ALICE CRISTINA RODRIGUES

TOPOGRAPHY DRIVE TREE SPECIES DIVERSITY, STRUCTURE AND ECOSYSTEM FUNCTION IN A TROPICAL ATLANTIC FOREST

Dissertação apresentada à Universidade Federal de Viçosa, como parte das exigências do Programa de Pós-Graduação em Botânica, para obtenção do título de *Magister Scientiae*.

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APROVADA: 20 de fevereiro de 2018.

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Dedico este trabalho a todas as pessoas que acreditaram em mim, à minha família e à eterna memória do meu tio Flávio que, ao passar por esse mundo, me mostrou a importância dos estudos.

[...]

Nós nunca descobriremos o que vem depois da escolha, se não tomarmos uma decisão. Por isso, entenda os seus medos, mas jamais deixe que eles sufoquem os seus sonhos... Não tenha medo de entrar nos lugares onde você acha que não cabe.

Lewis Carroll

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SUMÁRIO

ABSTRACT

RODRIGUES, Alice Cristina, M.Sc., Universidade Federal de Viçosa, February, 2018. **Topography drive species diversity, structure and ecosystem function in tropical Atlantic forest.** Advisor: Andreza Viana Neri.

The Brazilian Atlantic forest is considered one the most important centers of diversity of vascular plants in the world providing various ecosystem services. Nevertheless, the region is also one of the most threatened tropical forests in the world, due mainly to habitat fragmentation. Comprehending the role played by environmental drivers, such as topographic variables that determine the community assembly and ecosystem functioning of tropical forests is fundamental to establishing conservation and management strategies. Nevertheless, research that study the relationship of these drivers on the biodiversity, structure and ecosystem function of Atlantic Forest tree communities remains scarce. The objective of this research was to evaluate the relative contribution of topographic drivers on forest attributes and ecosystem functioning. The study was conducted in a seasonal semi deciduous Atlantic forest fragment (at Viçosa municipality, Minas Gerais state, Brazil. We selected two sampling areas with contrasting topographic conditions (a Southeast area and a Northeast area one). Each area (100 × 100 m) was sub-divided into 100 plots of 10 × 10 m a total 200 plots (2 ha). From each plot, all trees having diameter at breast height ≥ 3.2 cm were sampled and identified to the species level. In each plot we measured three topographic variables (slope, elevation, and convexity) using a Total Station and measure the soil physicochemical properties. We performed multivariate regression tree (MRT) analysis to classify habitat types according to topographic variables and species composition. We estimated the maximum number of species required accounting for 50% of stem abundance and biomass in each area and we considered as 'biomass hyperdominants' and 'stem hyperdominants' the species that accumulated 50% of the total biomass and stems, respectively. The two study areas showed significant differences in spatial distribution of topographical variables. According to the MRT, the Southeast area was topographically less heterogeneous whith five habitat types, whereas the Northeast area was topographically more heterogeneous with seven habitas types. All species richness indices differed significantly between areas, but only in Southeast area did they also differ between habitat types. Species richness in the Northeast area is 48% higher than that of Southeast area. Structural attributes and AGB did not show differences between areas. However when analyzed at the area scale, basal area, tree height and AGB showed significant differences between low valleys and high plateaus in the Southeast area. The number of stem hyperdominants varied significantly between areas. In the Southeast area, only two species accounted for 50% of the number of stems hyperdominants, while in the Northeast area 10 species accounted for 50% of stems hyperdominants. In the Southeast area, only two species were classified as biomass hyperdominants, in the Northeast area, on the other hand, five species accumulated 50% of the AGB. Our results showed that the diversity and distribution pattern of hyperdominant species were significantly correlated with topography in both areas, and that the structural and AGB attributes vary in the topographic gradient of the Southeast area. We presume that the relative functional contributions of species may substantially vary from one species to another, regardless of their abundance. Thereby, some particularly abundant species may not in fact contribute substantially to ecosystem processes. The variation of forest attributes among habitats is probably due to the heterogeneous distribution of resources such as water and nutrients because of the great difference in elevation between the extremes of the topographic. This fact can also be correlated with the existence of a marked fine-scale edaphic gradient in soil parameters among habitats in the Southeast area. In addition, species redundancy may explain the weak relation between richness and AGB found in our study. We conclude that topography is an important driver that determines the structure, diversity and ecosystem functioning. Our study is of great importance in the analysis of impacts on tropical forests on a local scale with global repercussions, which favors the establishment of basic criteria for conservation and management.

RESUMO

RODRIGUES, Alice Cristina, M.Sc., Universidade Federal de Viçosa, fevereiro de 2018. **Topography drive tree species diversity, structure and ecosystem function in a tropical Atlantic forest.** Orientadora: Andreza Viana Neri.

A Mata Atlântica é considerada um dos centros de diversidade de plantas vasculares mais importantes do mundo, desempenhando diversos serviços ecossistêmicos. No entanto, é uma das regiões de florestas tropicais mais ameaçadas devido à fragmentação. Dessa forma, compreender o papel dos modeladores ambientais, como as variáveis topográficas, que determinam a estruturação e funcionamento dessas florestas é fundamental para estabelecer estratégias de conservação e manejo. Porém, ainda são limitadas as pesquisas que estudam a relação destes modeladores sobre a diversidade, estrutura e funcionamento ecossistêmico de comunidades arbóreas da Mata Atlântica. Assim, o objetivo desta pesquisa foi avaliar a contribuição relativa dos modeladores topográficos sobre os atributos florestais e sobre funcionamento do ecossistema. O estudo foi realizado em um fragmento de floresta estacional semidecidual da Mata Atlântica no município de Viçosa, Minas Gerais, Brasil. Selecionamos duas áreas de amostragem (área Sudeste e área Nordeste) com condições topográficas contrastantes. Cada área (100 × 100 m) foi subdividida em 100 parcelas de 10 × 10 m, totalizando 200 parcelas (2 ha). Em cada parcela, todas as árvores com diâmetro a altura do peito ≥ 3.2 cm foram amostradas e identificadas em nível de espécie. Para cada parcela, medimos três variáveis topográficas (inclinação, elevação e convexidade) usando uma estação total e as propriedades físico-químicas do solo. Realizamos análises de regressão multivariadas (MRT) para classificar os tipos de habitats de acordo com as variáveis topográficas e a composição de espécies. Testamos diferentes tipos de modelos linearis para avaliar efeitos principais dos modeladores topograficos e parâmetros do solo sobre a estrutura e diversidade ao longo do gradiente topográfico. Consideramos como hiperdominantes em biomassa e hiperdominantes em caules, as espécies que acumularam 50% da biomassa total e caules, respectivamente. As duas áreas de estudo apresentaram diferenças significativas na distribuição espacial das variáveis topográficas. De acordo com a MRT a área sudeste foi topograficamente menos heterogênea, com cinco tipos de habitats, enquanto que a área nordeste foi topograficamente mais heterogênea com sete tipos de habitats. Todos os índices de riqueza de espécies diferiram significativamente entre as áreas, mas apenas na área

Sudeste também diferiram entre os tipos de habitats. A riqueza de espécies na área nordeste foi 48% maior do que a área sudeste. Os atributos estruturais e a biomassa acima do solo (AGB) não mostraram diferenças entre as áreas. No entanto, quando analisados na escala de área, área basal, altura e AGB mostraram diferenças significativas entre vales e platôs na área sudeste. O número de espécies hiperdominantes em caules e biomassa variou significativamente entre as áreas. Na área Sudeste, apenas duas espécies representaram 50% do número de hiperdominantes em caules, enquanto na área Nordeste esta represetanda por 10 espécies. Na área Sudeste, apenas duas espécies foram classificadas como hiperdominantes em biomassa. Na área Nordeste, por outro lado, cinco espécies acumularam 50% da AGB. Nossos resultados mostraram que a diversidade e o padrão de distribuição de espécies hiperdominantes foram significativamente correlacionados com a topografia em ambas as áreas, e que os atributos estruturais e AGB variam no gradiente topográfico da área sudeste. Presumimos que as contribuições relativas das espécies para o funcionamento ecossistêmico podem variar substancialmente de uma espécie para outra, independentemente da sua abundância. Assim, algumas espécies particularmente abundantes podem não contribuir substancialmente para os processos do ecossistema. A variação dos atributos florestais entre os habitats é provavelmente devido à distribuição heterogênea de recursos, como água e nutrientes, devido à grande diferença de elevação entre os extremos do gradiente topográfico. Esse fato também pode ser correlacionado com a existência de um gradiente edáfico de escala fina nos parâmetros do solo entre habitats na área Sudeste. Além disso, a redundância das espécies pode explicar a fraca relação entre riqueza e AGB encontrada em nosso estudo. Concluímos que a topografia é um importante modelador que determina a estrutura, diversidade e o funcionamento ecossistêmico. Sendo nosso estudo de grande importância na análise de impactos em florestas tropicais numa escala local com repercusão global, o que favorece o estabelecimento de critérios básicos de conservação e manejo

INTRODUÇÃO GERAL

As regras de montagem que determinam a composição florística e a estrutura das comunidades vegetais são baseadas na hipótese dos efeitos combinados de diferentes filtros ambientais sobre o pool regional de espécies (Diamond, 1975; Pausas & Verdu, 2010; Kraft & Ackerly, 2010). Diferentes eventos estocásticos podem determinar as espécies que são potencialmente disponíveis em um hábitat, porém os *drivers* abióticos locais selecionam as espécies que tem a capacidade para tolerar essas condições (Webb, 2000; Weiher et al., 2011). Por exemplo, nas florestas tropicais, a topografia têm efeitos significativos sobre a heterogeneidade do habitat e estruturação das comunidades de árvores ao longo de gradientes ambientais (Shen et al., 2013; Wang et al., 2016). Causando múltiplos efeitos no funcionamento ecossistêmico (Cardinale et al., 2012; Hooper et al., 2012; Naeem et al., 2012).

Vários estudos tem relatado que a distribuição das espécies está relacionada com variações na topografia e nas proprieades do solo em florestas tropicais (por exemplo, Guo et al., 2016). A topografia influencia o microclima, a intensidade de luz, a temperatura, a umidade do solo e do ar, a evaporação e a duração dos períodos de crescimento das plantas, e essas diferenças estão intimamente associadas às diferenças da composição e estrutura da vegetação (Pook & Moore, 1966). A topografia, sobretudo em escala regional e de paisagem está fortemente ligada com o padrão de distribuição das espécies (Grytnes, 2003; Sanders & Rahbek, 2012). No entanto, em escalas espaciais menores o efeito de pequenos gradientes de elevação, declividade e convexidade, sobre a estrutura, diversidade e funcioanmento ecossistêmico não é bem conhecido, srebretudo em florestas tropicais.

