réjou-Méchain et al. 2008, Toledo et al. 2011, 2012), we believe that it reflects measurable properties of the community that can be considered continuously across different habitats or scales, regardless of the strength of the pattern. Moreover, our results show that the comprehension of dominance and commonness patterns, including the oligarchy hypothesis, improves by interpreting the patterns in light of the species pool influence, as happens with other important aspects of community structure such as alpha- and beta-diversity gradients

(Ricklefs 1987, Kraft et al. 2011, Myers et al. 2013), among others (Lessard et al. 2012a, b). Finally, taking advantage of a quantitative approach to commonness could facilitate an understanding of the mechanisms creating commonness differences among species and shaping community commonness patterns at different scales.

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Supplementary material (Appendix ECOG-00546 at < www.oikosoffice.lu.se/appendix >). Appendix 1–2.