

# Commonness and rarity determinants of woody plants in different types of tropical forests

Gabriel Arellano · M. Isabel Loza · J. Sebastián Tello ·  
Manuel J. Macía

Received: 15 August 2014 / Revised: 23 October 2014 / Accepted: 18 November 2014 /  
Published online: 29 November 2014  
© Springer Science+Business Media Dordrecht 2014

**Abstract** The aim of this work is to examine whether there exists a link between local and landscape patterns of species commonness, and if these are related to morphological traits in tropical plant communities. The Madidi region (Bolivian tropical Andes) is selected as study location. We estimated local and landscape commonness, rarity classes, height, diameter, number of stems, and habit for >2,300 species. We employed correlations to evaluate the relationship between local scale commonness and landscape scale commonness. We performed ANCOVA and multinomial logistic regressions to predict commonness and rarity variables from the morphological traits. We repeated the analyses for six different forest types, including dry forests and wet forests along a 3,477 m elevation gradient. We found a positive relationship between local and landscape commonness in all

---

Communicated by Peter Ashton.

---

G. Arellano (✉) · M. J. Macía  
Departamento de Biología, Área de Botánica, Universidad Autónoma de Madrid, Calle Darwin 2,  
28049 Madrid, Spain  
e-mail: gabriel.arellano.torres@gmail.com

M. I. Loza  
Department of Biology, University of Missouri, St. Louis, MO 63121, USA

M. I. Loza  
Missouri Botanical Garden, P.O. Box 299, St. Louis, MO 63166-0299, USA

M. I. Loza  
Herbario Nacional de Bolivia, Campus Universitario Cota-Cota, Calle 27,  
Correo Central Cajón Postal 10077 La Paz, Bolivia

J. S. Tello  
Center for Conservation and Sustainable Development, Missouri Botanical Garden,  
P.O. Box 299, St. Louis, MO 63166-0299, USA

J. S. Tello  
Escuela de Biología, Pontificia Universidad Católica del Ecuador, Av. 12 de Octubre 1076 y Roca,  
Apdo. 17-01-2184 Quito, Ecuador

forest types. Additionally, we found that, plant height influences the local and landscape commonness, and that the apportioning of species into rarity classes depends greatly on the species habit and, at lesser degree, on the number of stems. Our main conclusions are: (1) Approaches to commonness and rarity based on abundance only or occurrence only could summarize most of the relevant information to characterize commonness and rarity patterns: both approaches, in practice, do not supply independent information. (2) The species traits determine which species are rare and which ones are common, which indicates that commonness and rarity patterns are the result of non-neutral trait-based community assembly processes.

**Keywords** Landscape commonness · Local commonness · Oligarchy · Plant traits · Rabinowitz's classification

## Introduction

The study of commonness and rarity has attracted the attention of ecologists and evolutionary biologists for decades (e.g. Preston 1948; Rabinowitz 1981), and even some authors have defined ecology as the study of commonness and rarity among and within species (Kelly et al. 1996). Understanding patterns of commonness and rarity of species has also fundamental implication for conservation (Gaston 2010, 2012), because rarity is associated with extinction risk, particularly for species that are rare in multiple aspects of their distribution and ecology (Rabinowitz et al. 1986). Despite the fundamental ecological and applied questions surrounding commonness and rarity, we lack a detailed understanding of patterns and mechanisms that produce this phenomenon.

Commonness and rarity can be expressed at different scales and along different ecological dimensions (Hanski 1982; Brown 1984; Rabinowitz et al. 1986; Pitman et al. 1999, 2001; Kristiansen et al. 2009). For example, the abundance of a species in a sample, the frequency with which a species appears across a given region, or the geographical extent of a species distribution, are three measures of commonness at three different spatial scales (Gaston 1994). Beyond spatial scales, species can be classified along other relevant ecological dimensions, such as the variety of habitats where the species appear, to distinguish different classes of rarity (Rabinowitz 1981; Rabinowitz et al. 1986).

Species commonness and rarity have been frequently related to species traits. In plants, studies have found that plant size is often correlated with species commonness at different scales: (1) At large scales across regions and continents, larger species have been found to be more widely distributed because of their greater dispersal ability (Ruokolainen and Vormisto 2000; Davidar et al. 2008; Kristiansen et al. 2009). (2) At local scales, large species could also be more abundant, because large plants have an advantage when they compete for light (Wright et al. 2007) and tend to have higher reproductive success (Nathan and Muller-Landau 2000; Westoby et al. 2002; Moles et al. 2004; Moles and Westoby 2004; Aarssen et al. 2006; Wright et al. 2007; Kristiansen et al. 2009).

The habit of species could also influence their commonness and rarity patterns, particularly across different environments. It is widely known that lianas decrease in abundance and richness at higher elevations in tropical ranges (e.g. Gentry 1991), but show the

opposite pattern in sites that suffer frequent disturbances, because of their particular suite of structural and physiological adaptations (Schnitzer and Bongers 2002; Pérez-Salicrup et al. 2004; Letcher and Chazdon 2012). Regarding shrubs, these can be common in the tropical forest communities, especially at higher elevations, where having multiple stems is an advantageous adaptation to low productivity levels and high frequency of disturbances due to steeper slopes (Bellingham and Sparrow 2000, 2009). Otherwise, it is poorly understood how different rarity and commonness classes are related with different plant habits in tropical forests, and whether the same patterns could apply to different forest types.

