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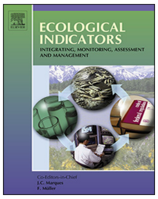

Original Articles

Fine-scale topography shape richness, community composition, stem and biomass hyperdominant species in Brazilian Atlantic forest

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ABSTRACT

Topography is an important driver that determines diversity patterns and ecosystem functioning in tropical forests. However, there are few studies analyzing contrasting topographical conditions on the relative importance of species to ecosystem functioning, mainly on those who have a greater contribution (i.e., hyperdominant species). We aimed to evaluate whether contrasting topographical conditions determine changes in tree species richness, community composition, and the number of stem and biomass hyperdominant species in a Brazilian Atlantic remnant forest fragment. We selected two areas on distinct hillsides with contrasting topographic conditions, at the biological reserve of the Federal University of Viçosa, Minas Gerais state, southeastern Brazil. Each area (100 × 100 m) was sub-divided into 100 plots of 10 × 10 m. From each plot, all trees having diameter at breast height (DBH) ≥ 10 cm were identified to the species level and tagged for measurement. We measured three topographic variables (slope, elevation, and convexity) in each plot, based on the assumption that these variables may affect tree species diversity, species composition, and ecosystem function (aboveground biomass). The AGB of individual stems was calculated in all plots. We performed a multivariate regression tree for estimating topographical heterogeneity in each area. We found that species richness differed significantly between areas. Species richness in the Northeast area (the more topographically heterogeneous one) was 48% higher than that in the Southeast area, which is less topographically heterogeneous. The tree species composition varied considerably between areas, with similar AGB patterns being registered among plots. The number of stem hyperdominants varied significantly between areas. In the Southeast area, only two species out of the 85 recorded (2.38%) accounted for 50% of the number of stems hyperdominants, while in the Northeast area 10 species (7.94%) accounted for 50% of stems hyperdominants. Our results showed that high topographic heterogeneity induces high species richness and that the number of stem and biomass hyperdominant species increase along with richness on a local scale. Based on our results, we presume that biomass hyperdominance can also strongly influence forest ecosystem functioning on a local scale.

1. Introduction

A key factor in maintaining heterogeneous forest landscapes is topography (Werner and Homeier, 2015; Jucker et al., 2018). Tropical forests, show high levels of habitat heterogeneity which plays a key role in the distribution of tree species (Dalling and Hubbell, 2002; Moeslund et al., 2013; Holl and Zahawi, 2014). Topographic variability cause small-scale heterogeneity in resources availability (Kubota et al., 2004; Townsend et al., 2008) and strongly affects forest species richness and community composition (Holl and Zahawi, 2014; Guo et al., 2016). However, woody species communities, not only differ in species richness, but also in species dominance and community composition (Maestre et al., 2012). Species dominance is typical for natural ecosystems (ter Steege et al., 2013; Lohbeck et al., 2016) and indirectly alters the relationship between species richness and a single cumulative ecosystem function, i.e., aboveground biomass (Hillebrand et al., 2008; Bastin et al., 2015). The relative contributions of species may substantially vary from one species to another, independent of their abundance (Lohbeck et al., 2016). Thus, some particularly abundant species may not in fact contribute substantially to ecosystem function, whereas other much rarer taxa may do so (Fauset et al., 2015; Bastin et al., 2015). Empirical evidence shows that a small subset of species

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contributes to most of a particular ecosystem function (Winfree et al., 2015, Lohbeck et al., 2016). This small subset of species often has particular functional trait values to optimally perform those functions (Mouillot et al., 2011), such as wood density and maximum height and are called hyperdominants species (Fauset et al., 2015). Identifying these key species is crucial to forecasting how tropical forests will respond to global environmental change and land-use change.

Recent studies have highlighted the importance of linking ecosystem function with tree species identity in diverse tropical forests, and they have shown that a few dominant species are the most representative of some vital ecosystem processes (Staggemeier et al., 2017). For example, studies conducted on the Amazonian basin showed that a small number of species contribute disproportionately to the global stem density and biomass, as they estimated that only 1.4% of tree species account for the half of the regional stem abundance and only 0.91% of tree species account for the half of the regional aboveground biomass (ter Steege et al., 2013; Fauset et al., 2015). These species were considered as stem hyperdominant and biomass hyperdominant respectively (Bastin et al., 2015; Fauset et al., 2015). This phenomenon of a disproportional influence of a small number of species on the ecosystem functioning has been called hyperdominance (e.g., Bastin et al., 2015; Staggemeier et al., 2017) and been applied to describe important ecosystem services such as biomass accumulation, carbon storage and seed production in Amazonian (Fauset et al., 2015; Thomas et al., 2018), woody productivity in Central Africa tropical forests (Bastin et al., 2015), and fruit production in Brazilian Atlantic rain forest (Staggemeier et al., 2017). However, little is known about the effects of environmental factors (e.g., climate, soil and topography) on the distribution of hyperdominant species, especially on fine scale in tropical forest.

Topography in small-scale is an important driver that determines the diversity patterns and functioning of tropical forests (Moeslund et al., 2013; Brown et al., 2013). In that sense, there is sufficient evidence that reveal the existence of a close positive relationship between topographic heterogeneity and tree species richness in tropical forests (Douda et al., 2012), where increasing habitat heterogeneity also increases the number of species coexisting along environmental gradients, being a determinant factor for community assembly (Brown et al., 2013; Liu et al., 2014). Topography heterogeneity may affect resources such as light, water and constrains local soil nutrient (Moeslund et al., 2013), within which trees grow, that in turn strongly affect forest species structure, composition and function (Jucker et al., 2018). Furthermore, topographic variability causes fine-scale heterogeneity of nutrient availability, meaning that species can then differentially explore patchily distributed resources, which can lead to higher species richness and species turnover (Questad and Foster, 2008). The environmental heterogeneity, determined principally landscape topography (Oliveira-Filho et al., 2001), are not only related to the distribution of the vegetation complexes of a particular region but are correlated with the spatial distribution of species within them; for example the Brazilian Atlantic forest (Ferreira-Júnior et al., 2007).