Essas mudanças na estrutura das comunidades podem também modificar a importância relativa das espécies em termos de sua contribuição para os processos ecossistêmicos (por exemplo, estocagem de biomassa e carbono, Poorter et al., 2017). Assim, algumas espécies particularmente abundantes podem não contribuir substancialmente para a produção de biomassa, enquanto outras que possuem uma ocorrência menos abundante contribuem de forma significativa (Fauset et al., 2015). O fenômeno da hiperdominâcia (i.e. a contribuição desproporcional para a biomassa ou a abundância de um pequeno número de espécies) é tipicamente natural nos ecossistemas e pode indiretamente alterar a relação entre riqueza de espécies e uma função ecossistêmica (Hillebrand et al., 2008; Lohbeck et al., 2016; Poorter et al., 2017). No entanto, ainda existem limitadas pesquisas que permitam estudar a relação de diferentes *drivers* ambientais (por exemplo, topografia) sobre a estruturação de comunidades arbóreas analisando a contribuição relativa das espécies no funcionamento ecossistêmico.

O domínio da Mata Atlântica (Oliveira-Filho & Fontes, 2000), é considerado como um dos centros globais de diversidade de plantas vasculares (Guedes-Bruni et al., 2009; Murray-Smith et al., 2009), e uma das regiões de floresta tropical mais ameaçadas no mundo devido à fragmentação (Myers et al., 2000; Laurance, 2009). Compreender o papel das variáveis ambientais que regem as mudanças na composição e estrutura destas florestas, bem como os fatores que controlam o funcionamento de seu ecossistema é necessário para apoiar a conservação da biodiversidade frente à perda e degradação das florestas (Guisan & Zimmermann, 2000, Margules & Pressey, 2000, Araújo & Guisan 2006, Ferrier et al., 2007). E prever respostas das espécies e das comunidades de plantas a mudanças nas condições ambientais (Guisan & Zimmermann, 2000; Araújo & Guisan, 2006; Ferrier et al., 2007).

O objetivo do presente trabalho foi avaliar a contribuição relativa dos drivers topográficos sobre os atributos florestais e sobre funcionamento do ecossistema num fragmento florestal da Mata Atlântica (Fig. 1). Para isso, essa dissertação foi estruturada em dois capítulos. No primeiro capítulo, analisamos se a topografia influencia os atributos estruturais e taxonômicos da comunidade de espécies arbóreas, e se com o aumento da heterogeneidade topográfica, há aumento da diversidade, como já foi relatado anteriormente para florestas tropicais (Kubota et al., 2004; Liu et al., 2014). Seguido disso, analisamos se a diversidade é positivamente associada à biomassa acima do solo. No segundo capítulo, analisamos se a maior heterogeneidade topográfica é responsável por uma maior riqueza de espécies e se a maior riqueza de espécies de árvores determina um maior número de espécies ‘*stem and biomass hyperdominants*’. Além disso, analisamos se as espécies ‘*stem hyperdominates*’ são também ‘*biomass hyperdominantes*’.

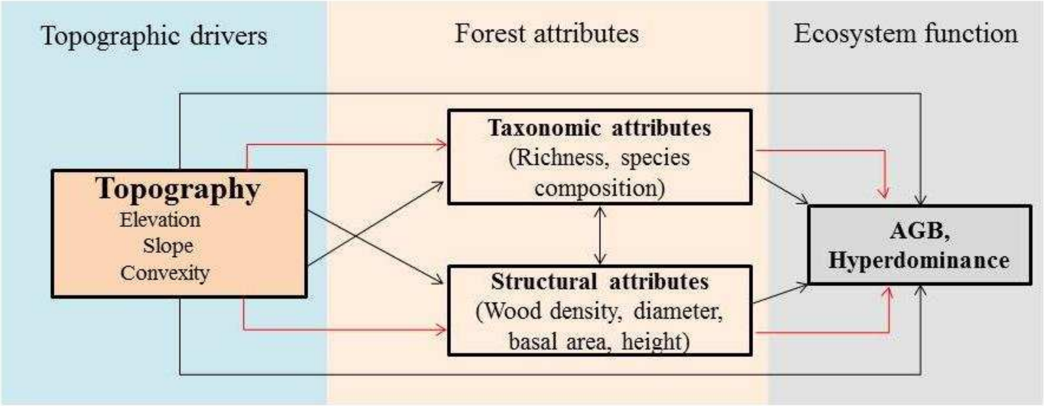

Figura 1. Modelo conceitual dos objetivos do estudo. As linhas em preto representam como a biomassa acima do solo pode ser afetada pelos atributos estruturais e taxonômicos, e pelo efeito direto e indireto da topografia (capítulo 1). As linhas em vermelho representam o possível efeito da topografia sobre a riqueza e estrutura da floresta e sua relação com as espécies hiperdominates em biomassa e caules (capítulo 2). Adaptado de Poorter et al., (2015).

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CAPÍTULO 1: Distribution patterns of tree species diversity, composition, stand structure and aboveground biomass along topographic gradients in relation to habitats in a tropical Atlantic forest

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1. ABSTRACT

The Brazilian Atlantic forest is considered one the most important centers of diversity of vascular plants in the world. Comprehending the role played by tropographic drivers that determine the community assembly and ecosystem functioning these forests is one of the main goals of current ecological research. In this study, we analyzed the effects of topographical variables and soil features on tree species diversity, composition and aboveground biomass along a topographic gradient in two areas of an Atlantic forest fragment from Minas Gerais state, Brazil. We investigated whether (1) topography influences structural and taxonomic attributes of the tree species community, and with increasing topographic heterogeneity, leads to an increase in diversity and (2) diversity is positively correlated with aboveground biomass. We carried out a standard census of wood stems ≥ 3.2 cm dbh in two sampling areas with contrasting topographic conditions: a Southeast area and a Northeast area one. We measured three topographic variables (slope, elevation, and convexity) and the soil physicochemical properties for each plot. We performed multivariate regression tree (MRT) analysis to classify habitat types according to topographic variables and species composition. The two study areas showed significant differences in spatial distribution of topographical variables. According to the MRT, the Southeast area can be divided into five habitats and the Northeast area in seven habitats. All species richness indices differed significantly between areas, but only in Southeast area did they also differ between habitat types, with exception Pielou's evenness index. Structural attributes and AGB did not show differences between areas. However in area scale, basal area, tree height and AGB showed significant differences between low valleys and high plateaus in the Southeast area. This variation among habitats is probably due to the heterogeneous distribution of resources such as water and nutrients because of the great difference in elevation between the extremes of the topographic gradient. This fact can also be correlated with the existence of a marked fine-scale edaphic gradient in soil parameters among habitats in the Southeast area. Species richness in the Northeast area is 48% higher than that of Southeast area, but we did not find a significant positive relationship between richness and AGB, probably due to species redundancy. A single topographical variable (Elevation) consistently explained more variation in species richness, abundance and composition than those with multiple effects of topography and soils. This suggests that soil fertility is not essential to maintain diversity in the study areas. Our results show that environmental filtering may be a fundamental process to community assembly in tropical forests, even on a local scale. This study represents a first approximation in the analysis of the relationship between structural and taxonomic attributes and ecosystem functions along topographic gradients, and might thus aid in the establishment of basic criteria for the management and conservation of the Atlantic forest.

Keywords: biodiversity; ecological mechanisms; ecosystem functioning; stand structure; topographic heterogeneity

2. INTRODUCTION

Understanding the roles of environmental factors for determining biodiversity, stand structure and ecosystem functioning of tropical forests is one of the central focuses in contemporary ecology (Ali et al., 2017; Poorter et al., 2017). Tropical forests harbor more than half of the global biodiversity and have a major influence on the mitigation of the current climate change while providing important goods and services that humans depend on (Lewis et al. 2015). For instance, the aboveground biomass in tropical forests plays a key role in the global carbon cycle (Lewis et al. 2015; Anderson-Teixeira et al. 2016) by sequestering carbon dioxide which is the main cause of the greenhouse effect (Anderson-Teixeira et al. 2016). Aboveground biomass stocks vary widely among forests due to the differential effects of abiotic (such as topography and soil fertility) and biotic (such as biodiversity and stand structural attributes) factors (Ali et al., 2016). Thus, aboveground biomass may be determined by taxonomic (e.g., species richness) and stand structural attributes (e.g., stem diameter, wood density, and tree height) as well as by direct and indirect effects of environmental (abiotic) factors that can affect the amount of biomass via effect on biodiversity and stand structural attributes (Ali and Yan, 2017; Poorter et al. 2017). Therefore, it is highly necessary to understand the main mechanisms underlying forest community assembly in order to establish conservation and management strategies, as well as to predict the responses of species richness to the variability of environmental factors.

Several studies have shown that topography is a proxy for resource availability, playing a key role in tree species distribution in tropical forests (e.g., Bohlman et al., 2008). Topographic factors, such as convexity, elevation and slope of the terrain, are well-known for not only determining a differential use of resources by tree species (McEwan and Muller, 2006) but also for molding edaphic gradients (e.g., soil nutrients and moisture contents) (John et al., 2007). Therefore, both topographic and edaphic gradients may influence demographic processes of tree growth, mortality and recruitment (e.g., Herwitz and Young 1994), and consequently may influence aboveground biomass (Valencia et al., 2009). Hence, the topography is considered as a good predictor of habitat formation, as it correlates with variables that are directly related to plant resources (Daws et al. 2002; Guo et al., 2016). Topographic heterogeneity may thus be a determinant driver in the relationship between diversity and productivity in tropical forests (Clark al. 1998; Takyu et al., 2002). Since environmental variables are spatially heterogeneous, they affect species distribution through the species-habitat association (Guo et al. 2016; Wang et al. 2016). For instance, variation in species richness along topographic gradients has been observed in several studies that have detected a clear habitat differentiation due to topographic heterogeneity (e.g., Homeier et al. 2010, Brown et al. 2013). In this context, there is a sufficient evidence for the existence of a close relationship between environmental heterogeneity and tree species diversity in tropical forests. However, increasing habitat heterogeneity leads to an increased number of species coexisting along environmental gradients, thereby configuring a determinant factor for community assembly (Brown et al. 2013; Liu et al. 2014). Yet, research on the distribution patterns of tree species diversity, stand structure and aboveground biomass along topographic gradients in relation to habitats in tropical forests remains scarce.