The present work explores the relationships between commonness at two different scales, rarity classes, and species traits within a  $200 \times 200$  km region that includes dry and wet tropical forests, along a 3,477 m elevation gradient in northwestern Bolivia. Specifically, we aim to answer the following questions: (1) Do different forest types show the same apportioning of species into different rarity classes? (2) Is local commonness of species correlated with landscape commonness within each forest type? (3) Are species traits (plant height, plant diameter, number of stems, habit) related to commonness at some scale and/or to rarity classes within each forest type?

## Materials and methods

### Study region, sampling design and floristic data

We established a network of 405 forest plots across the Madidi region of Bolivia (latitude  $-12.43^\circ$  to  $-15.72^\circ$ ; longitude  $-69.48^\circ$  to  $-66.66^\circ$ ), located in the eastern slope of the Andes and covering approximately 111,000 km<sup>2</sup> in the northern part of La Paz Department and the western part of the Beni Department (Fuentes 2005).

The plot network surveys mature forests of different habitats and covers a steep elevational gradient ranging from 254 to 3,731 m. The geological substrate ranges from alluvial and fluvial sediments of gravels, sands and clays of the Quaternary in the Amazonian forests, to predominance of Ordovician sandstones, siltstones, and slates at high elevations in the Andean slopes (Bolivian Geological and Mining Service map, <http://200.87.120.29/sigeboweb/>). All plots were installed avoiding big gaps and recent human disturbance. In each plot, we inventoried all woody plant individuals rooting within the plot limits with at least one stem with diameter equal or greater to 2.5 cm at 130 cm from the rooting point (“diameter at breast height”, dbh). For each individual, we measured and counted all stems with dbh  $\geq 2.5$  cm, and estimated the height reached by each individual. All species were collected at least once, and all individuals were identified to a valid species name or assigned to a morphospecies (“species” in the following). Extensive taxonomic work was conducted during 2010 and 2011 at Herbario Nacional de Bolivia to ensure that all species 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 identified to species level, neither assigned to a reliable morphospecies. Voucher specimens are kept in the Herbario Nacional de Bolivia and Missouri Botanical Garden. All plot characteristics, floristic inventories, and information on voucher specimens are available to query in the Tropicos<sup>®</sup> database ([www.tropicos.org/PlotSearch.aspx?projectid=20](http://www.tropicos.org/PlotSearch.aspx?projectid=20)).

## Definition of forest types

The study region is extremely heterogeneous both environmentally and floristically. To avoid results driven by such internal variability, we apportioned the plots into six different forest types. The most distinctive floristic formation is the semideciduous dry forest (DR; ranging from 650 to 1,350 m), which is tropical dry forest characterized by lack of precipitation during 4–5 months per year due to local rain shadow, clay loam soils with high nutrient contents and relatively organic soils. This forest type occurs in a large patch of ca.  $35 \times 35$  km in size within our study region.

The other five forest types were regular belts of tropical wet forests (>2,000 mm of annual precipitation) along the whole elevation gradient (Navarro et al. 2004; Fuentes 2005): lowland Amazonian forest (AM; below 1,000 m); lower montane forest (LM, from 1,000 to 1,700 m); intermediate montane forest (IM, from 1,700 to 2,400 m); upper montane forest (UM, from 2,400 to 3,100 m); and high Andean forest (HA; from 3,100 to 3,731 m). Temperature and precipitation changes with elevation are coupled with changes in soil properties. Soils are more acidic and present higher concentrations of carbon and nitrogen at higher elevations, caused by a progressive increase of the degree of soil moisture and soil waterlogging and a decrease in the mineralization rates when moving from the Amazonia to the Andes (Schawe et al. 2007). However, denitrification hydro-morphic processes occur in HA forests. Macro-nutrients contents are less predictable than changes in organic matter. Calcium and magnesium contents diminish with elevation, whereas potassium levels are maximum at intermediate elevations (LMF and IMF). Phosphorus content and texture are extremely variable across and within elevational belts, although Amazonian soils tend to be more sandy in average than other forest types. Each of these five wet forest types was distributed in more or less linear broad continuous belts across an area of ca.  $100 \times 100$  km.

Due to logistic constraints of the fieldwork, the plots within each forest type were not distributed at random, but significantly clumped around selected study localities (Table 1). The only exception to this aggregated pattern were some LMF and IMF plots that were isolated within the large patch dominated by semi-deciduous dry forests, and that were inventoried while sampling the DR forest in those localities.

## Species traits

We calculated four traits for each species as potential determinants of its commonness and rarity: (1) The maximum height of each species was estimated as the 95th percentile of the heights of all the individuals of that species found in the region. (2) The maximum diameter of each species was estimated as the 95th percentile of the diameters of all the stems of that species. (3) The average number of stems by species, considering the median of all individuals of that species. (4) The habit into four categories: (a) lianas: species with at least half the individuals considered liana in the field; (b) canopy trees: self-standing species with maximum stem diameter  $\geq 10$  cm; (c) treelets: self-standing species with maximum stem diameter  $< 10$  cm and whose individuals never presented multiple stems; and (d) shrubs: self-standing species with maximum diameter  $< 10$  cm and presented multiple stems. We excluded 23 hemiepiphytic species (species with  $\geq 50$  % of individuals considered hemiepiphytes in the field).

Once the traits were calculated for each species, all subsequent analyses were performed separately for each forest type (DR, AM, LM, IM, UM and HA forests).