The Brazilian Atlantic forest is the fifth richest biodiversity hotspot in the world (Myers et al., 2000), where 1 ha forest-plot can have up to more than 400 woody species (e.g., Rocha-Santos et al., 2017). Likewise, these forests have 49% plant endemism (Stehmann et al., 2009), but is one of the most threatened tropical forest in the world (Myers et al., 2000; Scarano and Ceotto, 2015). For example, 1544 plant species are endangered, the equivalent to 60% of the entire lists of threatened species for flora in Brazil (Rezende et al., 2018). Furthermore, the Brazilian Atlantic forest are reduced to about 20% of their original cover, but despite this, is important in the carbon storage in tree biomass and the maintenance of biodiversity (Magnago et al., 2015). However, little known whether fine-scale environmental heterogeneity generated by contrasting topographical conditions determines the species richness, community composition, and the number hyperdominant species in the Atlantic forest. The hyperdominance approach is essential to understand the ecosystem functioning, through these key species, as well as to establish effective management and conservation practices at fine spatial scales, since this ecosystem is found in small remnants forest fragments (Scarano and Ceotto, 2015). Furthermore, it is known that, most forest conservation projects apply mainly at global, continental and regional scales, because of the low cost effective of research and restoration activities, ecosystems are typically measured and monitored at fine spatial scales (Tovo et al., 2017). In addition, even within tropical landscapes, the structure, richness and function of forests can vary dramatically across very fine spatial scales (Werner and Homeier, 2015; Thomas et al., 2018).

In this context, we aimed to evaluate whether contrasting topographical conditions determine changes in tree species richness, community composition, and the number of stem and biomass hyperdominant species in a Brazilian Atlantic remnant forest fragment. We selected two areas on distinct hillsides with contrasting topographic conditions, at the biological reserve of the Federal University of Viçosa, Minas Gerais state, southeastern Brazil. In order to address the following question: 1) Does a contrasting topographical condition determine species richness? 2) Does higher tree species richness determine the occurrence of a higher number of stem and biomass hyperdominant species? 3) Are stem hyperdominant species also biomass hyperdominant? We hypostatized that 1) areas with high topographic heterogeneity; which is an indirect indicator of niche partitioning, (e.g., Brown et al., 2013; Liu et al., 2014), will present higher species richness and consequently a higher number of stem and biomass hyperdominant species and 2) the same stem hyperdominant species are not the same biomass hyperdominant because species may differ in their contribution to ecosystem functioning, despite its abundance (Lohbeck et al., 2016). Specifically, this study will contribute to understand the role of fine-scale hyperdominant species that can be essential for conservation and restoration activities in this Brazilian Atlantic remnant forest fragment.

2. Material and methods

2.1. Study area

The study was conducted in a seasonal semi deciduous Atlantic forest fragment (20°45′14″S, 42°45′53″W) at Viçosa municipality, Minas Gerais state, southeastern Brazil (Fig. 1). The forest fragment is located within the campus of the Federal University of Viçosa (UFV), extending over approximately 75 ha. The site had been used for shade coffee cultivation under natural forest cover up until 1926, but it has been fully protected ever since, which allowed for natural regeneration to occur. Later on, land use has been reserved. The study area has a moderate humid subtropical climate, with dry season occurring from May to September and wet season occurring between December and March. The mean annual relative humidity is ca. 80%, mean annual air temperature is 19 °C and mean annual precipitation is 1340 mm. The study area is located between 620 and 820 m elevation and the relief varies from strongly undulating to mountainous. The site is characterized by the presence of two dominant soil classes: a Dystric Red-Yellow Latosol covers hilltops and mountainsides, while a Cambic Red-Yellow Podzolic dominates the upper fluvial terraces (EMBRAPA, 1997).

2.2. Forest inventory and data collection

We selected two sampling areas with contrasting topographic conditions: a Southeast area (UTM 23 K 722758/7703626) and a Northeast area one (UTM 23 K 722234/7703330). Each area (100 × 100 m) was sub-divided into 100 plots of 10 × 10 m. A total 200 plots (2 ha) from the two areas were sampled from December 2016 to January 2017. From each plot, all trees having diameter at breast height (DBH) ≥ 10 cm were identified to the species level and tagged for measurement. All individuals were identified using specialized