The Atlantic forest is considered as one the most important hotspot of the diversity of vascular plants in the world (Murray-Smith et al., 2009). Additionally, this forest has a high capacity for carbon storage in the standing biomass (Magnago et al. 2015). Nevertheless, the region is also one of the most threatened tropical forests in the world, mainly due to the habitat fragmentation (Laurance, 2009; Ribeiro et al., 2011). The processes of transformation through which the Atlantic forest has been going to a series of negative consequences to ecosystem services. Currently, only as much as 10% of the mature forests therein are conserved and the remnants of native vegetation are restricted to ca. 20% of its original cover (Scarano and Ceotto, 2015). Hence, evaluating the distribution of abundance and diversity of tree species along environmental gradients in these forests is crucial for understanding their ecosystem functions. Furthermore, such an evaluation may also allow for understanding the management dynamics and the level of conservation of forest fragments, as well as how they would respond to different disturbance scenarios, by means of analyzing tree functional attributes associated with forest regeneration (Santo-Silva et al., 2016). Few studies, however, have so far addressed the relationships of environmental factors, species diversity and stand structural attributes with aboveground biomass along topographic gradients in Atlantic forest fragments.

In this study, we analyzed the effects of topographical factors and soil properties on tree species diversity, composition, stand structure and aboveground biomass along topographic gradients in two areas of an Atlantic forest fragment in Minas Gerais state, southeastern Brazil. We tested the following hypotheses: 1) topography influences stand structural and taxonomic attributes of the tree species community, with increasing topographic heterogeneity leading to increased diversity; and 2) diversity is positively related with aboveground biomass along topographic gradients. Based on that, we assumed that both tree species diversity and aboveground biomass would increase with increasing topographic heterogeneity.

3. MATERIAL AND METHODS

3.1. Study area

This study was conducted in a seasonal semideciduous 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 area 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 (Paula et al., 2002). The study area has a moderate humid tropical 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).

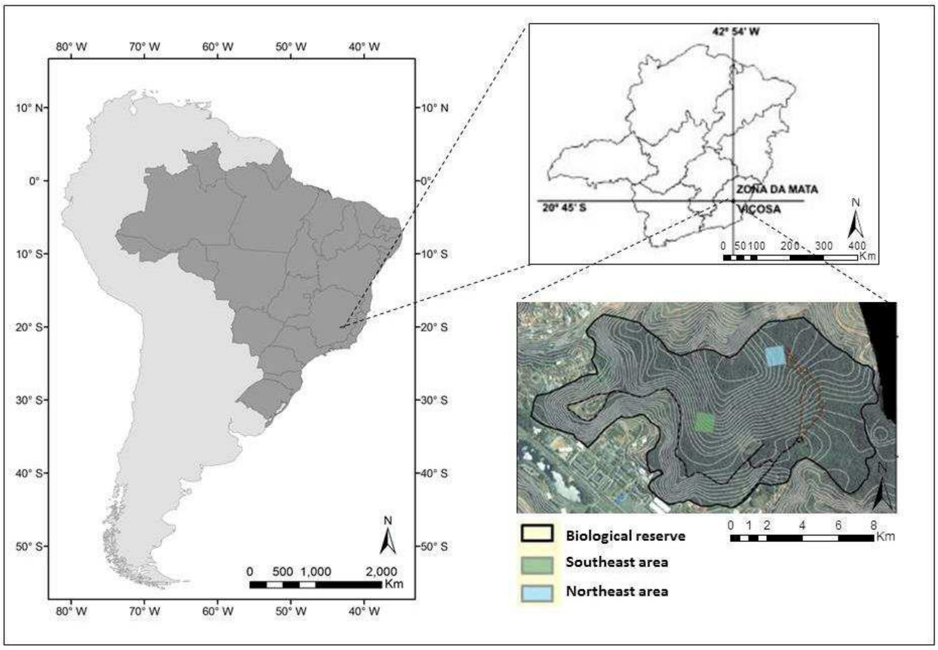

Figure 1: Map showing the location of the study area. Adapted from Ferreira-Júnior, et al., (2007) and Del Peloso, (2012).

3.2. Forest inventory and data collection

We selected two sampling areas with contrasting topographic conditions: a Southeast area (UTM 23K 722758/7703626) and a Northeast area (UTM 23K 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. Within each plot, all trees having a diameter at breast height (DBH) ≥ 10 cm were identified to the species level and tagged for measurement. All individuals were identified using specialized literature, through consultation with the VIC Herbarium of UFV, or by taxonomists. The Angiosperm Phylogeny Group IV (APG IV 2016) was used for taxon classification. Species nomenclature and the respective abbreviations of their authors were checked against the Tropicos.org list databases (MOBOT, 2015).

3.3. Measurements of topographical variables

We measured three topographic variables (slope, elevation, and convexity) within each plot, based on the assumption that these variables may affect tree species diversity, species composition, stand structure 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 (Guo et al. 2016). Convexity was determined by subtracting the elevation at the centre 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, 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 et al., 1988). The data was then transferred to a computer and analyzed with the software AutoCAD® for further procedures (Autodesk Inc., San Rafael, CA, USA).

3.4. Estimation of aboveground biomass

The aboveground biomass of individual stems was calculated using the general allometric equation (Eq. 1) proposed by Chave et al., (2014), based on tree DBH (cm), height (H, m) and species' wood density (ρ, g cm-3). We used Neotropical data from the Global Wood Density Database (Zanne et al., 2009; 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.

$$\boldsymbol{AGB = 0.0673\ (\rho \times DBH^{2} \times H)^{0.976}} \qquad \text{Eq. (1)}$$

The total aboveground biomass per plot was the sum of the aboveground biomass of all trees having DBH ≥ 10 cm, which was then converted to megagrams per hectare (Mg ha-1) (Ali et al., 2017). Species-level biomass was calculated as the sum of the biomass of all stems from a corresponding species.

3.5. Measurements of soil properties

In order to measure the soil chemical properties for each plot, a composite sample of the surface soil (0-10 cm depth) was collected. Soil chemical properties of the samples were measured in the Soil Analysis Laboratory of the Federal University of Viçosa, following standard protocols (EMBRAPA, 1997). The following parameters were assessed: soil organic carbon (C), total N, available P, K, Ca, Mg, Fe, Zn, effective cation exchange capacity (CEC), exchangeable acidity (H + Al); sum of bases (SB); base saturation (V); aluminum saturation (m); pH and organic matter (OM).

3.6. Quantification of biodiversity indices

Measurements of taxonomic diversity indices were calculated in each plot from forests at the four successional stages and from the old growth-forest. Measurements included species richness, Shannon-Weaver index and Pielou's evenness index (Magurran, 2004). Species richness refers to the total number of species recorded in each plot. Shannon-Weaver index (H') and Pielou's evenness index (J) were calculated by the following equations (Eq. 1 and 2).

$$\mathrm{H}' = -\sum_{\mathrm{i}=1}^{\mathrm{S}} \mathrm{pi} \ln \mathrm{pi} \qquad (1)$$

$$\mathrm{J} = \frac{\mathrm{H}'}{\ln(\mathrm{S})} \qquad (2)$$

Where S is the total number of species in a plot; pi is the species' relative abundance; and ln is the natural logarithm. These indices incorporate the species richness and the proportion of each species within each plot (Magurran, 2004). All diversity indices were calculated using the 'vegan' package (Oksanen et al., 2016) in software R 3.2.2. (R Development Core Team, 2016).

3.7. Data and statistical analyses

First, we constructed a map of two important topographic variables (i.e. elevation and slope) with the aim of mapping their spatial distribution in each study area, using the "*spatstat*" package (Baddeley et al., 2017). Second, we performed multivariate regression tree (MRT) analysis (De'ath, 2002; Larsen and Speckman, 2004) to classify habitat types according to the topographic variables and species composition (Guo et al., 2016; Wang et al. 2016). MRT is a method of constrained clustering that identifies clusters (a group of plots) that are most similar to 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). We represented the spatial distribution of habitats from each area using the "*Field*" package (Liu et al., 2014; Nychka et al., 2017).

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 of species (Hill number of order 0), being up to three times the sample size (Colwell et al., 2012). These estimates were obtained using the "*iNEXT*" package (Hsieh et al., 2016). 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., 2016). We used permutation 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., 2016).

Variables were tested for normal distribution with the Shapiro-Wilk test by evaluating the Q-Q plot. To compare the means of the variables between areas (i.e., soil chemical properties, stand structure, topographical variables) we used t-test (normally distributed data: structural attributes), and Mann-Whitney U test (non-normally distributed data: diversity, topographical variables, soil parameters). To compare means of the variables between habitats, we used a one-way ANOVA (for normally distributed data) followed by a posterior tukey's test ($p < 0.05$), and Kruskal-Wallis's test (for non-normally distributed data) followed by a posterior Dunn's test (Dinno, 2017). All these analyses were performed with the "*stats*" and "*dunn.test*" packages (Dinno, 2017). We employed partial Mantel tests to assess spatial autocorrelation of the sampling units within each area. The results of the Mantel test rejected the null hypothesis for the spatial autocorrelation among plots (P > 0.05). Here, we used the ‘*Mantel test*’ function in the “*ade4*” package (Dray *et al*. 2017).

We constructed a series of multivariate linear models to find the most parsimonious models for explaining the main effect of potential predictor variables (i.e. topography and soils parameters) on the response of species richness, abundance, and species composition across the topographical gradients. We used the generalized linear mixed effects model (GLMMs) with Poisson error distribution to investigate the effects of multiple predictors on species richness. Generalized linear models (GLMs) with negative binomial distributions with log link functions were used when the data showed significant overdispersion, and the effects of predictors on aboveground biomass and species composition were calculated using linear mixed effects models (LMMs) with Gaussian distributions. The identity link was identified for each model through the normality confirmed by the Shapiro–Wilk test and Q-Q plot. Explanatory or predictor variables were grouped into two categories, i.e., topographical variables and soil chemical properties. The topographic variables included elevation, slope and convexity, whereas soil chemical properties included pH. For species composition, we used axis-1 the non-metric multidimensional scaling (Euclidian distance) which explains the greater variance with absence/presence data (Oksanen, 2016). In these models, the identity of the plots in each area was included as a random factor. We assessed collinearity between selected predictor variables using Spearman correlation analysis, and when two variables were strongly correlated (r ≥ 0.6) were included in separate models.