**Table 1** Characteristics of the six forest types studied in the Madidi region, Bolivia

	Dry	Amazonian	Lower montane	Intermediate montane	Upper montane	High Andean
Number of plots	81	91	102	64	38	28
Mean (range) of inter-plot distances (km)	20 (0.03–49)	49 (0.03–132)	57 (0.01–175)	63 (0.07–135)	45 (0.05–111)	28 (0.07–118)
Mean (range) distance to the nearest plot (km)	0.56 (0.03–2.86)	0.54 (0.03–3.23)	1.24 (0.01–38.48)	0.95 (0.07–16.49)	0.41 (0.05–1.54)	0.56 (0.07–2.40)
Plot aggregation index (R)	0.17	0.15	0.37	0.28	0.12	0.16
Mean (range) number of species per plot	43 (12–65)	76 (39–130)	68 (21–126)	51 (22–102)	35 (13–59)	20 (5–46)
Regional number of species	389	1,080	1,151	715	344	157
Canopy tree species	223 (57 %)	577 (53 %)	674 (59 %)	420 (59 %)	187 (54 %)	78 (50 %)
Liana species	82 (21 %)	228 (21 %)	199 (17 %)	81 (11 %)	35 (10 %)	17 (11 %)
Shrub species	56 (14 %)	107 (10 %)	137 (12 %)	134 (19 %)	93 (27 %)	48 (31 %)
Treelet species	28 (7 %)	168 (16 %)	141 (12 %)	80 (11 %)	29 (8 %)	14 (9 %)

The plot aggregation index (R) is the Clark and Evans (1954) index of spatial aggregation; R = 1 means random distribution; R close to zero means clumped distribution; R close to 2 means regular distribution

## Commonness and rarity measures

For each forest type and species, we calculated commonness at local (i.e. plot-level) and landscape (i.e. forest-level) scales as follows: (1) Local commonness was measured as the logarithm of the maximum local abundance (i.e. within a plot) attained by a species in a given forest type. (2) Landscape commonness was measured as the logarithm of the proportion of plots within a given forest type where the species was present. We took logarithms because in all forest types, and at both scales, one or few species were very common, and we sought to highlight the differences among the other species, which represented the vast majority of the forests' diversity. Additionally, the logarithmic transformation served to fulfill the statistical assumptions of the Pearson's correlations and ANCOVA analyses (see below).

For each forest type and species we also calculated four rarity classes by combining maximum abundance and frequency: (1) Rare species were those present in less than 5 % of the plots of a given forest type, with always <5 individuals in any plot. (2) Abundant-but-infrequent species were those whose maximum abundance was  $\geq 5$  individuals, but that were present in less than 5 % of the plots of a given forest type. (3) Frequent-but-scarce species were those species present in at least 5 % of the plots in a given forest type but that were present always with <5 individuals in any plot. (4) Common species were those present in at least 5 % of the plots in a given forest type and whose maximum abundance was  $\geq 5$  individuals.

## Statistical analysis

To answer if different forest types show the same apportioning of species into different rarity classes, we performed  $G$  tests to test the null hypothesis of similar relative apportioning of species into the four rarity classes across the six forest types. The  $G$  test is a test of independence similar to the Chi-squared test, and measures if there exists independence or not between two categorical variables (in our case, forest type and rarity class).

To answer whether local-scale commonness of species correlates with landscape-scale commonness, we performed Pearson correlations between  $\ln(\text{maximum local abundance})$  and  $\ln(\text{landscape frequency})$  of species at each forest type.

To answer if species traits are related to commonness at some scale and/or to certain rarity classes, we performed two types of analyses for each forest type. First, to study the relationship between the commonness at both scales and its potential determinants, we performed two analyses of covariance (ANCOVA) at each forest type, by fitting models of the form:

$$Y = \beta_0 + \beta_1 MH + \beta_2 MD + \beta_3 NS + \beta_4 H_{liana} + \beta_5 H_{shrub} + \beta_6 H_{treelet}$$

where  $Y$  is the response variable:  $\ln(\text{maximum local abundance})$  in the case of the local scale commonness analysis, and  $\ln(\text{landscape frequency})$  in the case of the landscape scale analysis;  $MH$  is the maximum height;  $MD$  is the maximum diameter;  $NS$  is the average number of stems; and  $H_{liana}$  is a dummy variable indicating if a species is liana ( $H_{liana} = 1$ ) or not ( $H_{liana} = 0$ ), and the same applies for  $H_{shrub}$  and  $H_{treelet}$ .

Second, to evaluate the impact of species traits on the apportioning of species into rarity classes, we performed multinomial logistic regressions, by fitting three models in each forest type of the form

$$\ln\left(\frac{P(class_k)}{P(rare)}\right) = \beta_0 + \beta_1MH + \beta_2MD + \beta_3NS + \beta_4H_{liana} + \beta_5H_{shrub} + \beta_6H_{treelet}$$

where  $P(class_k)$  is the probability of a species of being of the rarity class  $k \in \{\text{common, abundant but infrequent, frequent but scarce}\}$  and  $P(rare)$  is the probability of a species of being rare (i.e., scarce and infrequent), which functions as a reference probability for the models. The  $P$  values of the whole models were calculated with likelihood ratio tests, and the  $P$  values for each coefficient were calculated with  $Z$  tests.

All calculations and analyses were performed with R 3.1.1. The level of significance for all analyses was 0.05, assessed over Bonferroni-corrected  $P$  values.