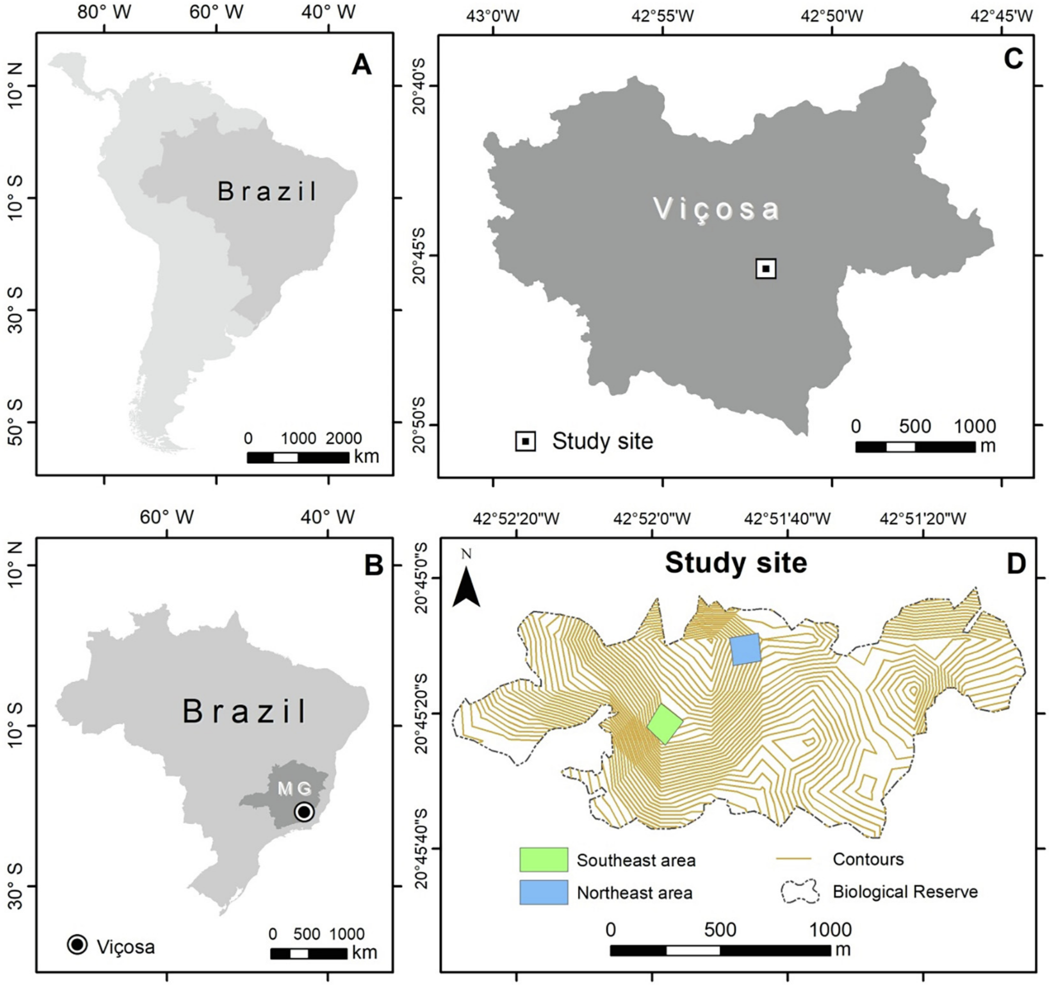

Fig. 1. Localization of the study area in relation to South America (A), the Minas Gerais State, Brazil (B), and the forest fragment within the campus of the Federal University of Viçosa (UFV), Viçosa municipality, Minas Gerais state, southeastern Brazil (C). The two samples plots are indicated within the forest fragment (D).

literature, through consultation to the VIC Herbarium of UFV, or by taxonomists. The *Angiosperm Phylogeny Group* IV (APG IV, 2016) was used for taxon classification.

2.3. Measurements of topographical variables

We measured three topographic variables (slope, elevation, and convexity) in each plot, based on the assumption that these variables may affect tree species diversity, species composition, and function (Liu et al., 2014; Guo et al., 2016). Elevation was calculated using the mean elevation at each of the four corners of the plot. The slope (measured in degrees) was the mean angular deviation of the horizontal of each of the four triangular planes formed by the connection of three of its edges (Harms et al., 2001). Convexity was determined by subtracting the elevation at the center of the quadrat from the mean elevation of the eight surrounding plots. On edge plots, convexity was calculated as the altitude of the plot of interest minus the mean altitude of the surrounding plots (Lan et al., 2011).

Topographic variables were obtained using a Total Station, which measures vertical and horizontal angles as well as linear distances. To take the measurements, the Total Station had to be positioned at an obstacle-free location and be aimed at the prism. The prism sits on a metal stick and should be placed over the point to be measured. The total station then emits a laser beam that reflects in the prism and returns to the equipment. By the time of response of the laser beam to the equipment and depending on the angle of rotation of the station's bezel, the internal computer calculates the angles and distances and stores the data in its internal memory (Kahmen and Faig, 1988).

2.4. Estimation of aboveground biomass (AGB)

The AGB of individual stems was calculated using the general allometric equation proposed by Chave et al. (2014), based on tree DBH (cm), height (H, m) and wood density (ρ, g cm^{-3}). We used Neotropical data from the Global Wood Density Database (Chave et al., 2009) to obtain the wood density of each species, using genus or family averages whenever species-level information was not available. Tree height was measured with a laser tape. The AGB was calculated as follows:

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

The total AGB per plot was the sum of the AGBs of all trees having DBH ≥ 10 cm, which was then converted to megagrams per hectare (Mg ha^{-1}) (Ali et al., 2016). Species-level biomass was calculated as the sum of the biomass of all stems from a species.

2.5. Data analysis

All data and statistical analyses were conducted in R.3.2.2 (R Core Team, 2016). We performed a multivariate regression tree (MRT) analysis (De'ath, 2002; Larsen and Speckman, 2004) to classify habitat types according to topographic variables and species composition (Guo et al., 2016; Wang et al., 2016). MRT is a method of constrained clustering that identifies clusters (group of plots) that are most similar to

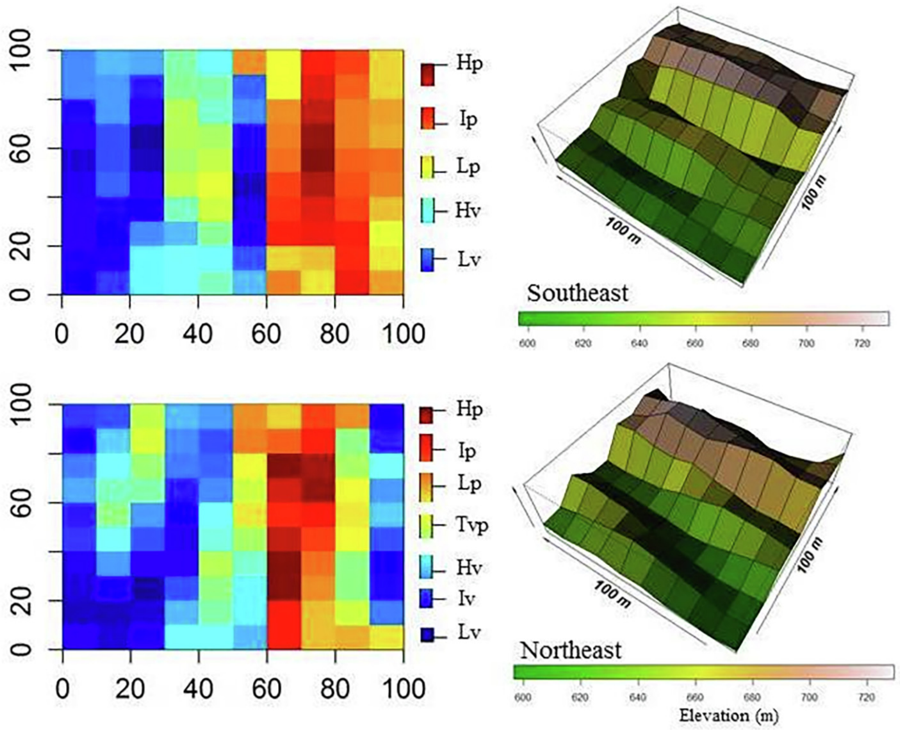

Fig. 2. Habitats types (left) and topographic maps (right) of the two study areas within 2-ha permanent plots in Atlantic forest, Minas Gerais, Brazil. According to the MRT, the areas were divided into of the following habitats: i) High plateau (Hp); ii) intermediate plateau (Ip); iii) low plateau (Lp); iv) high valley (Hv); v) low valley (Lv); vi) i) intermediate low valley (Iv), and ii) a transition area between high valley and low plateau (Tpv).

each other based on a set of predefined values (De'ath, 2002). We analyzed species dissimilarity (Euclidian distance) between each cluster as being defined by threshold values of topographic variables (De'ath, 2002). In this study, the root node consisted of all 100 plots (10 × 10 m) from each area. Subsequent clusters represented a species assemblage while the threshold values of topographic variables defined an associated habitat type (Guo et al., 2016; Wang et al., 2016). The algorithm determines the threshold value of topographic variables that splits the quadrats into two groups so as to minimize the species dissimilarity within groups (Larsen and Speckman, 2004). MRT analysis was performed using the "rpart" package (Therneau et al., 2017). The two study areas have marked differences in the spatial distribution of topographic variables, mainly elevation and slope (Fig. 2). We represented the spatial distribution of habitats from each area using the "*Field*" package (Nychka et al., 2017). According to the MRT, the Southeast area was less topographically heterogeneous, as determined by the two topographic variables (elevation and slope), and was divided into five potential habitats. Conversely, the Northeast area was more topographically heterogeneous (elevation, slope, and convexity) and was divided into seven habitats (Fig. A.1, Appendix/from Electronic Supplement Material, ESM hereafter).