To select the best models, we applied a multi-model inference approach (Burnham and Anderson, 2002) with the ‘*dredge*’ function in the “*MuMIn*” package (Barton, 2017), which allows all possible combinations of the explanatory variables included in the global model (Barton, 2017). To determine which of these variables were the most decisive in explaining changes in species richness, abundance, species composition, and aboveground biomass, we used an information theoretical approach based on the Akaike information criterion with a correction for small sample sizes (AICc) and AICc weights (Burnham and Anderson, 2002). We selected the best model with the lowest AICc and all models whose difference in AICc with the best model was less than four units (Burnham et al., 2011). All models were calculated in R using the packages ‘lme4’, ‘nlme’, and ‘MASS’ (Bates et al., 2017; Pinheiro et al., 2017; Ripley, 2017). All data and statistical analyses were conducted in R.3.2.2 (R-Core-Team, 2016).

4. RESULTS

4.1. Habitat types based on topography

The two study areas showed significant differences in spatial distribution of topographic variables, i.e., elevation and slope (Fig. 2). According to the MRT, the Southeast area was topographically less heterogeneous, with the habitat types determined by the two topographic variables, i.e., elevation and slope, and hence can be divided into five habitats: i) high plateau, ii) intermediate plateau, iii) low plateau, iv) high valley, and v) low valley (Fig. 3). The Northeast area was topographically more heterogeneous. The habitat types were determined by all three topographic variables including elevation, slope, and convexity, and hence can be divided into seven habitats. The Northeast area consisted of the same types of habitats as the Southeast area, but had two additional habitats types, i.e., i) intermediate low valley, and ii) a transition area between the high valley and low plateau (Fig. 3).

Elevation determined the first split of MRT for habitat types in both areas (break point: Southeast = 71, Northeast = 716), while accounted for 21-34% of species variance. In Southeast area elevation was also responsible for a second (breakpoint = 718), and third (breakpoint = 705) splits of habitat types, followed by slope, which determined fourth split (breakpoint = 29). Convexity was not included in the MRT for Southeast area but was responsible for second split (breakpoint = 0.37) in Northeast area. Elevation determined the third (breakpoint = 707) and fifth (breakpoint =703) split, and the slope was the fourth (breakpoint = 28) and sixth (breakpoint = 19) splits of habitats types in Northeast area (Fig. S1, Table S1). Differences presented by elevation were marginally significant between areas (Table 1). In the meantime, topographic variables by area showed consistent differences between habitats, with exception of slope in the Southeast area (Table S2).

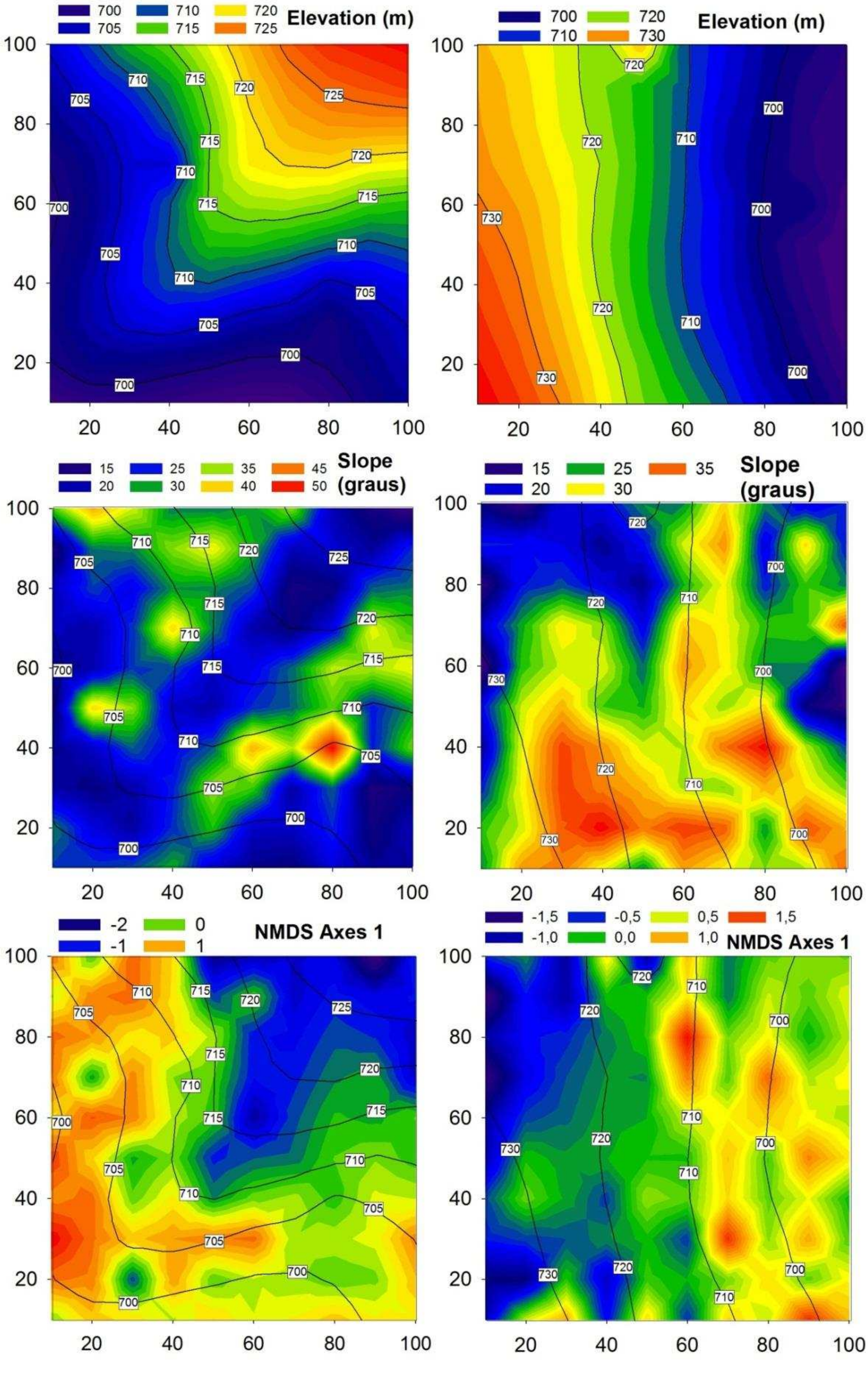

Figure 2. Map of spatial distribution of the two topographical variables more important (elevation and slope), and species composition (NMDS1) from each study area (100 x 100 m) with 10 by 10 m subplot size each. Northeast (figures on the left) and Southeast (figures on the right). Elevational contours are indicated by black lines.

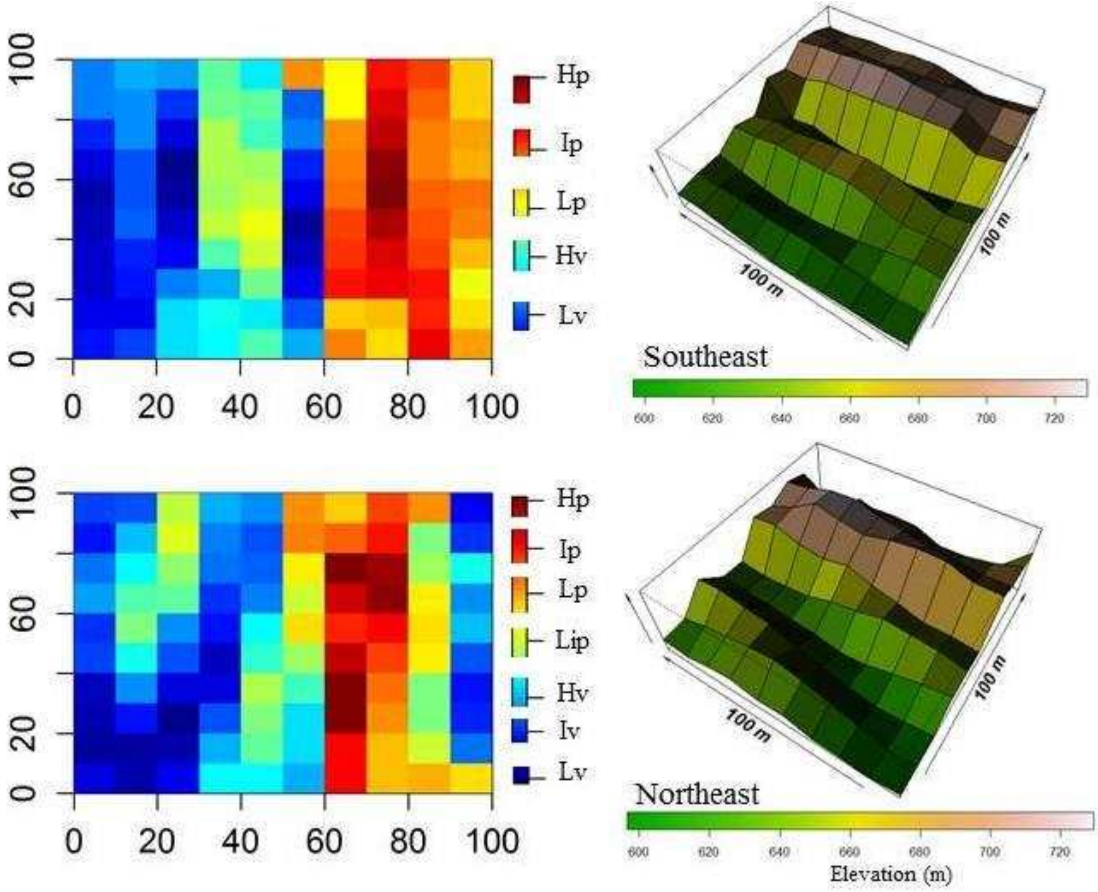

Figure 3. Habitats types (left) and topographic maps (right) of the two study areas within 2-ha permanent plots in Atlantic forest, Minas Gerais, Brazil. . According to the MRT, the areas were divided into of the following habitats: i) High plateau (Hp); ii) intermediate plateau (Ip); iii) low plateau (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 (Lip).

Table 1. Tree species diversity indices, stand structural attributes, topographic and soil variables (mean ± SD) of the study areas. T-test (normally distributed data: stand structural attributes), and Mann-Whitney U test (non-normally distributed data: species diversity indices, topographic variables, and soil properties).

