379
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Contribution of species abundance and frequency to aboveground forest biomass along an Andean elevation gradient

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ABSTRACT

Aims: To determine whether species that contribute most to a plot's biomass are the most abundant (high local abundance at plot scale) or the most frequent (occur the most across plots at landscape scale), or both. In the tropical Andes, these patterns may change with elevation. This study assesses the contribution to plot's aboveground biomass (AGB) of the plant community abundance pattern –the prevalence of within-plot dominant species– and the over-occurrence of regionally frequent species, in an elevation gradient.
Methods: We considered all trees ≥ 2.5 cm DBH from 446 0.1 ha plots in an Amazonia-Andes 260–4350 m elevation cline in N Bolivia. Plot AGB was calculated as the sum of AGBs for all stems contained. We grouped plots into four bins segregated by elevation and ran a bootstrap analysis over subsets of 58 random plots per bin with 100 iterations. Simpson evenness index (E_D) for all species in each plot was used as a measure for its species abundance. Values for each plot's species frequency was calculated as the mean of all species' in the plot mean frequencies across the bin (i.e. the fraction of plots where each species occurs). We used linear models to correlate plot AGB with (1) elevation and mean annual precipitation (MAP), and (2) E_D, plot species frequency and elevation. We performed all analyses at the species, genus and family levels.
Results: Plot AGB was related negatively with elevation, and thus positively with MAP, and also negatively with plot E_D and plot species frequency, all significant. Plot species abundance therefore contributes positively to explain the relationship with AGB along elevational gradients, while plot species frequency does so negatively (i.e. less frequent species contribute more to a plot's AGB across elevation). AGB, for both generic and familial levels was also significantly and negatively correlated with E_D, but not related with plot species frequency biomass at these taxonomic levels.
Conclusions: Plot AGB was mainly associated with elevation and floristic composition where species, genera and families tended to be abundant at the local (plot) scale. Species that were less frequent at the regional scale contributed with more AGB regionally, while frequency at generic and familial scales did little to explain AGB patterns. This association seems stronger at lower elevations for all taxonomic levels while decreases toward higher elevation. Our study reveals a relationship between plot structural features like C stocks –influenced by species local abundances– and the distribution of taxa across the landscape.

1. Introduction

Most carbon sequestration in the Neotropics takes place in tropical rain forests. These ecosystems are estimated to account for ~60% of global forest biomass and ~50% of terrestrial biomass (Houghton et al., 2009). Given the ecological importance of these forests, it is relevant to assess the contribution of species abundance patterns to a plot's aboveground biomass (AGB), hereafter referred to as an attribute of an entire

plot, including all individuals within.

Montane forests in the Andes are subject to great variation in environmental factors at relatively short geographic distances, which could affect their AGB and carbon storage (Clark & Clark, 2000; Alves et al., 2010; Girardin et al., 2013; Alvarez-Davila et al., 2017). In mountainous regions, growth is mainly constrained by physical characteristics, related to elevation such as temperature and precipitation. Both rainfall and temperature tend to diminish with elevation, although the overall reduction in rainfall with elevation is usually discontinuous due to a precipitation peak at middle elevation (Körner, 1999). In general, these climatic variables are good predictors of the variation in species composition, diversity, structure, and primary productivity along the elevation gradient (Poorter et al., 2017); mainly, high precipitation and seasonal water availability are strongly related with an increase of biomass in Netropical forest (Alvarez-Davila et al., 2017; Poorter et al., 2017). In turn, the number of individuals that an area can support tends to increase with primary productivity (Mittelbach, 2012).

In tropical rain forests, high scale of productivity is usually found in lowland and premontane forest, which also contain the richest species diversity likely due to warmer temperatures, and high water availability (Benner et al., 2010; Mittelbach, 2012; Alvarez-Davila et al., 2017; Poorter et al., 2017); although in mid-elevation tropical montane forests have also been found high scales of productivity (Huaraca et al., 2013; Arellano et al, 2017). At the same time, patterns of tree species dominance vary across the elevation gradient in terms of structure (i.e. tree density, basal area, canopy height, and biomass), floristic composition, or both (Richards, 1996; Guo & Rundel, 1997). Accordingly, very large trees and lianas practically disappear at the highest elevations, where shrubs become the prevalent growth form (Janzen, 1975). In addition to lower temperatures and less precipitation, other potential environmental factors that change with elevation are steeper slopes, greater wind speed, more intense UV radiation, more cloudiness, and poorer soils with lower pH (Körner, 1999; Unger et al., 2012; Girardin et al., 2013).