Species richness in the two sampled areas was evaluated using both individual-based rarefaction and extrapolation curves, which were constructed with the first Hill numbers (Chao et al., 2014). Extrapolations were made based on presence/absence data (Hill number of order 0), up to thrice the sample size (Colwell et al., 2012). These estimates were obtained using the "*iNEXT*" package (Hsieh et al., 2016). The Hill number was estimated as the mean of 100 replicate bootstrapping runs to estimate 95% confidence intervals. Whenever the 95% confidence intervals did not overlap, species numbers differed significantly at $P < 0.05$ (Colwell et al., 2012).

Non-metric multidimensional scaling (NMDS) was performed to examine differences between areas and among habitats in terms of species composition by using Jaccard dissimilarities (Clarke, 1993). We performed the NMDS using the '*metaMDS*' function of the "*vegan*" package (Oksanen et al., 2018). We used permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) to determine differences in species composition by using the '*adonis*' routine available within the "*vegan*" package (Oksanen et al., 2018), and to test for significant clustering of areas across the AGB gradient. We finally constructed Venn diagrams with the 'gplots' package in R to check the number of exclusive and shared species between areas.

To address the second question, does higher tree species richness determine the occurrence of a higher number of stem and biomass hyperdominant species? We estimated the maximum number of species required to account for 50% of stem abundance and biomass in each area. With that, we were able to assess the number of stem hyperdominants and biomass hyperdominants in each area.

To address the third question, are stem hyperdominant species also biomass hyperdominant?, we considered as 'biomass hyperdominants' and 'stem hyperdominants' the species that accumulated 50% of the total biomass and stems, respectively, when ranked by decreasing order of contribution to the total AGB and stem abundance, based on the definitions adopted by Bastin et al. (2015) and Fauset et al. (2015). We also calculated the contribution of stem hyperdominants to the total biomass in each area and regressed the percentage contribution of each species to the biomass of the whole dataset against their percentage contribution to the number of stems of the whole dataset, following the methods adopted by Fauset et al. (2015). To compare the mean AGB between areas, we performed t-tests (normally distributed data). Data was tested for normal distribution with the Shapiro-Wilk test and a Q-Q plot.

The importance value (IV) of each species was calculated by the sum of its relative density (RD), relative frequency (RF), and relative dominance (Rd), following the method adopted by Gonçalves et al. (2017). Species-level stem abundance was determined using phytosociological analysis, in which the absolute (Ab) and relative (Ar) abundance of each species was calculated by the following equations (Eqs. (1) and (2)).

$$\text{Ab} = \text{total number of individuals per species} \\ /\text{total number of plots that contain species} \tag{1}$$

$$\text{Ar} = \text{Ab of the species} \times 100/\text{Total abundance} \tag{2}$$

The most important species were those with the highest numbers of individuals per unit area; therefore, the proportional analysis of IVI

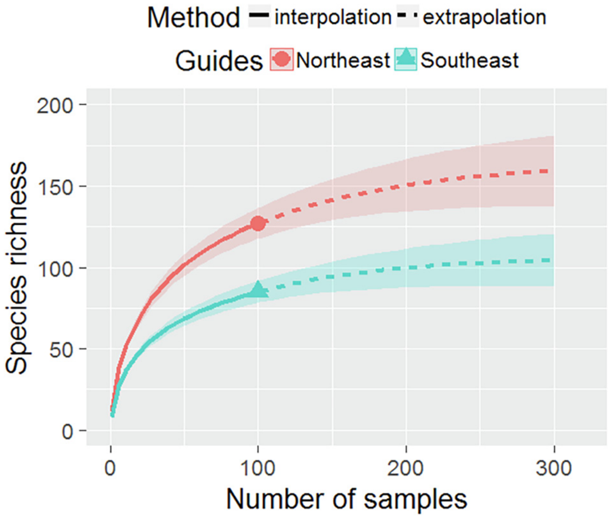

Fig. 3. Sample-based rarefaction (solid line) and extrapolation curves (dashed lines) of tree richness for the two study areas (Southeast and Northeast). Rarefaction and extrapolation curves present the lines that represent the mean values and the bands the standard deviation with 95% confidence intervals.

enabled us to evaluate the relative contribution of each species within the community (Gonçalves et al., 2017). Lastly, we constructed species rank curves based on both species abundance and distribution (number of species per area; Magurran, 2004). To obtain species rank curves, all species were ranked from the most to the least abundant. We then obtained the species rank curves using the *'radfit'* function of the "*vegan*" package (Oksanen et al., 2018).

3. Results

3.1. Species richness and composition

We recorded a total of 4130 individuals belonging to 157 species across a total sampled area of 2 ha, which 55 species are shared between the two areas (Fig. A.2., from ESM). Species richness differed significantly between areas (Fig. 3). Species richness in the Northeast area (the more topographically heterogeneous one) was 48% higher than that in the Southeast area, which is less topographically heterogeneous. The NMDS revealed that tree species composition varied considerably between areas, with similar AGB patterns being registered among plots (Fig. 4). The NMDS ordination distribution separated the two study areas along the second axis.

3.2. Phytosociology and stem hyperdominant species

The number of stem hyperdominants varied significantly between areas (Fig. 5). In the Southeast area, only two species out of the 85 recorded (2.38%) accounted for 50% of the number of stems hyperdominants, while in the Northeast area 10 species (7.94%) accounted for 50% of stems hyperdominants. The Top 20 highest stem dominant species are given in Table 1. Data on all species is found in Appendix Table A.1. from ESM.