	Sample area		**Mann-Whitney U Test/ t-test**	
Site parameter	Northeast	Southeast	z/t	*p valeu*
Diversity				
Species richness	11.37 ± 2.89	8.11 ± 2.73	1.04	***
Shannon's species diversity	2.22 ± 0.37	1.57 ± 0.50	1.23	**
Pielou's species richness	0.92 ± 0.05	0.75 ± 0.16	1.93	**
Stand structural attributes				
Total stems	1843	2297		
Number of stems	18 ± 2.23	23 ± 2.74	5.2	*
Tree DBH (cm)	11.02 ± 3.16	10.01 ± 2.81	3.9	ns
Stem wood density (g/cm^3)	0.66 ± 0.03	0.66 ± 0.04	1.14	ns
Tree max. height (m)	16.28 ± 3.53	17.07 ± 4.35	5.35	ns
Basal area (m^2/ha)	30.12 ± 18.50	33.96 ± 16.14	5.47	ns
AGB (Mg/ha)	209.60 ± 184.24	235.53 ± 171.81	1.02	ns
Topographical variables				
Elevation (m)	709.34 ± 8.82	713.19 ± 12.84	5.82	*
Slope	25.36 ± 7.28	26.17 ± 6.11	1.06	ns
Convexity	0.08 ± 1.80	0.12 ± 3.0	4.61	ns
Soil chemical properties				
pH (H_2O)	5.43 ± 0.70	4.83 ± 0.45	2.41	***
H+Al	5.87 ± 2.08	10.36 ± 2.17	6.47	***
SB	4.52 ± 2.55	2.27 ± 2.67	2.23	***
(t)	4.89 ± 2.17	3.71 ± 2.24	3.69	***
V	43.03 ± 22.68	17.00 ± 16.14	1.72	***
Mo	5.41 ± 0.62	6.51 ± 1.07	6.80	**

t-test significance (black color, ns = non-significant, * = $p < 0.05$); and z-Mann-Whitney significance test (gray color, ns = non-significant, ** = $p < 0.01$, *** = $p < 0.001$).

4.2. Distribution patterns for taxonomic diversity, stand structural attributes and aboveground biomass

All species richness indices differed significantly between areas (Table 1), but only in Southeast area did they also differ between habitat types, with exception Pielou's evenness index (Table S2). Species richness in the Northeast area is 48% higher than that of Southeast area (Fig. 4). Species richness differed among habitats in Southeast area, but did not differ between habitats in Northeast area (Fig. 4 & Table S2). The NMDS showed that tree species composition varied considerably among areas with strong influence of the distribution pattern of the topographic variables, mainly elevation and slope (Fig. 2 & 5). The NMDS ordination separated the two study areas along the second axis. Species composition also showed differences among habitat types in Southeast area, mainly between high plateau and low valley (Table S2 & Fig. S2).

Stand structural attributes and aboveground biomass did not show differences between areas (Table 1). The aboveground biomass ranged from 23.11 to 690 Mg ha^{-1} in Northeast, and 26.94 to 664.65 Mg ha^{-1} in Southeast. However, when analyzed at the area scale, basal area, tree height and aboveground biomass showed significant differences between low valleys and high plateaus in the Southeast area. Subplots in depressions were dominated by species that had high tree maximum height and aboveground biomass, but the low basal area. On the contrary, there were no differences between habitats in Northeast area (Table S2).

4.3. Shifts in species richness, abundance and composition between areas and habitats

The multi-model comparison between areas and habitats within areas showed that models including a single topographical variable (i.e. elevation) consistently explained more variation in species richness, abundance and composition than those with multiple effects of topography and soils (Table 2 and Fig. S3). In our analysis scale, topographic variables were better predictors than soil parameters. Aboveground biomass did not showed change with main effects of different predictors (topography, soils, and richness). Thus, we observed as the main pattern that there are non-significant positive relationship between species richness and aboveground biomass at site and habitat scale (Fig. 6).

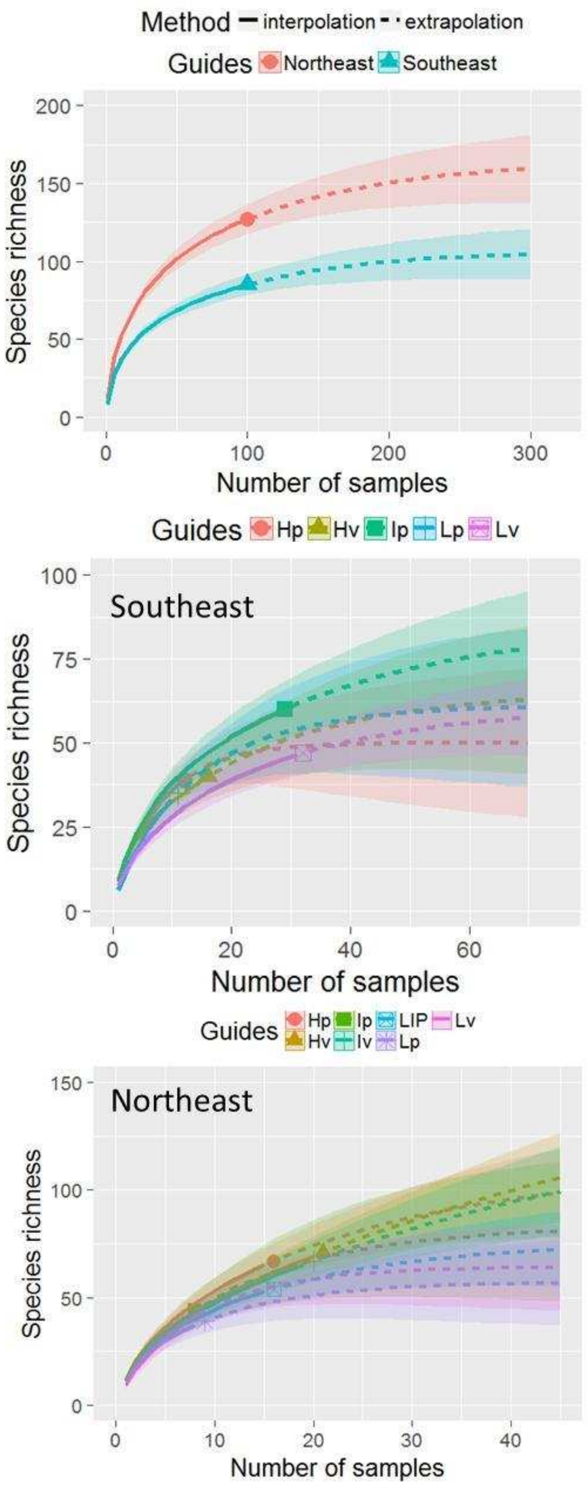

Figure 4. Sample-based rarefaction (solid line) and extrapolation curves (dashed lines) of tree species richness for the two study areas and different habitats by area.

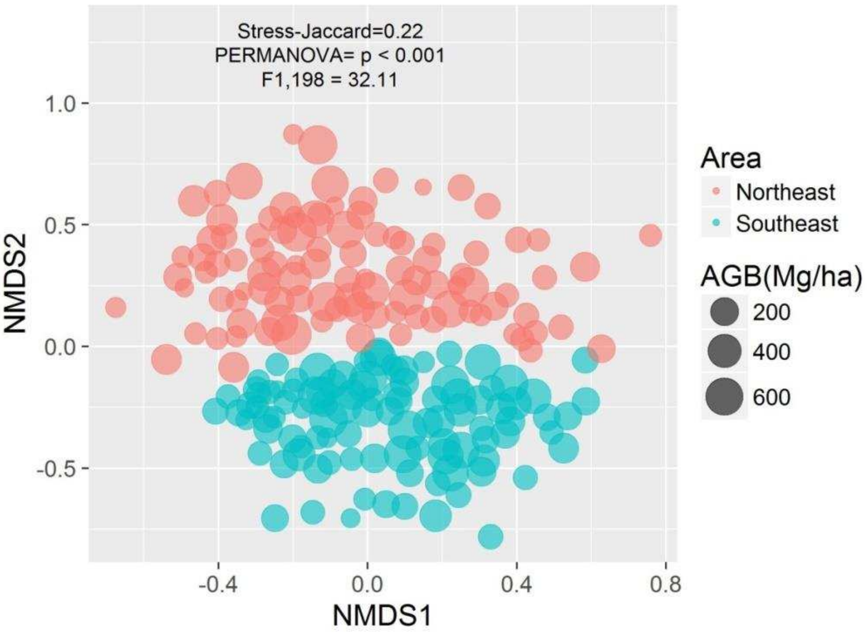

Figure 5. Non metric multidimensional scaling based on species composition according to aboveground biomass (circles sizes) and study areas (point colors).

Table 2. Subset of models predicting the species richness (generalized linear mixed effects model); abundance (negative binomial generalized linear model); and species composition (linear mixed effect model). Result of information-theoretic–based model selection is indicated. We present only the models with values of ΔAICc < 4. Predictors are elevation (m). The Akaike information criterion corrected for small samples (AICc), difference between one estimated AICc and the lowest AICc the best model (ΔAICc), and model weights (AICcwt).

Model type	**Distribution**	**Response variable**	**Predictors**	**AICc**	**ΔAICc**	**AICcwt**	**R2**
GLMMs	*Poisson glmer*	Richness	~ Elev	154,6	0	0.86	0.78
			~ Elev + slope	158.7	1.12	0.43	0.54
GLM	*Negative binomial*	Abundance	~ Elev + habitat	491.32	0	0.56	0.69
LMMs	*Gaussian lme*	Species composition	~ Elev	446.32	0	0.80	0.82
			~ Elev + slope	453.6	1.63	0.3	0.72
			~ Elev+ convex	455.23	2.37	0.15	0.38
			~ Elev+ pH	455.62	3.59	0.14	0.36
LMMs	*Gaussian lme*	Species composition	Southeast models	AICc	ΔAICc	AICcwt	r2
			~ Elev	196,5	0	0.56	0.82
			~ Elev + slope	197.4	0.53	0.42	0.63
			Northeast models				
			~ Elev	226.7	0	0.84	0.73
			~ Elev + slope	229.9	3.34	0.15	0.46

5. DISCUSSION

Our results showed that topography is an important driver for determining species diversity, stand structure and aboveground biomass at the local scale. We found that topographic variables such as elevation, slope and convexity are causing significant changes in the environmental heterogeneity of a Brazilian Atlantic forest, and consequently influencing species richness, composition and stand structure. To best of our knowledge, this is the first study on the relationship between diversity and ecosystem functioning in an Atlantic forest mosaic by evaluating the effects of multiple stand structural and taxonomic attributes along the topographic gradients. We, therefore, discuss herein how our results could contribute to improving biodiversity conservation in highly fragmented forest landscapes.