## Results

The six forest types differed 4-fold and 7-fold in the local and regional number of species, respectively (Table 1). The proportion of canopy trees was fairly constant among different forest types, 50–59 % of the species, but the proportion of shrub species increased at higher elevations, whereas the proportion of liana and treelet species decreased with elevation.

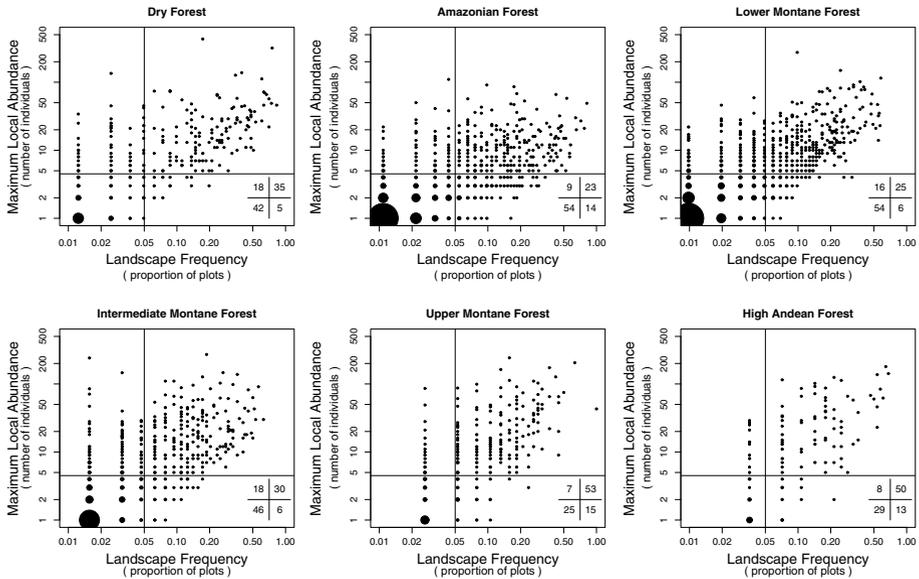
### Rarity classification and relationship between local commonness and landscape commonness

In all forest types 76–79 % of species were included in the rare and common classes (Fig. 1). However, below 2,400 m (DR, AM, LM and IM forests) there were more rare species than common species (42–54 vs. 23–35 %), whereas above 2,400 m (UM and HA forests) there were more common species than rare species (50–53 vs. 25–29 %). In all forest types the abundant-but-infrequent and the frequent-but-scarce classes only included relatively few species. Overall, the six forest types differed significantly in the proportion of species into the four rarity classes ( $G = 308.07$ ,  $P < 0.001$ ). Despite these differences, there was always a strong linear positive relationship between  $\ln(\text{maximum abundance})$  and  $\ln(\text{landscape frequency})$  of species in all forest types: DR ( $r = 0.72$ ), AM ( $r = 0.65$ ), LM ( $r = 0.72$ ), IM ( $r = 0.65$ ), UM ( $r = 0.69$ ) and HA ( $r = 0.71$ ); ( $P < 0.001$  in all cases).

### Relationship between local and landscape commonness and traits

The ANCOVA models indicated that species traits and commonness at plot-level and forest-level scales are significantly related (the models had  $P < 0.001$  in both cases). Taller species showed a significant trend to be more common at both local and landscape scales in AM and LM (Table 2). However, the inverse trend was found at landscape scale in the DR forest. On the other hand, species with larger maximum diameters tended to be uncommon at local scale in AM and LM forests, and also at landscape scale in LM forest.

There was a general trend for treelets and lianas to be less common at local scale than canopy trees (significantly in all forest types, except for lianas in the DR forest) (Table 2). The same applies at landscape scale (significantly in all forest types, except for lianas in the DR and HA forests; marginally significant for treelets at HA forest). Noteworthy, liana species tended to be slightly more common at landscape scale than canopy trees in the DR forest, although this trend was not statistically significant. In general, there was a trend for species with more stems per individual to be less common at the local and landscape scales in all forest types, but only significantly in the AM forest. However, shrub species were as common as canopy trees in all forest types.



**Fig. 1** Classification of species into four rarity classes in six tropical forest types in northern Bolivia. The horizontal lines separate the species with maximum local abundance  $\geq 5$  individuals from the others. The vertical lines separate the species present in 5 % or more of the plots from the others. These two criteria are combined to classify the species into four rarity classes. Each point corresponds to one species; several species of exactly the same characteristics are represented by points of increasing size. The bottom-right corner diagram represents the percentage of species in these four rarity classes

Relationship between the four rarity classes and traits

Overall, traits of species were significantly related to their rarity class in all forest types (multinomial logistic regression models with  $P < 0.001$  in all cases). The models coefficients indicated that being treelet or not was the most relevant factor across forest types (Fig. 2). Compared to canopy trees, treelet species were more likely to be rare than common (in all forest types), and more likely to be rare than abundant-but-infrequent (significantly in DR, IM and HA forests). Besides, treelet species were more likely to be rare than frequent-but-scarce in the DR forest.

The effect of being liana was similar at the highest elevations, although less pronounced. Compared to canopy trees, liana species were more likely to be rare than common in UM and HA forests, and more likely to be rare than abundant-but-infrequent in the HA forest. Although being shrub did not have any significant effect on the rarity class, species with more stems in average were less likely to be common than rare in the DR forests, less likely to be abundant-but-infrequent than rare (in AM and UM forests), and less likely to be frequent-but-scarce than rare in AM, LM and IM forests.