3.3. Biomass hyperdominant species

On average, the AGB ranged from 23.11 to 690 Mg ha^{-1} in the Northeast area and from 26.94 to 664.65 Mg ha^{-1} in the Southeast area. No difference was detected between areas (Fig. A.3. from ESM). In the Southeast area, only two species (2.38%) were classified as biomass hyperdominants, i.e., accounting for more than 50% of the biomass (Fig. 5). In the Northeast area, on the other hand, five species (3.97% of all identified species in the data set) accumulated 50% of the AGB (Fig. 5). The 20 most dominant species by AGB are given in Table 2. Data on all species is found in appendix Table A.2. from ESM.

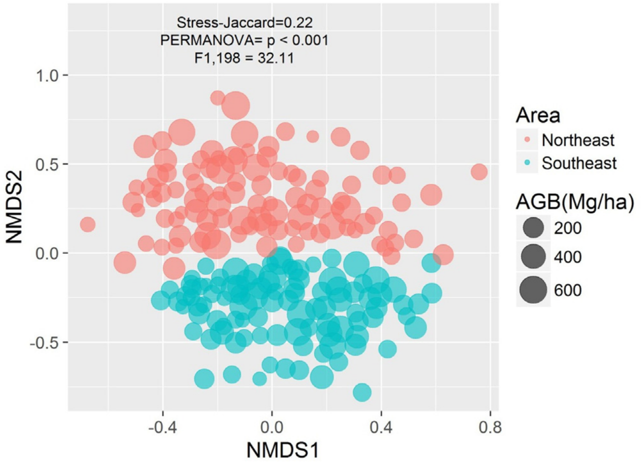

Fig. 4. Non metric multidimensional scaling based on species composition according to aboveground biomass gradient (circles sizes) and study areas (point colors) within 2-ha permanent plots in Atlantic forest, Minas Gerais, Brazil.

4. Discussion

4.1. Topographic heterogeneity and species richness

Our results revealed opposing patterns in species richness and community composition between the two areas with contrasting topographical conditions. Thus, we presume that an increase in species richness with increasing topographic heterogeneity, with the less heterogeneous Southeast area, which has five habitats, having lower species richness (84 species) than the Northeast area which has seven habitats (126 species). This positive relationship is similar to that observed in different tropical forests (Brown et al., 2013). In that sense, studies based on the habitat heterogeneity hypothesis have demonstrated how a higher topographic heterogeneity induces a higher diversity (e.g., Douda et al., 2012; Liu et al., 2014). Higher habitat heterogeneity is associated with heterogeneous resource distribution, which in turn results in higher variation in woody plant structural diversity (e.g., Lippok et al., 2014; Jucker et al., 2018). The same association is observed on local scales, especially at the forest stand level, as resource distribution thereat is affected by topography, resulting in spatial heterogeneity under different topographic conditions (Moeslund et al., 2013; Brown et al., 2013). The spatial distribution of species, allied with the correlation between richness and topography, indicate the existence of habitat preferences and provide evidence for differences in regeneration niches produced by the direct and indirect effects of topography (Brown et al., 2013; Guo et al., 2016).

4.2. The relationship between species richness and hyperdominance

In our study, the Southeast area not only had a lower number of species but also had one species with high dominance; for instance *Sorocea bonplandii*, which accounted for 46% of the total stem abundance in the area. In contrast, the Northeast area had no species with high dominance. This result may be due to the fact that in heterogeneous environments plants are distributed in space among patchy microhabitats based on interspecific tradeoffs of resources and environmental requirements (Guo et al., 2016). Strong environmental contrasts among microhabitats enable the coexistence of a large number of plant species with different life histories (Douda et al., 2012). Conversely, a limited number of species may coexist in a homogeneous environment, as the best competitors overgrow the area

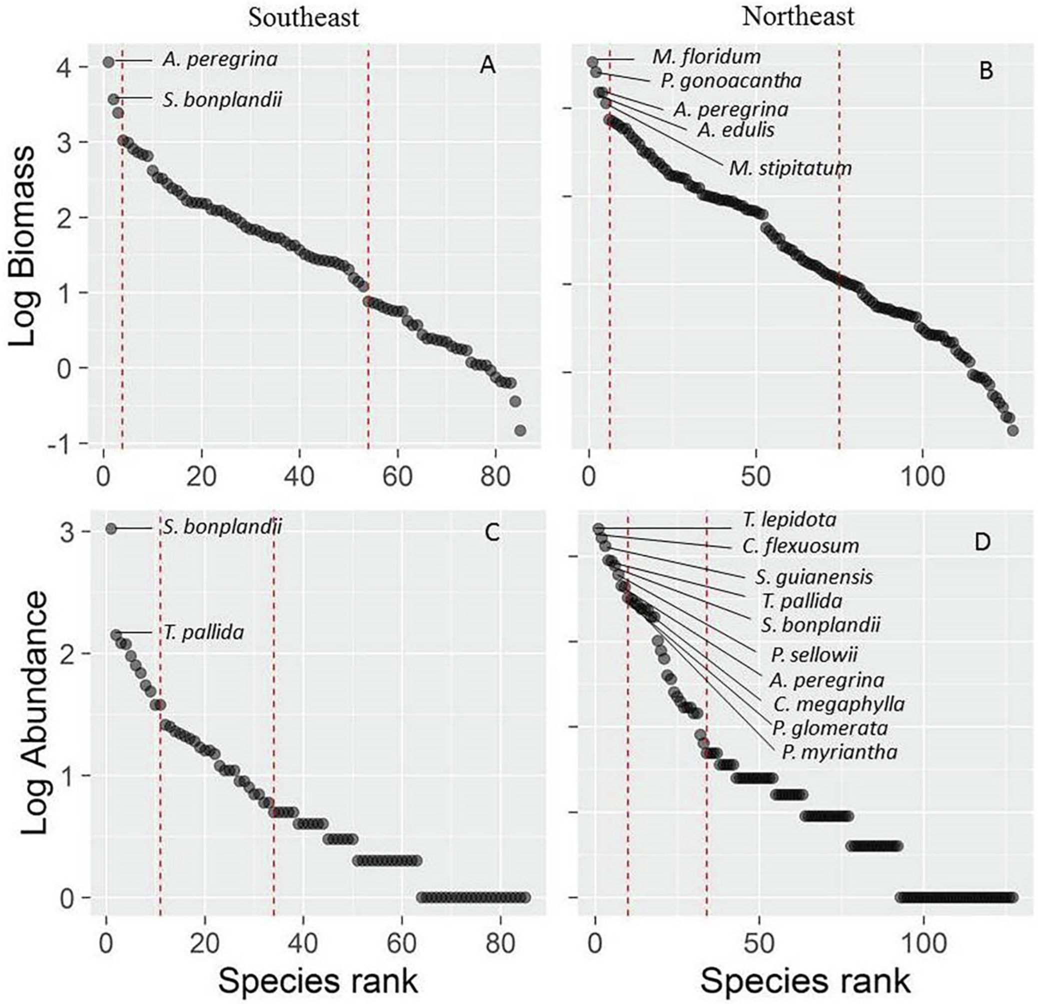

Fig. 5. Species abundance distribution for the two study areas (Southeast and Northeast) separate for stem and biomass hyperdominants species within 2-ha permanent plots in Atlantic forest, Minas Gerais, Brazil. First red line indicate the limit of species that accumulate up to 50% of the total biomass (A-B), or represent 50% of total community abundance (C-D) in each study area.