5.1. Topographic heterogeneity promotes habitat formation on a local scale

The MRT analysis showed that the Southeast and Northeast areas are topographically classified into five and seven habitats, respectively. In the former, two topographic variables, namely elevation and slope, are responsible for habitat structuring, while in the latter three topographic variables, including elevation, slope and convexity, structured the habitats. Recent studies have used MRT analyses for habitat classification (i.e., Guo et al., 2016; Punchi-Manage et al., 2013; Wang et al., 2016). We found that topography is a major driver of habitat formation in both areas, determining changes in species richness and composition. Our results corroborate the hypothesis that topographic variables, especially elevation and slope, determine habitats formation and strongly correlate with tree species richness and composition. Furthermore, the topography is considered as a proxy that controls spatial variation of nutrient and water contents, thereby affecting plant distribution along topographic gradients (John et al., 2007; Moeslund et al., 2013).

5.2. Effects of topography on species diversity and stand structure

Our results indicated that diversity correlates significantly with topography, especially with elevation and slope, in both study areas, indicating that floristic composition changed along topographic gradients. This shows that environmental filtering is a fundamental process for shaping community assembly in tropical forests (e.g., Liu, et al., 2014), even at a local scale. A significant difference in species richness was observed between areas, with the higher topographic heterogeneity in the Northeast area determining an increased diversity therein. Although the Southeast area had a number of stems up to 20% higher than the Northeast area, the former had lower species richness. This is consistent with the niche complementarity hypothesis, i.e., the occurrence of a positive diversity effect at the more heterogeneous area due to an increased resource use via niche differentiation or partitioning (Tilman, 1999; Poorter et al., 2017) caused by the higher topographic heterogeneity. However, at the habitat scale, we found that taxonomic attributes differed among habitats in the Southeast area only, which is the less heterogeneous one. Such variation among habitats is probably due to the heterogeneous distribution of resources such as water and nutrients (e.g., Katabuchi, et al., 2012). We expected these attributes to be strongly correlated with topography in both areas, yet tree species diversity can be positively, negatively or unimodally linked to environmental conditions (Pausas and Austin, 2001). We presume that the differences in diversity observed among habitat types in the Southeast area may be due to the great difference in elevation between the extremes of the topographic gradient, which is yet accompanied by no variation in convexity, thereby possibly determining a consequent marked gradient in the distribution of resources (e.g., water and nutrients).

Stand structural attributes did not differ significantly between areas, despite the differences in topographic heterogeneity. However, at the habitat scale, the stand structural attributes including maximum tree height and basal area as well as aboveground biomass differed among habitats only in the Southeast area. In our analyses, maximum tree height decreased along habitats, from valleys to plateaus. It is well-known that valley areas have a higher availability of soil water and nutrients as compared to plateau areas (Moeslund et al., 2013; Liu et al., 2014). The increased tree height observed in valleys is a typical feature of trees growing at conditions of high resource availability, whereas the decreased height of trees from plateau habitats is, in contrast, characteristic of plants growing at low resource availability conditions (Poorter, 2009; Reich, 2014). These results are consistent with the findings of a previous study that species distribution along the topographic gradients can be influenced by habitat filtering, which selects features such as tree height and basal area, being related to resource use or to the colonization strategy adopted (e.g., Liu et al, 2014).

In our study, the difference in tree height observed among habitats from the Southeast area correlated with differences in basal area, whereby overall the habitats with lower tree heights showed higher basal areas whereas the habitat with highest values of tree height, i.e. the low valley, showed the lowest basal areas. Our data support the results of a previous study which reported that the conditions at high-elevation habitats are apparently well suited for slow-growing canopy tree species and that these habitats show higher tree densities and basal areas per unit area, compared to low-elevation habitats (Punchi-Manage et al., 2013). Furthermore, there is a strong correlation between these attributes and the abiotic environment (Cornwell and Arkerly, 2010), as a trade-off to better withstand conditions of strong winds, nutrient-poor soils or low soil water availability (Poorter, 2009). We also found a significant decrease in aboveground biomass among subplots in the Southeast area, from valleys to plateaus, probably due to the difference in tree height and basal area among habitats and to the decrease in nutrient availability along the elevation gradient. Similar results have also been reported in other tropical forests (e.g., Leuschner et al. 2007).

Thus, local topography seems to control the distribution of taxonomic and structural attributes, with plain, smooth habitats harboring larger trees with higher biomass and lower basal area than steeper areas. This fact may be correlated with the existence of a marked fine-scale edaphic gradient since we detected significant differences in soil parameters among habitats from the Southeast area (Table S2).

5.3. Diversity but not aboveground biomass increases with increasing topographic heterogeneity

The Northeast area, which had a higher number of habitats, had also a higher number of species than the Southeast area. However, we found a non-significant positive relationship between species richness and aboveground biomass. Previous studies on forests have reported positive relationships between species richness and biomass (Paquette and Messier, 2011; Zhang et al. 2012). Nevertheless, our results show an inverse pattern, presumably due to the scale effect on the relationship between species richness and biomass. Our results at larger spatial scale (1 ha) are consistent with the findings of previous studies that the relationship between species richness and aboveground biomass is either weak or negative, while at small spatial scales (0.04 and 0.1 ha) species richness is strongly positively related with aboveground biomass (Chisholm et al. 2013; Poorter et al. 2015).

The positive relationship between richness and biomass reported in the aforementioned studies is consistent with the sampling, niche complementarity and facilitation effects (e.g., Tilman, 1999). On the other hand, the negative relationship between species richness and aboveground biomass indicates that different abiotic and biotic effects may operate at larger spatial scales (Poorter et al. 2015). The effect of environmental variables such as edaphic and topographic factors could explain such weak relationship between species richness and aboveground biomass, but we found a nonsignificant relationship between species richness and soil fertility. This suggests that these species sorting at fine-scale heterogeneity creates opportunities for plant establishment due to niche differences, which translates into increased plant diversity at the plot scale (e.g., Williams and Houseman, 2014; Muledi et al. 2017). For instance, in the Northeast area, there are a lower number of stems and a higher number of species, probably due to the higher topographic heterogeneity therein, which increases the species coexistence. In the Southeast area, on the other hand, the inverse situation is observed, with the presence of a higher number of stems and lower number of species, which could analogously be caused by the lower topographic heterogeneity of the area.

In this study, the weak relationship between species richness and aboveground biomass may be due to the species redundancy in the Northeast area. A recent study has found a weak relationship between species diversity and aboveground biomass at larger spatial scales due to species redundancy (Poorter et al. 2015). Furthermore, other studies on tropical forests have reported that functionally-dissimilar species may be playing equivalent roles in the ecosystem processes, e.g., biomass production (Lohbeck et al. 2016; Poorter et al. 2017). Presumably, the higher species richness in the Northeast area compensates for the aboveground biomass produced by the higher number of stems in the Southeast area. This indicated the observed equivalent stocks of aboveground biomass between the two areas, despite the fact that the Northeast area showed a 48% higher number of species and 20% lower number of stems as compared to the Southeast area.

5.4. Implications for conservation and forest management

This study shows an approximation regarding the effects of topographic drivers on the relationship between species diversity and ecosystem functioning in an Atlantic forest. Such effects were evaluated through taxonomic and stand structural attributes at the fragment scale as well as at the habitat scale within fragments. This approach has major importance for the global-scale analysis of the impact of environmental drivers on tropical forests. We also consider this approach to be of high relevance at a local scale in fragmented landscapes of the Atlantic forest, considering that the management and conservation strategies are usually aiming to recover ecosystem services (e.g., biomass and carbon stock) at a local scale. Therefore, comprehending how topographic heterogeneity determines the diversity-biomass relationship at a fragment scale and along topographic gradients may allow for establishing critical areas (with higher biodiversity conservation value and higher carbon stock) for the management and conservation of forests, from a REDD+ perspective. Nevertheless, we propose that future studies focus on a more specific relationship between species and habitats, which would allow for identifying the relative contribution of species to ecosystem functioning along topographic gradients. For instance, the loss of these hyperdominant species at a local scale (e.g., through logging activity) may prove to be an important issue in the near future due to not only to the ecosystem functions they support but also to their carbon storage capacity.

6. CONCLUSIONS

This study reveals that higher topographic heterogeneity promotes higher species richness but does not implicate significant changes in biomass storage. However, our habitat-scale analyses indicate that in the less heterogeneous area there is a more uniform distribution pattern of elevation along with no variation in convexity across the gradients, which induces changes in stand structural and taxonomic attributes. On the other hand, the more heterogeneous area shows no difference among habitats along the topographic gradients. We provide here the first indications of the relative importance of topographic drivers to species composition, stand structure and aboveground biomass along topographic gradients in a tropical Atlantic forest. Topographic drivers strongly correlated with the distribution of floristic composition in both study areas, but only in the Southeast area, which is the less heterogeneous one, did it strongly correlate with the distribution of stand structural attributes and aboveground biomass. In the Southeast area, there is higher nutrient availability in valley areas, and consequently, these habitats have larger trees and higher aboveground biomass. Species richness and composition at an area scale was best explained by the elevation of the study area, with no significant change being mainly due to the effect of soil chemical properties. This study represents a first approximation in the analysis of the relationship between diversity and ecosystem functions along topographic gradients, and might thus help in the establishment of basic criteria for the management and conservation of the Atlantic forest.

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8. APPENDICES

Figure S1. Results of multivariate regression tree (MRT) in each area.