In addition to environmental drivers, the diversity and composition of species may determine biomass in Neotropical rain forests (Poorter et al., 2017; Sullivan et al., 2017) on the basis of how dominant species are in a particular area. Any forest community taken at a regional scale includes a subset of species that are considerably more abundant locally, and at the same time may have a broad range of distribution, thus becoming considerably frequent across localities. These species have often been named as "common" (Brown, 1984; Pitman et al., 2001). This pattern has been supported by some studies showing that most abundant species (at the plot scale) often are also frequent at the landscape scale (Pitman et al., 2001, 2012; Arellano & Macía, 2014). Thus, any species can be defined according to two components: abundance (local relative number of individuals) and frequency (occurrences across landscape). Although the reasons why a given species is abundant ("numerically") are many and difficult to discern, some generalizations could be made: (1) numerically abundant species can be assumed to have a higher capacity to mobilize resources and assimilate energy (Hall et al., 1992), or (2) more resistance to pathogens, herbivores, or any source of frequency-dependent mortality (as pointed out by ter Steege et al., 2013), or (3) species density depends on its population long-term dynamics (balance between mortality and recruitment), for instance, by exhibiting low mortality rates (Lines et al., 2010). Regarding frequent species, they are assumed to be generalists, sharing with dominant species traits that allow them the use of a broader range of resources across environmental gradients (Condit et al., 2000). These species-level properties could have an impact on forest-level AGB, given that local species compositions and their respective distributional patterns change: in some places "numerically abundant" species will prevail over "numerically scarce" species (or vice-versa), and/or species "frequent in the landscape" will prevail over those "infrequent in the landscape" (or vice-versa) (Pitman et al., 2001). Although in different ways, both components contribute to local

plot scale AGB. Unless they exhibit very low wood density, numerically abundant species will obviously contribute more to AGB, while species that are frequent at the landscape scale are expected to have greater ability to exploit a wider range of resources (Higgins & Richardson, 1999), thus contributing to a more complete exploitation of resources within plots. The latter would increase plot productivity and AGB, an effect reinforced because frequent species are also expected to disperse more efficiently, reaching more plots. Moreover, this tendency ought to persist at the genera and family levels as well because those taxonomic groups with more abundant and/or frequent species would contribute to a biomass pattern that extrapolates to the landscape scale (ter Steege et al., 2013).

In tropical montane forests, abiotic environmental gradients that affect plot AGB are well summarized by elevation (Malhi et al., 2006), but the relative contribution of species abundance and frequency is often not discriminated when community biomass is considered as a whole. Amazonian lowland forests have very high species richness at the plot scale (alpha-diversity) (Gentry, 1988), and their pattern of dominance in terms of abundance and frequency is likely favored by environmental homogeneity (essentially soil and climate) across a rather flat landscape. When environmental filtering becomes more stringent in higher elevation forests, this pattern of species dominance turns out to be weaker (Pitman et al., 2001, 2012; Trujillo et al., 2019). Therefore, species abundance and frequency could help to explain elevational patterns of AGB at the plot scale (i.e., low AGB at higher elevation) since their values decline with elevation largely due to the increase of environmental harshness and heterogeneity along the gradient (Stein et al., 2014). Despite the importance of Andean mountain forests in providing ecosystem services to the entire region (Körner, 1999), intimate knowledge of the biotic and abiotic factors determining biomass is scant (Gentry, 1988; Chave et al., 2003; Unger et al., 2012; Girardin et al., 2013; Alvarez-Davila et al., 2017). Most studies have explored the relationship between biomass and structure of the tropical forest focusing on lowland forests (Clark & Clark, 2000; DeWalt & Chave, 2006; Anderson et al., 2009), but there are fewer studies that consider the role of dominant species on biomass in tropical montane forests (Fauset et al., 2015), much less on this relationship across elevation gradients.

Here, we aim to investigate the relationship between AGB at the plot scale and the dominance patterns (abundance, frequency) of species, genera and families across an Amazon-Andes elevation gradient. We also analyzed data to taxonomic levels above species because dominance patterns have sometimes been assessed at the genus and family levels (ter Steege et al.,2013). AGB was calculated from allometric functions based on stem diameter, height and wood density (Kebede & Soromessa, 2018; Chave et al., 2015). We consider dominance value as a stand (plot) attribute, which is a function of its tree community assemblage. While plot AGB is expected to decrease with elevation, we hypothesize that the effect of elevation on AGB will be smaller in plots where dominance is higher.