and reduce the number of other species (Tilman and Pacala, 1993; Tabarelli et al., 2012). From a practical point of view, we consider fundamental to understand how environmental drivers (e.g., topography) determine richness patterns on a fine scale, and how environmental conditions can limit or favor tropical forest management and conservation activities.

Our results showed that the number of stem and biomass hyperdominants species (i.e., the disproportionate contribution to the biomass in the area, or the abundance of a small number of species) increases with increasing richness on a fine scale. Thus, we presume that the relative functional contributions of species may substantially vary from one species to another, regardless of their abundance, corroborating a previously observed pattern in tropical forests (e.g., Fauset et al., 2015). Thereby, some particularly abundant species may not in fact contribute substantially to ecosystem processes, whereas other much rarer taxa may do so (Fauset et al., 2015; Lohbeck et al., 2016). On the other hand, it is possible that abundance fluctuations of dominant species drove ecosystem service delivery, whereas richness changes were relatively unimportant because they primarily involved rare species that contributed little to function (Winfree et al., 2015). Reports with this type of analysis are quite scarce for tropical forests, mainly on a fine scale, with most such studies having been conducted on a regional scale (e.g., Amazon and African forests; Fauset et al., 2015; Bastin et al., 2015). However, our results shed a light on how a fine-scale analysis might also be important to understand the distribution of ecosystem functions within tree communities, which could provide insight into establishing more specific criteria for forest management and conservation, especially in small remnant forest fragment.

The Southeast area has lower richness and lower number of stem hyperdominant species; with only two species accounting for 50% of the total stem abundance (i.e., *Sorocea bonplandii*, is the most dominant species in our dataset). The species, however, despite being the most stem dominant in the area (Table 1), was not biomass dominant, having placed second in the rank of biomass hyperdominant species, with 37.06 $\mathrm{Mg\,ha^{-1}}$ (Table 2). The Northeast area, on the other hand, has higher richness and higher number of biomass hyperdominant species, with ten species accounting for 50% of the total stem abundance. Of these ten, only *Anadenanthera peregrina* is among the species that accounted for 50% of the AGB, contributing with 16.77 $\mathrm{Mg\,ha^{-1}}$ (Table 2). Additionally, we found no species with high stem dominance in this area, as all ten species contributed similarly to the total of stems, indicating a relatively more uniform biomass distribution in the tree community. Previous studies have indicated that the contribution of each species to the biomass stock depends on not only its abundance (e.g., Fauset et al., 2015) but also on the functional properties (e.g., tree size, lifespan, growth rate, and wood density) of each individual of the species as well as on traits that determine how much carbon the species stores and for how long (Paula et al., 2011; Fauset et al., 2015; Poorter

Table 1
The 20 most abundant tree species in study area. The data were obtained through a phytosociology analysis. Number of individuals (Ni). Relative density (R.De). Relative abundance (R.Ab) and relative frequency (R.Fr). Importance value (IV) of species are also indicated for the two study areas.

Species/Southeast	Family	Ni	DenR	AbuR	FreR	IVI	IVI (%)
Sorocea bonplandii	Moraceae	1053	45.88	8.79	12.32	66.99	22.33
Trichilia pallida	Meliaceae	142	6.19	2.16	6.77	15.12	5.04
Protium warmingianum	Burseraceae	122	5.32	2.61	4.80	12.73	4.24
Siparuna guianensis	Siparunaceae	119	5.19	2.92	4.19	12.29	4.10
Casearia ulmifolia	Salicaceae	95	4.14	1.65	5.91	11.70	3.90
Plinia glomerata	Myratceae	80	3.49	1.71	4.80	10.00	3.33
Machaerium nyctitans	Fabaceae	69	3.01	1.44	4.93	9.37	3.12
Apuleia leiocarpa	Fabaceae	55	2.40	1.31	4.31	8.02	2.67
Anadenanthera peregrina	Fabaceae	53	2.31	1.16	4.68	8.15	2.72
Rollinia sylvatica	Annonaceae	38	3.49	1.71	4.80	10.00	3.33
Coutarea hexandra	Rubiaceae	38	1.66	1.13	3.45	6.24	2.08
Chrysophyllum gonocarpum	Sapotaceae	26	1.13	1.09	2.46	4.68	1.56
Eugenia leptoclada	Myrtaceae	25	1.09	1.90	1.35	4.34	1.45
Brosimum guianense	Moraceae	23	1.00	1.28	1.85	4.13	1.38
Allophylus edulis	Sapindaceae	22	0.96	1.53	1.48	3.97	1.32
Piptadenia gonoacantha	Fabaceae	20	0.87	1.19	1.72	3.79	1.26
Trichilia lepidota	Meliaceae	20	0.87	1.11	1.85	3.83	1.28
Amaioua guianensis	Rubiaceae	19	0.83	0.99	1.97	3.79	1.26
Luehea grandiflora	Malvaceae	17	0.74	1.01	1.72	3.48	1.16
Ocotea odorifera	Lauraceae	16	0.70	1.03	1.60	3.33	1.11
Species/Northeast	Family	Ni	DenR	AbuR	FreR	IVI	IVI (%)
Trichilia lepidota	Meliaceae	145	7.88	1.48	5.53	14.88	4.96
Chrysophyllum flexuosum	Sapotaceae	128	6.95	1.71	4.21	12.87	4.29
Siparuna guianensis	Siparunaceae	115	6.25	1.57	4.12	11.94	3.98
Trichilia pallida	Meliaceae	95	5.16	1.24	4.30	10.70	3.57
Sorocea bonplandii	Moraceae	94	5.11	1.31	4.04	10.45	3.48
Prunus sellowii	Rosaceae	88	4.78	1.13	4.39	10.29	3.43
Anadenanthera peregrina	Fabaceae	81	4.40	1.08	4.21	9.69	3.23
Citronella megaphylla	Cardiopteridaceae	67	3.64	1.26	2.98	7.89	2.63
Plinia glomerata	Myrtaceae	66	3.59	1.63	2.28	7.49	2.50
Psychotria myriantha	Rubiaceae	57	3.10	1.26	2.54	6.90	2.30
Xylosma prockia	Salicaceae	56	3.04	1.16	2.72	6.92	2.31
Protium warmingiana	Burseraceae	53	2.88	0.87	3.42	7.17	2.39
Machaerium stipitatum	Fabaceae	52	2.82	1.15	2.54	6.52	2.17
Guapira opposita	Nyctaginaceae	49	2.66	0.85	3.25	6.76	2.25
Dalbergia nigra	Fabaceae	49	2.66	1.75	1.58	5.99	2.00
Ocotea dispersa	Lauraceae	48	2.61	0.79	3.42	6.82	2.27
Piptadenia gonoacantha	Fabaceae	44	2.39	0.81	3.07	6.27	2.09
Allophylus edulis	Sapindaceae	44	2.39	0.81	3.07	6.27	2.09
Luehea grandiflora	Malvaceae	32	1.74	0.79	2.28	4.81	1.60
Nectandra lanceolata	Lauraceae	28	1.52	0.86	1.84	4.22	1.41