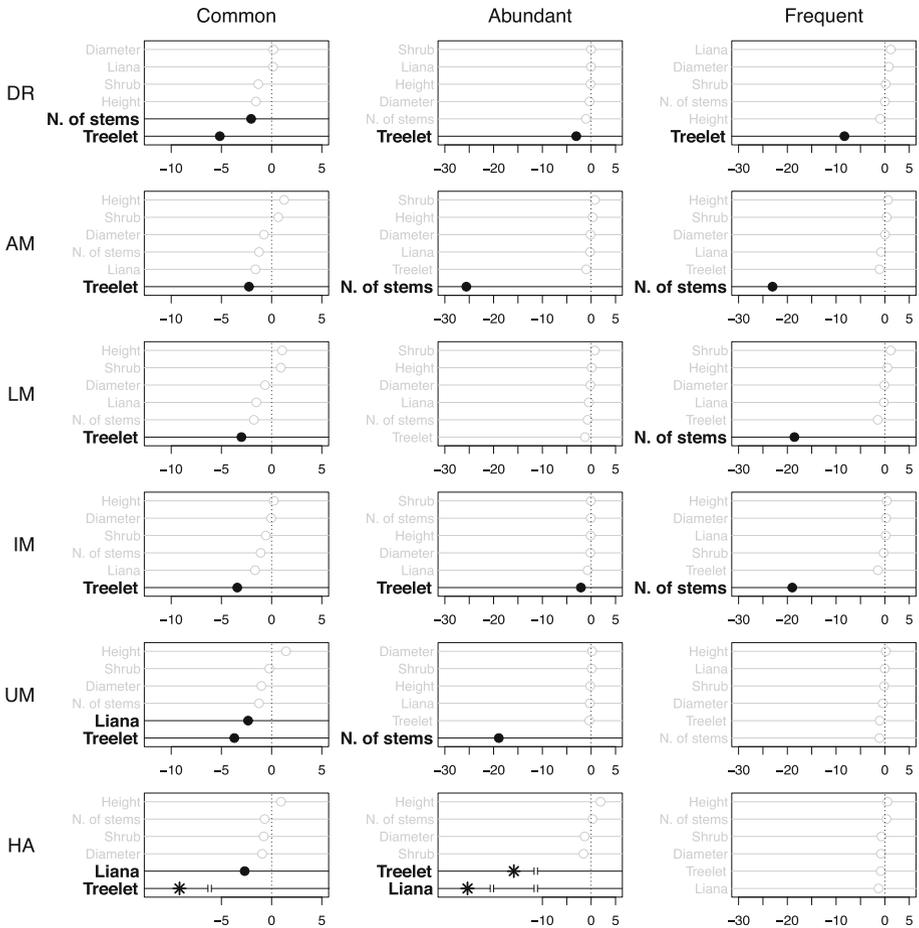
Discussion

The positive relationship between abundance and spatial distribution found in the six forest types implies that most of the species are ordered along a single commonness-rarity axis, with most of the species being infrequent and scarce or frequent and abundant (Fig. 1). Our

**Table 2** Results of the ANCOVA test between (a) local scale commonness [ $=\ln(\text{maximum local abundance})$ ] and traits, and (b) landscape scale commonness [ $=\ln(\text{landscape frequency})$ ] and traits

Response variables	Explanatory variables	Dry forest	Amazonian forest	Lower montane forest	Intermediate montane forest	Upper montane forest	High Andean forest
Local commonness	Maximum height	-0.04	<b>0.04***</b>	<b>0.02*</b>	-0.01	0.05	0.04
	Maximum diameter	-0.01	<b>-0.01***</b>	<b>-0.01**</b>	-0.01	-0.02	-0.01
	Median number of stems	-0.70	-0.29	-0.30	-0.45	-0.48	-0.21
Habit: liana	Habit: liana	-0.33	<b>-0.61***</b>	<b>-0.79***</b>	<b>-0.95***</b>	<b>-1.68***</b>	<b>-2.07**</b>
	Habit: shrub	-0.13	0.25	0.30	-0.09	-0.04	-0.24
	Habit: treelet	<b>-1.94***</b>	<b>-0.71***</b>	<b>-0.89***</b>	<b>-1.41***</b>	<b>-1.44***</b>	<b>-2.13***</b>
Landscape commonness	Maximum height	<b>-0.07***</b>	<b>0.04***</b>	<b>0.04***</b>	0.01	0.04	-0.01
	Maximum diameter	0.01	-0.01	<b>-0.01*</b>	<0.005	-0.01	0.01
	Median number of stems	-0.54	<b>-0.34*</b>	-0.41	-0.32	-0.24	-0.19
Habit: liana	Habit: liana	0.07	<b>-0.77***</b>	<b>-0.79***</b>	<b>-0.54**</b>	<b>-0.71**</b>	-0.54
	Habit: shrub	-0.52	0.07	0.21	-0.19	-0.16	-0.09
	Habit: treelet	<b>-1.85***</b>	<b>-0.67***</b>	<b>-0.81***</b>	<b>-0.78***</b>	<b>-0.91***</b>	-0.81

The values are ANCOVA coefficients; significances are indicated with \*\*\*  $P < 0.001$ , \*\*  $P < 0.01$ , or \*  $P < 0.05$ ; significant results are highlighted in bold case