Our specific hypotheses thus are: 1) stand AGB, estimated from trees contained in a plot, decreases as MAP decreases and elevation increases; 2) the two components of dominance —abundance and frequency, both considered as stand attributes— are positively correlated with AGB, which also makes elevation and AGB be negatively related; 3) the effect of both components of plot-scale dominance on AGB across elevation is consistent at different taxonomic levels: species, genus and family.

2. Methods

2.1. Study area

We analyzed plot data from Parque Nacional Madidi and surrounding areas, a region 18,854 km^2 in northern Departamento de La Paz, Bolivia. The study was carried out in this tropical region, between
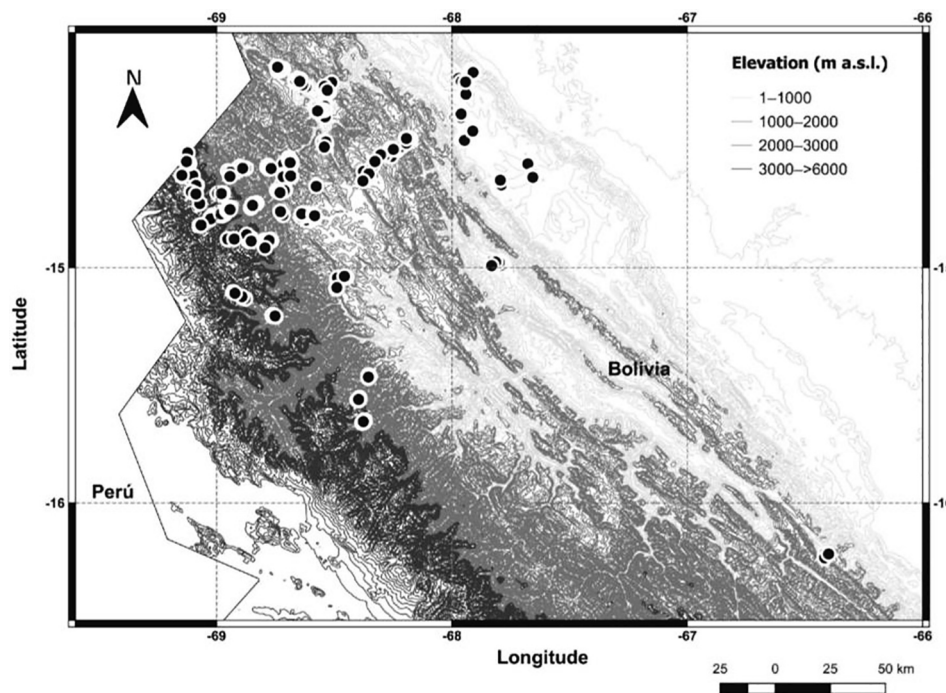
Fig. 1. Study area in the Madidi region, Bolivia. Points show study plots.

14°33́52″S, 67°40́24″W and 14°36́26″S, 69°08́52″W, which includes large swaths of the Bolivian Amazonia and the Andes mountains, ranging from lowland rain forests and dry savannas below 200 m a.s.l., to cloud and mid to high elevation montane forests, to summits above 5000 m with subnival vegetation (Fuentes, 2005; Forrest et al., 2008) (Fig. 1).

The Madidi region encompasses large physiographic units that include the Cordillera Oriental and the Subandino mountain systems, with rainy and dry bioclimates. Precipitation varies with elevation and topography, from the mean annual 2,335 mm of the Amazon lowlands (Navarro et al. 2004) to the broad 100–3,500 mm range of Andean uplands. Annual mean temperature ranges from 25 °C in the eastern lowlands to −2.5–0.5 °C near the summits (Fuentes, 2005).

Data was obtained from 446 inventories of 0.1 ha forest plots carried out by various researchers between 2001 and 2011 as part of the Madidi Project (https://madidiproject.weebly.com/). The location of plots ranged from the Amazonian lowlands ca. 260 m a.s.l. to the high elevation Andes up to 4,350 m, with most plots between 1,000 and 3,000 m. Inventory data consisted of tree height and diameter at breast height (DBH, 130 cm above ground) of all woody individuals (≥2.5 cm DBH), including palms, tree ferns and lignified Poaceae (Arellano et al., 2016), while lianas were excluded from the analyses. All stems of the multiple stemmed individuals were accounted only once for the analysis. The height of each stem, necessary to estimate biomass of individuals, was estimated visually, with some prior training or experience.