et al., 2015).

It should be noted that neotropical plant communities of dominant tree species that are essential for the ecosystem functioning, such as large trees with higher biomass production and carbon storage capacities, occur predominantly in mature forests (Tabarelli and Peres, 2002; Tabarelli et al., 2010; Fauset et al., 2015). Nevertheless, typical secondary forests may be found in landscapes undergoing human intervention, which might considerably change the current and future state of community assembly and ecosystem functioning (Pütz et al., 2014; Santos-Silva et al., 2016). Accordingly, studies have shown how the winner–loser species replacement dynamics may be responsible for up to a 50% reduction in the AGB of fragmented habitats and tropical forests (e.g., Paula et al., 2011). Should such forest degradation persist, the AGB stock is expected to gradually decrease due to the biotic homogenization caused by the high proliferation and dominance of pioneer trees with short life cycles (Tabarelli et al., 2012; Pütz et al., 2014).

In that sense, it is worth remembering that the Atlantic forest is undergoing a scenario in which large tropical landscape extensions have already been lost and the currently existing ones are fragmented, which thus significantly reduces the biomass and carbon stocks therein (Pütz et al., 2014; Magnago et al., 2015). The aforementioned novel approach based on analyzing hyperdominant species has only recently started to gain relevance, especially due to the implications that key species from tropical forests may have on the ecosystem functioning on a global scale (e.g., carbon cycling in the Amazon forest, Fauset et al., 2015). Although the hyperdominance analyses herein were performed on a regional scale, we highlight that the actions aiming at the management and conservation of tropical forests are also of high relevance on a local scale, due mainly to technical and economic limitations (Tovo et al., 2017). Therefore, we consider fine-scale hyperdominance analyses to be necessary for devising management and conservation actions on that same scale, on which small remnant forest fragment. may have specific environmental conditions.

4.3. Biomass and stem hyperdominants species

We found two biomass and stem hyperdominant species in the Southeast area, against five biomass hyperdominant and ten stem hyperdominant species in the Northeast area. We also found that among the top 20 biomass hyperdominants in each area, only 25% of species were common to both areas. On the other hand, half the stem hyperdominants were shared by the areas. Based on our results, we presume that hyperdominance strongly influences forest ecosystem functioning on a local scale. Furthermore, our results are consistent with the ones obtained in the Amazon basin, where a strong species hyperdominance in terms of stem density and biomass has been found (ter Steege et al., 2013). Analogously, a recent study conducted in the

Table 2
Top 20 most hyperdominat species in aboveground biomass (AGB) in biological reserve.

Species Southeast	AGB (Mg ha^{-1})	AGB (Mg ha^{-1}) Cumulated	%AGB/ species	% AGB cumulated
Anadenanthera peregrina	74.31	74.31	32.12	32.12
Sorocea bonplandii	37.06	111.37	16.02	48.14
Casearia ulmifolia	24.44	135.81	10.56	58.70
Apuleia leiocarpa	10.51	146.32	4.54	63.24
Myroxylon peruiferum	9.79	156.11	4.23	67.47
Copaifera langsdorffii	8.11	164.22	3.50	70.98
Machaerium nyctitans	7.33	171.55	3.17	74.15
Protium warmingiana	6.85	178.40	2.96	77.11
Allophylus edulis	6.50	184.90	2.81	79.91
Plinia glomerata	4.19	189.09	1.81	81.73
Luehea grandiflora	3.36	192.45	1.45	83.18
Ocotea odorifera	3.27	195.71	1.41	84.59
Dalbergia nigra	2.81	198.52	1.21	85.80
Casearia decandra	2.43	200.95	1.05	86.85
Cordia sellowiana	2.28	203.23	0.98	87.84
Ceiba speciosa	2.00	205.23	0.86	88.70
Siparuna guianensis	1.67	206.89	0.72	89.42
Pterocarpus rohrii	1.57	208.46	0.68	90.10
Brosimum guianense	1.56	210.02	0.67	90.77
Rollinia sylvatica	1.53	211.55	0.66	91.44
Species Northeast	AGB (Mg ha^{-1})	AGB (Mg ha^{-1}) Cumulated	% AGB/ species	% AGB cumulated
Machaerium floridum	49.80	49.80	19.45	19.45
Piptadenia gonoacantha	33.23	83.03	12.98	32.42
Anadenanthera peregrina	16.77	99.80	6.55	38.97
Allophylus edulis	15.11	114.91	5.90	44.87
Machaerium stipitatum	15.04	129.96	5.87	50.74
Trichilia lepidota	11.32	141.28	4.42	55.16
Cedrela fissilis	7.37	148.65	2.88	58.04
Nectandra lanceolata	7.07	155.72	2.76	60.80
Maytenus aquifolium	6.67	162.39	2.61	63.41
Cariniana legalis	6.35	168.74	2.48	65.89
Ficus enormis	5.88	174.62	2.30	68.18
Luehea grandiflora	5.85	180.47	2.28	70.47
Prunus sellowii	5.14	185.61	2.01	72.48
Dalbergia nigra	4.59	190.20	1.79	74.27
Cariniana estrellensis	3.89	194.09	1.52	75.79
Persea pyrifolia	3.33	197.42	1.30	77.09
Apuleia leiocarpa	3.16	200.58	1.23	78.32
Xylosma prockia	3.08	203.66	1.20	79.52
Chrysophyllum flexuosum	3.06	206.72	1.20	80.72
Casearia sylvestris	2.70	209.42	1.06	81.77