**Fig. 2** Standardized coefficients of species traits (maximum height, maximum diameter, median number of stems, habit) on rarity class, as computed for multinomial logistic regression models. The *first column* represents the coefficients for the  $\ln(\text{probability of being common}/P_{\text{rare}})$ , the *second column* represents the coefficients for the  $\ln(\text{probability of being abundant but infrequent}/P_{\text{rare}})$ , and the *third column* represents the coefficients for the  $\ln(\text{probability of being frequent but scarce}/P_{\text{rare}})$ , being  $P_{\text{rare}}$  the probability of being scarce and infrequent. The *dotted vertical line* in zero represents the lack of effect. *Filled dots* represent significant deviations from zero, according to Z tests on the coefficients. *Asterisks* represent extreme (and significant) values of the coefficients for lianas and treelets in HA forests, which are caused by the lack of species in those rarity classes in that forest type. *DR* dry forest, *AM* Amazonian forest, *LM* lower montane forest, *IM* intermediate montane forest, *UM* upper montane forest, *HA* high Andean forest

results add to past studies reporting such a positive abundance-frequency relationship at different scales on tropical woody plants, the so-called oligarchic pattern (reviewed by Pitman et al. 2013). Although such relationships have been found to be stronger within a given region or habitat, a positive relationship between abundance and spatial distribution of species is one of the most general patterns in ecology at any scale (Gaston et al. 2000), strongly suggesting tight links from local and landscape commonness at <20,000 km<sup>2</sup> to regional and continental commonness at >2,000,000 km<sup>2</sup> (Kristiansen et al. 2009; ter Steege et al. 2013).

A novel strength of our work is to classify species into different rarity classes using the same thresholds to define rarity classes. This approach has been seldom adopted before, which has prevented from a general understanding of commonness/rarity patterns among habitats and study regions (Rabinowitz 1981; Rabinowitz et al. 1986; Ricklefs 2000). By doing so we find, on the one hand, that the positive relationship between abundance and distribution is a general pattern, as previous classifications of species in other tropical forests suggested (Pitman et al. 1999; Romero-Saltos et al. 2001). This indicates that the oligarchy hypothesis could apply from the Amazonia to the Andes up to  $\sim 3,700$  m in elevation (Pitman et al. 2001, 2013). On the other hand, we find that the proportion of rare and common species depends on the habitat considered, given that forests at higher elevations show increasingly stronger oligarchic patterns, by containing more common and fewer rare species (Fig. 1). Although most of the papers that support the oligarchic hypothesis have been focused in the lowland forests (e.g. Pitman et al. 2001; Vormisto et al. 2004; Macía and Svenning 2005), it is known that species richness and the degree of dominance of species are negatively correlated (Bazzaz 1975; Huston 1979) and then it seems plausible that the species are more common, in average, at higher elevations, where there are fewer species (Arellano et al. 2014).

Being treelet or liana has a great impact in the commonness/rarity of a species

Overall, habit was the most important factor related to the commonness and rarity patterns at both scales. Lianas were less common at local and landscapes scales, and more likely to be infrequent and/or scarce than canopy trees. This is something partially determined by how we chose the sampling sites: disturbed areas or liana-dominated gaps were avoided. The pattern was most distinct above 2,400 m, as expected for the elevational trend in abundance and diversity of lianas that is known to be a very general trend in tropical mountains, and caused by the low tolerance of lianas to the potentially lower temperatures at higher elevations (Schnitzer and Bongers 2002; Schnitzer 2005; Jiménez-Castillo et al. 2006).

Treelet species were also less common at local and landscapes scales, and were more likely to be infrequent and/or scarce than canopy trees in most forest types. In other words, these relatively small species do not show dominance in any sense, at any of the scales considered, which rises questions on how small and large plants can coexist, and why these relatively small species have not disappeared from the community, displaced by the small or juvenile individuals of potentially larger species.

A first hypothesis that could explain such phenomenon is that small species compete at finer scales than large species, and therefore the apparent success of large species is more a sampling effect than reflecting true competitive interactions (Aarssen et al. 2006). In this regard, the employed cut-off of 2.5 cm may have considered as rare some small species that seldom reach such size, being otherwise common. Considering this, other plot size, diameter cut-off, or sampling design, could have been more appropriate to correctly describe the commonness and rarity patterns of such subset of small species.

Alternatively, a second hypothesis sustains that smaller species, although not being highly competitive at the short-term when compared with larger species, tend to originate more derived species due to shorter life cycles and greater speciation rates (Aarssen et al. 2006). If this idea were true, groups of small and rare species would tend to share a common origin, and to be more closely related among them than large species. Previous research indicate that commonness and rarity are not randomly distributed among all the species of the community (e.g. ter Steege et al. 2013), but further research on the different

functional and evolutionary roles of tropical forest species is needed to gain insight into the role of evolution in shaping the patterns studied here.

Multi-stemmed or shrub species are not more common at any scale

We found evidence of no advantage of shrub or multi-stemmed species at local or landscape scales, neither any elevational trend in the commonness/rarity patterns of these species. In fact, species with more stems have a generalized trend to be scarce and/or infrequent, compared with single-stemmed species. This is surprising specially in the case of montane forests, since previous results showed that having multiple stems is an advantageous adaptation to low productivity levels and high frequency of disturbances due to steeper slopes typical of montane forests (Bellingham and Sparrow 2000, 2009). Moreover, this is in contrast with the observed increase in the proportion of shrub species with elevation, which somewhat suggests that shrubs do well at higher elevations. However, it could be explained if the higher prevalence of the shrub habit among montane species is related to evolutionary heritage of very diversified clades in the Andes (e.g. *Psychotria*, *Miconia*, *Clusia*), and not so much to competitive advantages of these species at ecological scales.