The dataset contained a total of 123,856 individuals belonging to 2,060 species (including morphospecies), 527 genera, and 126 families. Vouchers were deposited at the Herbario Nacional de Bolivia in La Paz (LPB, with duplicates at the Missouri Botanical Garden, MO). Analyses were conducted separately at three levels of taxonomic resolution: species, genus and family.

The mean annual precipitation (MAP) was obtained from the WorldClim-Global Climate Data (version 2.0, Fick & Hijmans, 2017), at a spatial resolution of ca. 1 km².

2.2. Analyses

To estimate plot AGB we used allometric measures that include tree height, diameter and wood density, using the equation proposed by Chave et al. (2015):

$$AGB = 0.0673(\rho Di^2 H)^{0.976}$$

where ρ is wood density (g/cm³), Di is diameter (cm) and H is tree height (m). Di and H were measured for each individual within each plot, while data for wood density were obtained from the Global Wood Density Database (Zanne et al., 2009). Since measurement of wood density was not available for many species, we assigned those the mean wood density of congenerics that have one. We then calculated plot AGB as the sum of all stems' biomass within the plot.

To determine the species abundance at the plot scale we estimated the prevalence of within-plot dominant species by calculating the Simpson Evenness index (E_D), applied to the number of stems of all species present in each plot (plot species evenness). A high value of the evenness index indicates that species are equally abundant (none dominates), while a low value indicates that a few species account for most of the stems (i.e., high co-dominance of those few). Plots whose community assemblage contain species with high abundance will have low E_D values. This indicator allows to relate AGB with the degree of occurrence of many individuals or stems of a few species, or alternatively with the degree of plot homogeneity in terms of species relative abundance.

To calculate E_D, we first estimated the Inverse Simpson index (D) as the inverse of the sum of the squared proportions of every taxon (p_i).

$$D = \frac{1}{\sum_{i=1}^{S} p_i^2}$$

E_D was calculated as the quotient between D and the maximum value of D, corresponding to species evenly distributed in the community, where S = species richness.

$$E_D = \frac{D}{D_{max}} = \frac{1}{\sum_{i=1}^{S} p_i^2} \times \frac{1}{S}$$

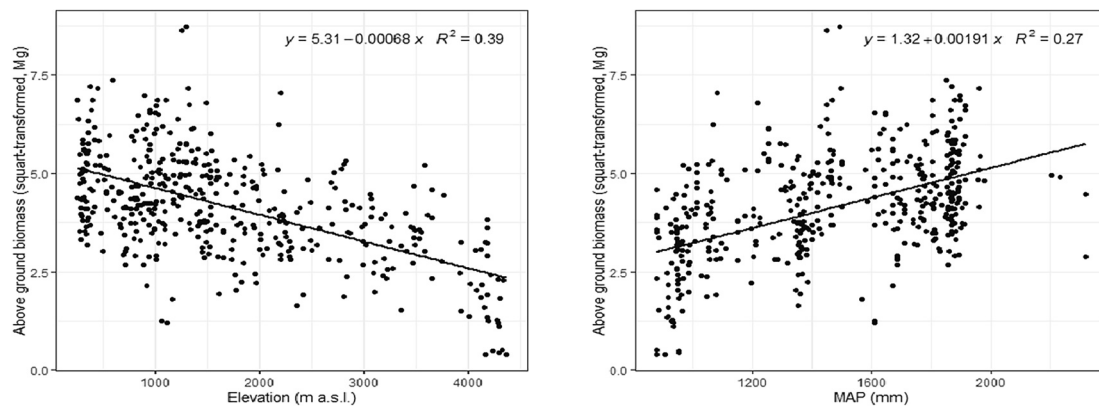We used a bootstrap analysis using 100 iterations to determine plot

Fig. 2. Linear regressions relating plot AGB with elevation (a): $R^2 = 0.39$, $P < 0.001$, and MAP (b): $R^2 = 0.27$, $P < 0.001$.

species frequency variable in order to minimize the asymmetry between the very many plots from the dataset from lowland Amazonian forests and the very few from the uplands. We segregated the total 446 plots into four bins corresponding to four elevation bands: 260–1000 m, 1000–2100 m, 2100–3200 m and 3200–4400 m, where the bin with the least plots (those above 3200 m) contained 59 plots. So, subsets of 58 plots were randomly sampled for each elevational bin; then, 100 iterations of this procedure were conducted.