Amazon region has found that only five of the top 20 species contribute to abundance, biomass and productivity, and that approximately one third of the biomass and productivity hyperdominant species do not even register as stem hyperdominants (Fauset et al., 2015). Our local-scale study revealed a similar pattern, with 35% of the main biomass hyperdominant species in the Southeast area not being stem hyperdominant, in contrast with a 45% value being registered to such variable in the Northeast area (Table 1). Despite that, these species may still contribute to forest biomass stocks (Table A.2 from ESM).

Our results indicated that *Myroxylon peruiferum* (with only two stems) and *Copaifera langsdorffii* (eight stems) altogether in the Southeast area and *Machaerium floridum* (eight stems) in the Northeast area accounted for 7.73% and 19% of the biomass in our dataset, respectively (Table 2). None of those species were listed as main stem hyperdominants, and despite ranking 51st, 28th and 33rd in stem abundance, respectively (Table A.1 from ESM); they all contributed considerably to biomass production. *M. peruiferum* and *C. langsdorffii* ranked 5th and 6th in biomass, contributing 4.23% and 3.50%, respectively, to the total in the Southeast area; in contrast, *Machaerium floribum* ranked first in biomass production in the Northeast area. Such inconsistency is due to two plant traits: extreme maximum size (DBH = 94 cm, 58 cm and 150 cm, in *M. peruiferum*, *C. langsdorffii* and *M. floridum,* respectively) and maximum height (16 m, 12.5 m and 16 m in those species, respectively). Together, these traits explain why these three species contribute so much to biomass despite having so few stems.

The study by Fauset et al. (2015) in the Amazon basin has also shown that a small number of species contributes disproportionately to the global density of stems and biomass, with only 1.4% of tree species representing half the regional abundance (stem hyperdominant species) and only 0.91% of tree species representing half the regional AGB production (biomass hyperdominant species). This dominance phenomenon is typically natural in ecosystems and may indirectly alter the relationship between species richness and an ecosystem function (Hillebrand et al., 2008; Lohbeck et al., 2016; Poorter et al., 2017). Such relationship may be linear with low species dominance, or be asymptotic when there is prevailing high dominance of a few species with higher contribution to ecosystem processes along with the presence of several species with low contribution (Dangles and Malmqvist, 2004, Lohbeck et al., 2016). These differences in the relationship between species richness and ecosystem functioning have been attributed to differences in functional redundancy (Petchey et al., 2007), i.e., when different species play equivalent roles in the ecosystems (Lohbeck et al., 2016; Poorter et al., 2017).

4.4. Implications for forest management and conservation

Our results present an approximation on how the ecosystem functioning of small remnant forest fragment in Atlantic forest can be evaluated through stem and biomass hyperdominant species in areas with different topographic conditions. This approach is of major importance for analyzing the impacts of tropical forests on a global scale (i.e., cycling carbon). Thus, we consider this hyperdominance approach to be of high relevance also to fine scale. For instance, it allows to identify the level of contribution of species in ecosystem functions, but above all to plan management decisions to eliminate species that reduce ecosystem functions, and substitute species that could increase them, without affecting local species richness. Forest ecosystem services are highly suppressed by fragmented habitats, which themselves are dominated by pioneer species and invade typically mature forests conditions, impacting biomass production and carbon storage thereat (Pütz et al., 2011; Pütz et al., 2014). Nonetheless, Atlantic remnant forest fragment still have high biodiversity and carbon storage conservation value under a REDD + perspective (Magnago et al., 2015). Therefore, knowing biomass hyperdominant species is of great importance to protect them from the logging activity that takes place in tropical forest, which itself may be leading to an important reduction of the current carbon stock in the highly diverse forest.

On the other hand, we consider important to understand the implications of this approach when analyzing different forest types (i.e., mature and secondary forests). For that reason, we presume that assessing hyperdominance in mature forests, specifically by analyzing species with higher functional contributions (i.e., trees with high capacity to store biomass and carbon), would be fundamental for conservation. Moreover, applying this approach on secondary forests, in communities with transient species dominance during succession, may be important for management by directed succession. Through hyperdominance analysis, it is possible to identify the relative contribution of species to ecosystem processes as well as the species that limit the establishment of mature forest species with higher functional values. Thereby, it is ultimately possible to control the succession trajectories by directly managing the species with lowest functional contributions, especially in landscapes undergoing human modification.

Lastly, we argue that even knowing that secondary forests are fundamental for conserving ecosystem functioning (Gibson et al., 2011), considerable attention must be devoted to managing degraded lands so that they can return to a forest condition and keep their functioning as well as their carbon sequestration dynamics. Forests undergoing regeneration should thus become the focus of conservation practices, as they play a key role in increasing biomass resilience, carbon sequestration and storage, and biodiversity restoration on a local scale (Chazdon et al., 2016).

5. Conclusions

Our results showed that high topographic heterogeneity induces high species richness at fine scale. Species richness in the more topographically heterogeneous area (Northeast) is almost 50% higher than in the Southeast area, which in turn is the less topographically heterogeneous. Furthermore, species composition varied considerably between areas, but with similar patterns of aboveground biomass being observed among plots. Thus, our results also revealed that the number of stem and biomass hyperdominant species increase along with richness on a fine scale. The Southeast area has lower richness and lower number of stem hyperdominant species, with only two species accounting for 50% of the total stem abundance, whereas the Northeast area has higher richness and higher number of biomass hyperdominant species, with ten species accounting for 50% of the total stem abundance. Additionally, our results indicated that higher tree species richness can influence the number of biomass or stem hyperdominant species. Moreover, in our fine-scale study we observed similar patterns between areas, with 35% of the main 'biomass hyperdominant' species in the Southeast area not being 'stem hyperdominant', in contrast with a 45% value being registered to such variable in the Northeast area. Based on our results, we presume that biomass hyperdominance can also strongly influence forest ecosystem functioning on a fine scale.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2019.02.033.

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