Being taller and having larger diameter are very different things

Contrary to our expectations, maximum height and maximum diameter of species presented very contrasting results, and more clearly for wet forest below 1,700 m elevation, where taller species are more common at both scales, whereas species with greater maximum diameters show the opposite pattern.

The relative success of taller species is in agreement with previous works focused on tropical forests at low elevations (Ruokolainen and Vormisto 2000; Davidar et al. 2008; Kristiansen et al. 2009). Overall, it seems that greater dispersal abilities associated with potentially higher individuals make the species to perform well at landscape level, which, in turn, could lead to high local abundances. This could be caused because taller species that disperse well are more likely to find highly suitable habitats where local populations can grow and develop well.

In contrast, species that attain greater diameters do not seem to outcompete other species at local or landscape scales, despite being hypothesized to have higher reproductive success (Nathan and Muller-Landau 2000; Westoby et al. 2002; Wright et al. 2007). What we find resembles the pattern reported by Itoh et al. (1997), who found that some large tree species were characterized by negative autocorrelation at the local scale (i.e., low local densities). They proposed the Janzen–Connell dynamics as the underlying mechanism for such distribution (Janzen 1970; Connell 1971). It is appealing to think about large (likely long-lived) individuals as long-term and stable reservoirs of host-specific predators and/or pathogens with greater influence over their surrounding area than smaller plants, but more research would be required to point towards a mechanistic cause for the pattern.

## Conclusions

Two main conclusions arise from the present study. First, the positive relationship between commonness at local and landscape scales indicates that very simple approaches to commonness and rarity based on abundance only or occurrence only, could summarize

most of the relevant information to characterize species commonness and rarity patterns. Both approaches, in practice, do not supply independent information, which indicates that a wide array of tools could be used to characterize the species, with direct consequences for applied ecology, such as employing presence/absence maps to estimate the total population size of a given species (Hui et al. 2009, 2010). Finally, the species traits determine which species are to be rare and which to be common, which indicates that commonness and rarity patterns do not result solely from stochastic processes, but are the result of non-neutral trait-based community assembly (McGill et al. 2006a, b, 2007; Violle et al. 2012).

**Acknowledgments** We are very grateful to P. M. Jørgensen, coordinator of the Madidi Project, and to L. E. Cayola, A. F. Fuentes, A. Araújo-Murakami, M. Cornejo, V. W. Torrez, J. M. Quisbert, T. B. Miranda, R. Seidel, N. Y. Paniagua, and C. Maldonado, who provided very valuable plot data for the present study. We also appreciate the indispensable help of many students and volunteers who collaborated in the field and herbarium. We thank the Dirección General de Biodiversidad, the Servicio Nacional de Áreas Protegidas, Madidi National Park, and local communities for permits, access, and collaboration during the fieldwork. An anonymous reviewer provided useful comments to the manuscript. We received financial support from the following institutions: Consejería de Educación (Comunidad de Madrid), National Geographic Society (8047-06, 7754-04), US National Science Foundation (DEB#0101775, DEB#0743457), and Universidad Autónoma de Madrid—Banco Santander, for which we are grateful.

## References

- Aarssen LW, Schamp BS, Pither J (2006) Why are there so many small plants? Implications for species coexistence. *J Ecol* 94:569–580
- Arellano G, Cayola L, Loza I et al (2014) Commonness patterns and the size of the species pool along a tropical elevational gradient: insights using a new quantitative tool. *Ecography* 37:536–543
- Bazzaz FA (1975) Plant species diversity in old-field successional ecosystems in Southern Illinois. *Ecology* 56:485–488
- Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. *Oikos* 89:409–416
- Bellingham PJ, Sparrow AD (2009) Multi-stemmed trees in montane rain forests: their frequency and demography in relation to elevation, soil nutrients and disturbance. *J Ecol* 97:472–483
- Brown JH (1984) On the relationship between abundance and distribution of species. *Am Nat* 124:255–279
- Clark PJ, Evans FC (1954) Distance to nearest neighbor as a measure of spatial relationships in populations. *Ecology* 35:445–453
- Connell JH (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: Boer P, Gradwell G (eds) Dynamics of populations. Centre for Agricultural Publications and Documentation, Wageningen
- Davidar P, Rajagopal B, Arjunan M, Puyravaud JP (2008) The relationship between local abundance and distribution of rain forest trees across environmental gradients in India. *Biotropica* 40:700–706
- Fuentes A (2005) Una introducción a la vegetación de la región de Madidi. *Ecología en Bolivia* 40:1–31
- Gaston KJ (1994) *Rarity*. Chapman & Hall, London
- Gaston KJ (2010) Valuing common species. *Science* 327:154–155
- Gaston KJ (2012) The importance of being rare. *Nature* 487:46–47
- Gaston KJ, Blackburn TM, Greenwood JJD et al (2000) Abundance-occupancy relationships. *J Appl Ecol* 37:39–59
- Gentry AH (1991) The distribution and evolution of climbing plants. In: Putz FE, Mooney HA (eds) *The biology of vines*. Cambridge University Press, Cambridge
- Hanski I (1982) Dynamics of regional distribution: the core and satellite species hypothesis. *Oikos* 38:210–221
- Hui C, McGeoch MA, Reyers B et al (2009) Extrapolating population size from the occupancy-abundance relationship and the scaling pattern of occupancy. *Ecol Appl* 19:2038–2048
- Hui C, Veldtman R, McGeoch MA (2010) Measures, perceptions and scaling patterns of aggregated species distributions. *Ecography* 33:95–102
- Huston M (1979) A general hypotheses of species diversity. *Am Nat* 113:81–101