To determine plot species frequency, we estimated the prevalence of frequent species across plots within a bin by calculating the proportion of total plots (58 randomly sampled plots in each elevational bin) in which each species occurred. We then used the average value from all species present in the plot. A high value for plot species frequency means that such plot has many species that are frequent at the landscape scale. The same procedure was applied when estimating plot E_D and plot taxon frequency at the genus and family levels by pooling the values for all species belonging to the same genus and to the same family, respectively.

To test the first hypothesis, which establishes that stand AGB decreases with the MAP associated with greater elevation, we used univariate linear models to explain the relationship between plot AGB with elevation and MAP separately. To test the second hypothesis, which relates the plot AGB with the patterns of species abundance and frequency at the plot scale, we used general linear models, with plot AGB as the response variable and plot elevation, E_D (high local abundance) and plot species frequency (high occurrence of species on plots across landscape) as predictor variables. The same linear models were used for subsequent analyses at the genus and family levels in order to answer the third hypothesis.

The statistical linear models were assessed with the Akaike information criterion (AIC) for selecting the better fitting linear model (lower AIC). We also used the variance inflation factor (VIF) to detect multicollinearity between variables and then selected the linear models with lower VIF. AGB data were square-root-transformed to meet the assumptions of normality. All analyses were carried out in R (R Core Team, 2018).

3. Results

Among the 123,856 recorded individuals, 3,010 belonged to *Oxandra espintana*, 2,828 to *Polylepis pepei*, 1,800 to *Hedyosmum racemosum*, and 1,700 to *Iriartea deltoidea*. The rest of species each had < 1,500 individuals throughout the dataset. For genera, we registered 7,597 individuals belonging to the genus *Miconia*, 4,411 to *Polylepis*, 3,338 to *Weinmannia*, and 3,135 to *Trichilia*; the rest of genera had each fewer than 3,000 individuals. Melastomataceae was the family with most individuals (9,225), followed by Rubiaceae (7,834), Arecaceae (6,239) and Myrtaceae (6,117); the rest of families had each fewer than

6,000 individuals (Supplementary material, Table 1).

The species that occurred in the most plots were *Euterpe precatoria* (125 plots of the total 446), *Alchornea glandulosa* (1 2 0), *Tapirira guianensis* (1 1 5), *Iriartea deltoidea* (1 0 4), and *Guatteria punctata* (1 0 2); the rest were found in fewer than 100 plots. The genera present in most plots were *Miconia* (267 plots), *Ocotea* (234 plots), *Piper* (216 plots), *Inga* (214 plots), and *Myrcia* (202 plots); the rest were found in fewer than 200 plots. The families that occurred in most plots were Myrtaceae (336 plots), Lauraceae (329 plots), Rubiaceae (326 plots) and Fabaceae (308 plots); the rest occurred in fewer than 300 plots (Supplementary material, Table 1).

We found a total of 8542.211 Mg of AGB over all the plots. Plot AGB ranged between 0.16 and 76.14 Mg (mean = 19.15, SD = 11.3). The species that contributed the most to plot AGB, throughout the whole elevation gradient, were *Anadenanthera colubrina* (315.57 Mg), *Schinopsis brasiliensis* (147.91 Mg), *Pseudolmedia laevis* (105.12 Mg) and *Pouteria bilocularis* (103.89 Mg). The genera that contributed with the most AGB throughout were *Anadenanthera* (315.57 Mg), *Polylepis* (225.07 Mg), *Ocotea* (222.31 Mg) and *Pouteria* (216.94 Mg). We found Fabaceae (1044.97 Mg), Moraceae (676.49 Mg), Lauraceae (506.89 Mg) and Malvaceae (341.77 Mg) to be the families with greatest AGB.

3.1. Relationships between plot AGB, elevation and MAP

Plot AGB was significantly and negatively correlated with elevation ($R^2 = 0.39$, $P < 0.001$. Fig. 2). There were significantly positive linear relationships between plot AGB and MAP ($R^2 = 0.27$, $P < 0.001$). Also, we found a negative relationship between MAP and elevation ($R^2 = 0.85$, $P < 0.001$) (Supplementary material, Fig. 1).