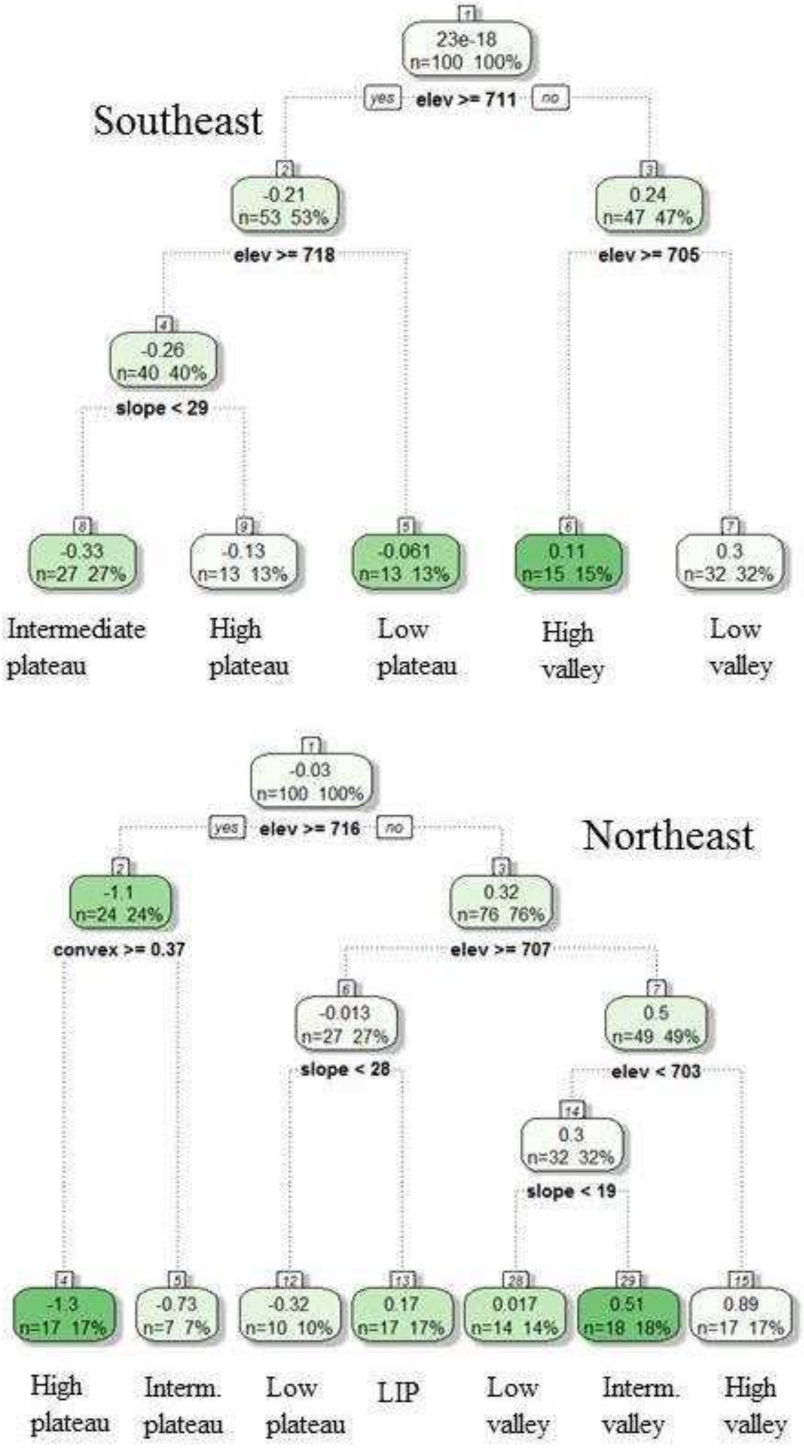


Table S1. Habitats of each area based the results of MRT

Habitat -Northeast	**Topographical variables**
High plateau	Elev≥716. convex≥0.37
Intermediate plateau	Elev≥716. convex<0.37
Low plateau	Elev≥707. slope<28
Transition plateau/valley	Elev≥707. slope≥28
High valley	Elev≥703
Intermediate valley	Elev<703. slope≥19
Low valley	Elev<703. slope<19
Habitat-Southeast	
High plateau	Elev≥718. slope>29
Intermediate plateau	Elev≥718. slope<29
Low plateau	Elev<718
High valley	Elev≥705
Low valley	Elev<705

Table S2. Tree diversity pattern, tree structural attributes, topographic and soil variables (mean ± SD) of the habitats by area. 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 (LIP).

Varibles	**Northeast**							**Southeast**				
	Hp	**Ip**	**Lp**	**LIP**	**Hv**	**Iv**	**Lv**	**Hp**	**Ip**	**Lp**	**Hv**	**Lv**
Diversity												
S	12.1 ± 2.4	11.7 ± 2.5	11.0 ± 3.5	10.9 ± 3.50	12.0 ± 3.02	11.5 ± 2.80	9.2 ± 1.69	8.42 ± 3.3^{bc}	8.96 ± 2.8^{b}	6.18 ± 2.40^{d}	9.12 ± 2.9^{ab}	7.37 ± 1.9^{cd}
Si	2.27 ± 0.2	2.21 ± 0.3	2.21 ± 0.4	2.21 ± 0.32	2.33 ± 0.57	2.2 ± 0.32	1.94 ± 0.28	1.49 ± 0.6^{ab}	1.74 ± 0.4^{a}	1.11 ± 0.62^{b}	1.71 ± 0.6^{a}	1.53 ± 0.3^{ab}
Pi	0.92 ± 0.1	0.91 ± 0.1	0.93 ± 0.03	0.93 ± 0.02	0.93 ± 0.03	0.91 ± 0.05	0.91 ± 0.09	0.78 ± 0.2	0.81 ± 0.1	0.80 ± 0.23	0.77 ± 0.17	0.78 ± 0.1
Structure												
dbh	12.0 ± 3.3	12.0 ± 2.2	10.6 ± 2.62	10.1 ± 2.43	10.5 ± 3.06	10.3 ± 2.22	11.4 ± 1.90	10.4 ± 3.2	10.5 ± 3.2	9.8 ± 3.4	10.3 ± 2.1	9.38 ± 2.5
wd	0.65 ± 0.1	0.65 ± 0.02	0.67 ± 0.02	0.65 ± 0.03	0.66 ± 0.04	0.67 ± 0.35	0.67 ± 0.03	0.66 ± 0.02	0.66 ± 0.03	0.66 ± 0.03	0.64 ± 0.05	0.67 ± 0.1
Hmax	14.9 ± 1.7	16.37 ± 3.9	16.9 ± 2.8	16.4 ± 4.34	16.0 ± 3.96	16.3 ± 3.38	17.9 ± 4.08	14.7 ± 1.5^{b}	15.7 ± 2.6^{b}	14.6 ± 2.1^{b}	16.9 ± 2.5^{ab}	20.2 ± 5.7^{a}
BA	21.74 ± 7.3	21.94 ± 8.3	28.9 ± 16.9	33.2 ± 23.40	32.8 ± 21.35	34.5 ± 18.34	30.1 ± 21.90	33.1 ± 9.7^{b}	42.2 ± 15.2^{a}	31.3 ± 14.4^{bc}	43.7 ± 19.8^{a}	22.8 ± 9.3^{d}
AGB	119.2 ± 60.6	125.9 ± 70.7	214.1 ± 158.0	234.1 ± 220.6	244.2 ± 209.43	242.1 ± 203.6	232.3 ± 225.9	217.4 ± 117.2^{a}	205.6 ± 165.1^{a}	198.1 ± 164.4^{a}	262.3 ± 225.0^{ab}	228.3 ± 78.7^{bc}
Topography												
Elev.	722.6 ± 4.4^{a}	721.3 ± 3.4^{a}	711.5 ± 2.1^{b}	711.5 ± 2.9^{b}	705.2 ± 1.2^{c}	700.0 ± 1.7^{d}	700.3 ± 2.3^{d}	725.6 ± 4.4^{a}	726.2 ± 5.8^{a}	716.0 ± 3.3^{b}	708.6 ± 2.3^{c}	698.0 ± 3.7^{d}
Slope	21.8 ± 6.2^{bc}	28.7 ± 6.8^{ab}	23.7 ± 2.9^{b}	32.8 ± 4.7^{a}	26.1 ± 9.1^{b}	24.4 ± 5.0^{b}	17.5 ± 1.4^{c}	32.9 ± 2.6^{a}	21.8 ± 4.8^{c}	26.4 ± 6.2^{b}	29.4 ± 3.1^{a}	25.8 ± 6.1^{b}
Convex.	1.1 ± 0.5^{a}	0.1 ± 0.3^{b}	0.9 ± 0.8^{a}	0.3 ± 0.9^{b}	0.4 ± 3.2^{b}	-1.1 ± 0.9^{c}	-0.9 ± 1.1^{c}	2.8 ± 2.9	-0.3 ± 4.1	0.8 ± 2.7	0.04 ± 1.5	-0.6 ± 1.7
Soil												
pH (H_2O)	5.8 ± 0.8	5.5 ± 0.9	5.6 ± 0.5	5.2 ± 0.7	5.4 ± 0.7	5.2 ± 0.4	5.2 ± 0.4	4.6 ± 0.1^{b}	4.5 ± 0.1^{b}	4.6 ± 0.1^{b}	4.8 ± 0.1^{ab}	5.2 ± 0.5^{a}
H+Al	4.9 ± 2.5	5.3 ± 2.9	5.1 ± 1.4	5.2 ± 1.9	5.8 ± 2.1	5.6 ± 1.2	5.9 ± 1.0	10.9 ± 0.9^{ab}	12.0 ± 1.1^{a}	10.6 ± 1.2^{ab}	10.4 ± 1.2^{bc}	8.4 ± 2.4^{c}
SB	6.0 ± 3.2	4.8 ± 3.6	5.4 ± 1.8	3.9 ± 2.5	4.4 ± 2.6	3.7 ± 1.5	3.5 ± 1.5	1.1 ± 0.2^{c}	1.1 ± 0.2^{c}	1.2 ± 0.3^{c}	1.7 ± 0.4^{b}	4.3 ± 4.0^{a}
(t)	6.3 ± 2.7	5.3 ± 3.1	5.6 ± 1.6	4.4 ± 2.1	4.8 ± 2.2	4.1 ± 1.1	3.9 ± 1.1	2.8 ± 0.2^{b}	3.1 ± 0.4^{b}	2.8 ± 0.2^{b}	3.2 ± 0.4^{b}	5.1 ± 3.6^{a}
V	55.5 ± 28.7	44.9 ± 32.6	50.5 ± 16.6	36.9 ± 22.0	41.3 ± 23.3	35.6 ± 13.8	32.8 ± 13.7	9.3 ± 2.1^{d}	8.7 ± 1.7^{d}	10.6 ± 3.1^{cd}	12.4 ± 1.7^{b}	30.8 ± 22.8^{a}
mo	5.7 ± 0.7	5.4 ± 0.8	5.6 ± 0.6	5.3 ± 0.7	5.3 ± 0.6	5.2 ± 0.1	5.2 ± 0.2	6.3 ± 0.9^{b}	7.4 ± 1.2^{a}	6.2 ± 0.8^{b}	6.3 ± 0.5^{b}	5.8 ± 0.4^{bc}

Different letters indicate significant differences at posteriori analyses ($P < 0.05$) between habitats.