- Itoh A, Yamakura T, Ogino K et al (1997) Spatial distribution patterns of two predominant emergent trees in a tropical rainforest in Sarawak, Malaysia. *Plant Ecol* 132:121–136
- Janzen DH (1970) Herbivores and the number of tree species in tropical forests. *Am Nat* 104:501–528
- Jiménez-Castillo M, Wiser SK, Lusk CH (2006) Elevational parallels of latitudinal variation in the proportion of lianas in woody florals. *J Biogeogr* 34:163–168
- Kelly C, Woodward F, Crawley M (1996) Ecological correlates of plant range size: taxonomies and phylogenies in the study of plant commonness and rarity in Great Britain. *Philos Trans Biol Sci* 351:1261–1269
- Kristiansen T, Svenning J-C, Grández C et al (2009) Commonness of Amazonian palm (Arecaceae) species: cross-scale links and potential determinants. *Acta Oecol* 35:554–562
- Letcher SG, Chazdon RL (2012) Life history traits of lianas during tropical forest succession. *Biotropica* 44(6):720–727
- Macía MJ, Svenning J-C (2005) Oligarchic dominance in western Amazonian plant communities. *J Trop Ecol* 21:613–626
- McGill BJ, Enquist BJ, Weiher E, Westoby M (2006a) Rebuilding community ecology from functional traits. *Trends Ecol Evol* 21:178–185
- McGill BJ, Maurer BA, Weiser MD (2006b) Empirical evaluation of neutral theory. *Ecology* 87:1411–1423
- McGill BJ, Etienne RS, Gray JS et al (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol Lett* 10:995–1015
- Moles AT, Westoby M (2004) Seedling survival and seed size: a synthesis of the literature. *J Ecol* 92:372–383
- Moles AT, Falster DS, Leishman MR, Westoby M (2004) Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per life-time. *J Ecol* 92:384–396
- Nathan R, Muller-Landau H (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends Ecol Evol* 15:278–285
- Navarro G, Ferreira W, Antezana C et al (2004) Bio-corredor Amboró Madidi, zonificación ecológica. Editorial FAN, Santa Cruz
- Pérez-Saliciprup DR, Schnitzer S, Putz FE (2004) Community ecology and management of lianas. *For Ecol Manage* 190:1–2
- Pitman NCA, Terborgh J, Silman MR, Núñez P (1999) Tree species distributions in an upper Amazonian forest. *Ecology* 80:2651–2661
- Pitman NCA, Terborgh JW, Silman MR et al (2001) Dominance and distribution of tree species in upper Amazonian terra firme forests. *Ecology* 82:2101–2117
- Pitman NCA, Silman MR, Terborgh JW (2013) Oligarchies in Amazonian tree communities: a ten-year review. *Ecography* 36:114–123
- Preston FW (1948) The commonness, and rarity, of species. *Ecology* 29:254–283
- Rabinowitz D (1981) Seven forms of rarity. In: Syngé H (ed) *The biological aspects of rare plant conservation*. Wiley, New York
- Rabinowitz D, Cairns S, Dillon T (1986) Seven forms of rarity and their frequency in the flora of the British Isles. In: Soulé ME (ed) *Conservation biology: the science of scarcity and diversity*. Sinauer Associates Inc, Sunderland
- Ricklefs RE (2000) Rarity and diversity in Amazonian forest trees. *Trends Ecol Evol* 15:83–84
- Romero-Saltos H, Valencia R, Macía MJ (2001) Patrones de diversidad, distribución y rareza de plantas leñosas en tres tipos de bosque en la Amazonia nororiental ecuatoriana. Evaluación de recursos forestales no maderables en la Amazonía noroccidental. IBED-Universiteit van Amsterdam, Amsterdam
- Ruokolainen K, Vormisto J (2000) The most widespread Amazonian palms tend to be tall and habitat generalists. *Basic Appl Ecol* 1:97–108
- Schawe M, Glatzel S, Gerold G (2007) Soil development along an altitudinal transect in a Bolivian tropical montane rainforest: podzolization versus hydromorphy. *Catena* 69:83–90
- Schnitzer SA (2005) A mechanistic explanation for global patterns of liana abundance and distribution. *Am Nat* 166:262–276
- Schnitzer SA, Bongers F (2002) The ecology of lianas and their role in forests. *Trends Ecol Evol* 17:223–230
- ter Steege H, Pitman NCA, Sabatier D et al (2013) Hyperdominance in the Amazonian tree flora. *Science* 342. doi:10.1126/science.124309
- Violle C, Enquist BJ, McGill BJ et al (2012) The return of the variance: intraspecific variability in community ecology. *Trends Ecol Evol* 27:244–252
- Vormisto J, Svenning J-CC, Hall P, Balslev H (2004) Diversity and dominance in palm (Arecaceae) communities in terra firme forests in the western Amazon basin. *J Ecol* 92:577–588

- Westoby M, Falster DS, Moles AT et al (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annu Rev Ecol Syst* 33:125–159
- Wright IJ, Ackerly DD, Bongers F et al (2007) Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Ann Bot* 99:1003–1015