3.2. Relationships between plot AGB, elevation and dominance

Various models were considered before determining that that the model: elevation, E_D and frequency, made the best predictor. There was a significant negative linear relationship of plot AGB with elevation and with E_D at all three taxonomic levels: species, genus and family (Fig. 3a, b, c; Table 1). Thus, along the elevational gradient, plots with higher AGB contained few taxa contributing with the most individuals. The negative significant interaction between AGB and E_D indicates that plots with greater AGB tended to contain individuals from species, genera and families that were abundant. In other words, there are some within-plot dominant taxa that contribute positively to the AGB. AGB was also negatively correlated with plot species frequency (Fig. 3d, Table 1). This means that there are plots with higher AGB that contain fewer species that occur frequently at the landscape scale, although this result is not consistent at the generic and familial levels.
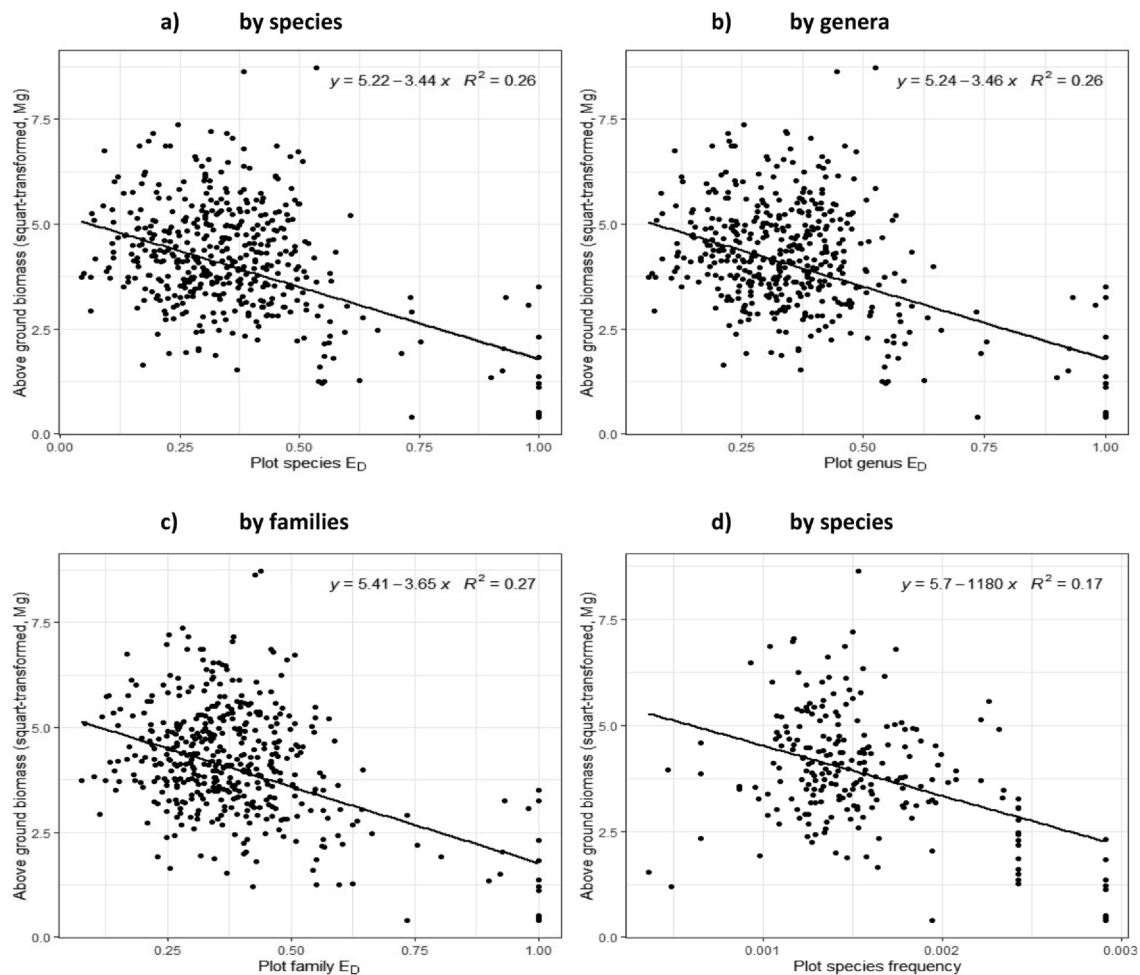
Fig. 3. Linear regressions relating the AGB with plot-scale species E_D at the a) species, b) genus, and c) family level; d) relationship of AGB with plot-scale species frequency.

Table 1

Statistical summary of the general linear model results for plot AGB and elevation, plot species evenness (E_D) and plot species frequency (Frequency) as predictors. The models were also applied to the genus and family levels. Statistically significant in bold ($P < 0.05$*; $P < 0.01$**; $P < 0.001$***). E: regression coefficient.

Sqrt Biomass (Mg)		
	E	P
Species		
Elevation	− 0.0005	**0.000***
E_D	− 1.048	**0.053***
Frequency	− 445.278	**0.039***
R^2 (adjusted) = 0.44		
Genus		
Elevation	− 0.001	**0.000***
E_D	− 1.389	**0.005****
Frequency	66.414	0.216
R^2 (adjusted) = 0.42		
Family		
Elevation	− 0.001	**0.000***
E_D	− 1.749	**0.000***
Frequency	58.874	0.07
R^2 (adjusted) = 0.43		

4. Discussion

In this study we show that above-ground biomass, one of the most important structural properties of tropical forests, is negatively correlated to elevation and, as expected, is greater where precipitation (MAP) is higher, (i.e., plots in the rainier Amazonian lowland forests had greater ABG than plots from montane forests). The Andean elevational gradient exhibits the common pattern of a gradual change in forest structure as elevation increases, paralleled with a general decline in AGB and woody species richness (Girardin et al., 2013; Alvarez-Davila et al., 2017), although often hump-shaped (Trujillo et al., 2019; de la Cruz-Amo et al., 2020). The relationship between climate variables and forest primary production (Körner, 1999; Reich et al., 2014; Alvarez-Davila et al., 2017) is largely determined by water availability, one of the variables most responsible in determining forest structure and carbon stocks (Alvarez-Davila et al., 2017; de la Cruz-Amo et al., 2020). Unsurprisingly, we found the greatest number of stems –and the highest values of plot AGB– in the rainier lowlands. According to the second hypothesis, the two components of dominance —abundance and frequency— were significantly correlated with AGB, which makes them relevant to elucidate the pattern of AGB, in our case along the elevation gradient. The significant negative relationship of AGB with E_D, for all taxonomic levels, showed that plots whose woody plant assemblage contains some species that are locally abundant, contribute more to the AGB and productivity of an area (Fauset et al.2015). AGB is also negatively correlated with plot species frequency (presence of species with high occurrence across an altitudinal band), meaning that to

landscape scale few species contributed with greater biomass. This negative effect of frequency on AGB, however, is present only at the species but not at the generic and familial levels.

In this study we show that plots with less frequent species attain more AGB than plots containing species that are widely distributed. That could mean that species with larger stem sizes –one may argue– are perhaps less frequent, –specifically in the lowlands– but still, due to their large size may be contributing disproportionally to those few plots where they are present. According to Fauset et al., 2015, both, abundance of species and their maximum stem size are the principal predictors of species contribution to regional biomass and productivity (Fauset et al., 2015).

As our study shows, the presence of plots dominated by abundant species –mainly those in low-elevation forests–, with higher AGB, is likely the result of relative environmental homogeneity (Pitman et al., 2001; ter Steege et al., 2013; Fauset et al., 2015). In low-elevation tropical forest a few abundant species have been found to account for most of the biomass to these forests, contributing to their dominance in the landscape in the same way that frequent species do (Pitman et al., 2001, ter Steege et al, 2013; Fauset et al., 2015). We hypothesize that many of these species are distributed according to similar ecological requirements, including edaphic and climatic factors (Brown, 1984; Pitman et al., 2001; ter Steege et al., 2013. We found few studies that assessed the contribution of common taxa to community biomass at regional or plot scales. Fauset et al. (2015) showed that few species account for most biomass regionally, this is mainly because they are more common, and they only contribute to high AGB in plots if they are common regionally and/or have high wood density. There is evidence that the stem density increase toward high elevations (Culmsee et al., 2010), however the biomass decrease in these areas. Then, according to Moser et al. (2008) it is likely that the highest biomass contribution does not depend on abundance but also on structural attributes such as wood density, basal area or plant height. Then, commonness in plots could also lead to dominance in the landscape (ter Steege et al., 2013).

The greater AGB at low elevations may be explained not only by the general trend of tropical lowlands harboring species that are more common, but also by those with large individuals (Pitman et al., 2001, Ghazoul & Sheil, 2014; Mittelbach, 2012; DeWalt & Chave, 2006). The gentle topography of the lowlands favors the establishment of large trees (Valencia et al. 2009), less present in the steep slopes of mountains. Nutrient limitation due to limited soil microbial activity, low sunlight, reduced transpiration and strong winds result in the smaller but multiple-stem trees of highland forests that may end up containing greater biomass (Leuschner et al., 2007; Ghazoul & Sheil, 2014). The overall association between common species and AGB could therefore be better explained by the existence of species by the number of individuals representing them locally than for the widely distribution that they may have at the landscape scale, overall in lowlands; while, the highlands AGB is most dependent on small-sized multi-stemmed trees and shrubs (Janzen, 1975). We found that the observed negative relationships between plot taxon frequency and plot AGB did not carry over at the genus and family taxonomic levels, probably because there are many genera represented by few common species, or families represented by few common genera. Palms are represented by several abundant species in Madidi and most Amazonian forests, but with few genera, as the *Arecaceae* that contribute greatly to the number of stems in a given plot, or *Iriartea* that is one of the genus found most predictably in any plot of *terra firma* forest in Amazonia (Pitman et al., 2001, Fauset et al., 2015), probably Arecaceae is one of the families with the most overall biomass.

It is noteworthy that two palm species from those forests, *Iriartea deltoidea* and *Euterpe precatoria,* were mostly responsible for the family pattern we observed due to their broad distribution and total AGB (90.78 Mg and 26.54 Mg, respectively).

One explanation for this taxonomic patterns in relationship to their contribution to AGB is that for certain families with a low speciation rate, the few extant species would tend to have broad distributional ranges (Domínguez-Lozano & Schwartz, 2005). In tropical rainforests, although high tree diversity implies a low relative density of individuals for most species (Huston, 1979; Condit et al, 2000), some genera and families may dominate in number of individuals, so there will be genera and families with more specificity for a particular environment and thus show higher local abundance.

At the genus level, we found ubiquitous genera such as *Ocotea* (222.31 Mg), *Pouteria* (216.94 Mg), *Pseudolmedia* (185.14 Mg), *Miconia* (166.79 Mg) and *Tetragastris* (98.88 Mg), that accumulated large AGB, mainly because of their many large-sized individuals. In the uppermost Andean highlands, on the other hand, many plots are strongly dominated by any number of species of *Polylepis* (Gareca et al., 2010), each contributing greatly to plot AGB with their many stems.

It is also likely that AGB of tropical forests may be determined by species traits and shifts in the structure and composition on species with elevation (Culmsee et al., 2010), because there may be structural features that can be phylogenetically conserved (Moser et al., 2008). Then will be interesting to assess the traits of the taxa in relation with community proprieties in elevational gradients.

As a conclusion, we found that in the Madidi region AGB values, as expected, decreased towards higher elevations, thus increasing with the higher MAP of low elevations. The more favorable climatic conditions of wet low elevations facilitate spatial patterns of density distribution of taxa that are very different from montane forests. These biotic and abiotic conditions allow for low elevation forests to be most productive. From our results we found AGB –a rough proxy for productivity– to be associated with species that occur most abundantly within plots, particularly at low elevations. Thus, a few species with many individuals at the local scale and with narrow distribution along elevational gradients could contribute the most to total forest biomass and productivity. The pattern is particularly important for lowland forests, which accumulate the largest aboveground reserves of carbon (Ghazoul & Sheil, 2014; Chave et al., 2015; Muelbert et al., 2018). To Fauset et al. (2015), half of the carbon stock and half of the woody plant productivity in Amazonia are the contribution of just 1% of all species. In terms of biomass, these few common species at the local and few at the landscape scale provide a large proportion of ecosystem services to the region, such as regulation of regional and global climate by sequestering CO_2, by microclimate regulation of moisture and temperature, and by providing shade and shelter (Gaston, 2010; Daba & Dejene, 2018).

CRediT authorship contribution statement

Verónica Sandoya: Formal analysis, Funding acquisition, Investigation, Validation, Writing - original draft. **Sandra Saura-Mas:** Conceptualization, Formal analysis, Methodology, Supervision, Validation, Writing - review & editing. **Iñigo Granzow-de la Cerda:** Conceptualization, Formal analysis, Methodology, Supervision, Validation, Writing - review & editing. **Gabriel Arellano:** Data curation, Methodology, Validation, Writing - review & editing. **Manuel J. Macía:** Data curation, Validation. **J. Sebastián Tello:** Data curation, Project administration. **Francisco Lloret:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Supervision, Validation, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118549.

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