Figure S2. Non metric multidimensional scaling based on species composition according to structural attributes (circles sizes) and habitats (point colors) by study area, Southeast (A,B,C) and Northeast (D,E,F). 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 (LIP).

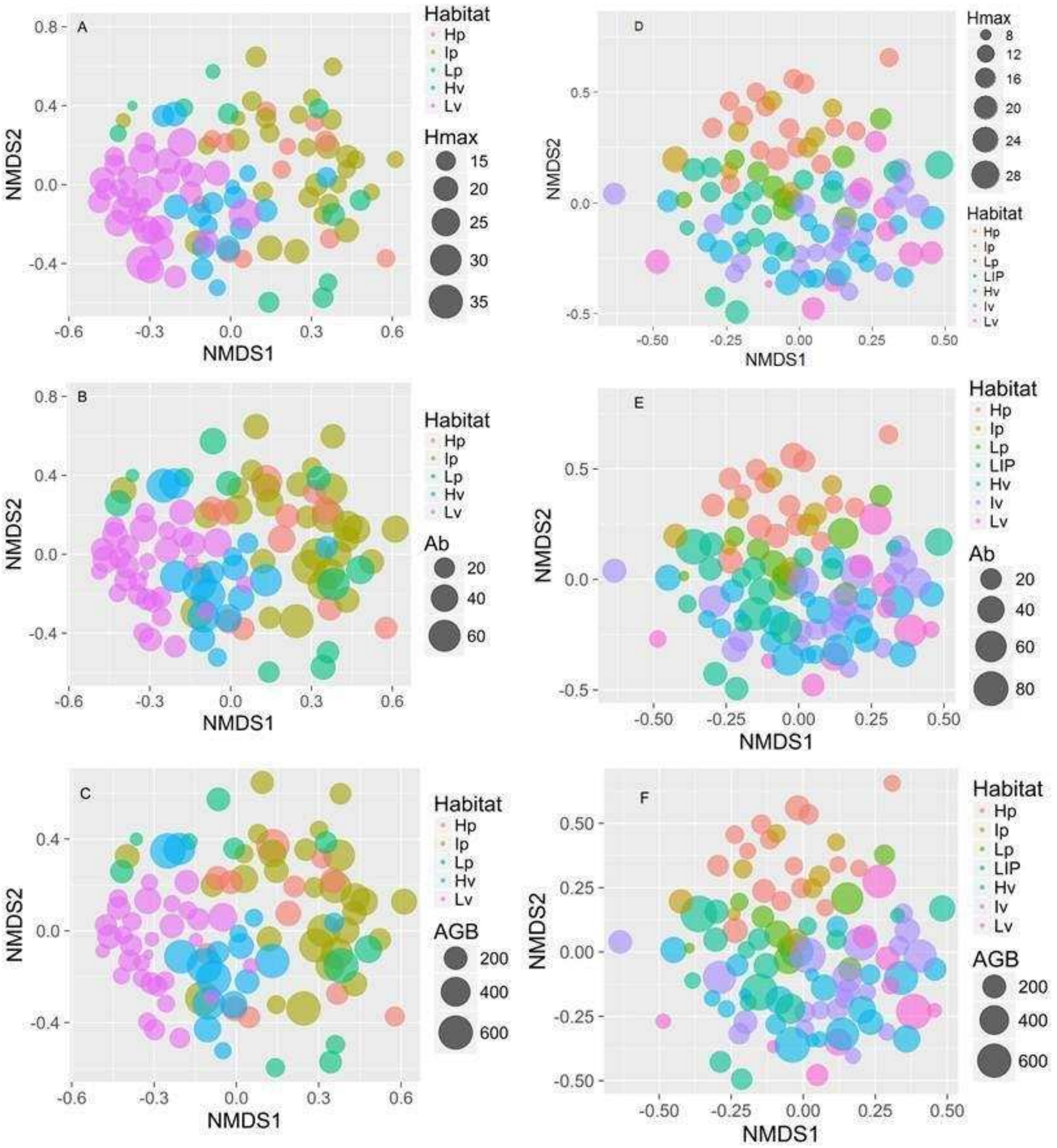
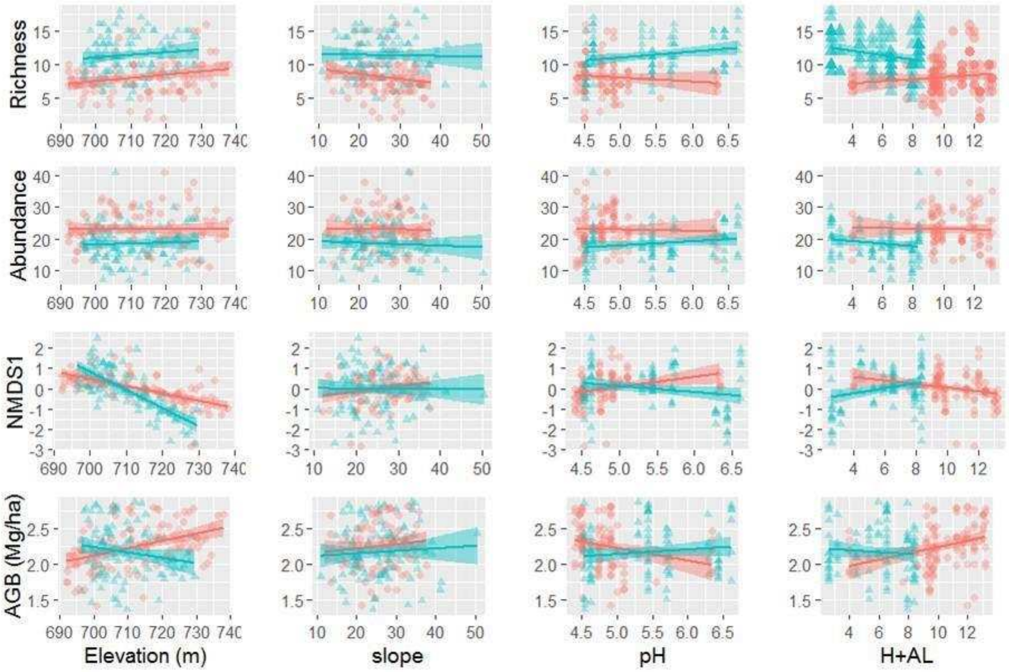


Figure S3. The relationships between tree species richness, abundance, species composition (NMDS1), aboveground biomass (AGB) and topographic –soil variables (elevation, slope, pH, H+AL). Solid lines represent fit (predicted) values of the LMM, and the shaded polygons the 95 % associated with the modeled predictions.



In the multi-model comparative applied between areas and habitats by area, we found that models including single topographic variable consistently explained more variation in richness, abundance and species composition than those with multivariate effects of topographic and soils drivers. In this sense, according to our best model (ΔAICc = 0; Table 2), both response variable was best explained by elevation in the study area. Richness was significantly affected by elevation between areas (GLMM: t = 2.29, P < 0.004, Fig. S3), but no significant change with main effects of soils parameters. Richness was significantly greater in Northeast than Southeast area (GLMM: t = 3.47, P < 0.002, Fig. S3). For Abundance, our best model (ΔAICc = 0) was composed of elevation and habitats (GLM, z = 2.17, P < 0.01). The linear mixed-effects models between areas showed that species composition is explained by both topographic and soils drivers through seven potential models (ΔAICc < 7). The linear mixed-effects models by area revealed significant shifts of species composition across the topographic gradient (Table 2). Species composition of both sites was significantly associated with elevation and slope considering our best models with values ΔAICc < 2.

CAPÍTULO 2: Local-scale topography determines high tree diversity and hyperdominance in secondary Atlantic forests: implications for ecosystem functioning

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1. ABSTRACT

Topography is an important driver of diversity patterns and ecosystem functioning in tropical forests. However, few studies have analyzed the topographic heterogeneity in the relative importance of species to ecosystem functioning, mainly of those with high contribution (i.e., hyperdominant species). We aimed to evaluate the effect of topographic heterogeneity on the relationship between species richness and hyperdominant species distribution in an Atlantic 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) $\geq$ 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 – AGB). The AGB of individual stems was calculated in all plots. We performed a multivariate regression tree to estimate the topographic 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. 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 stem hyperdominants, while in the Northeast area 10 species (7.94%) accounted for 50% of stem hyperdominants. Our results showed that high topographic heterogeneity induces high species richness and that the number of stem and biomass hyperdominant species increases 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.

Keywords: aboveground biomass; ecosystem functioning; species abundance distribution; secondary forests; topographic heterogeneity

2. INTRODUCTION

Predicting how multiple drivers shape plant community assembly along environmental gradients and across spatio-temporal scales is one of the most important questions in ecology and conservation biology (Götzenberger et al., 2012). Community assembly may be driven by different processes at different spatial scales, selecting species from a regional species pool into a local habitat (i.e., environmental filtering and biotic filtering; Kraft and Ackerly, 2010). Biotic assembly rules are expected to be apparent mainly on relatively small spatial scales, by means of analyzing abundance-mediated species interactions (Bycroft et al., 1993). Conversely, environmental filtering can be the main driver of community assembly (e.g., climate, soil, topography) at larger spatial scales (Götzenberger et al. 2012; Wang et al., 2016). On the continental scale, other drivers are responsible for plant community assembly, such as the biogeographic processes that limit dispersal and immigration or promote species extinction (e.g., Cavender-Bares et al., 2009). However, the relative importance of environmental drivers to the spatial and temporal changes in community assembly and their effects on the ecosystem functioning of tropical forests remain poorly understood.

Global-scale topography is an important driver that determines the diversity patterns and functioning of tropical forests (Baldeck et al., 2012; 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 diversity 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 (Lundholm, 2009; Liu et al., 2014). Environmental heterogeneity may affect abiotic resources such as light and soil nutrients, which in turn strongly affect forest species composition and diversity (Clark et al.1993; Balderrama and Chazdon, 2005). Furthermore, topographic variability causes small-scale heterogeneity of nutrient availability, meaning that species can then differentially explore patchily distributed resources, which can lead to higher species diversity and spatial turnover (Questad and Foster, 2008).

Moreover, tropical forest landscapes have been rapidly converted into human-modified landscapes by intense land use (Laurance et al., 2014). Intensification of land use has been recognized as an important driver of community assembly and loss of biodiversity in tropical forests (Arroyo-Rodríguez et al. 2015; Poorter et al., 2017; de

Ávila et al., 2018), although secondary forest regrowth following disturbance may also contribute to biodiversity recovery (Gibson et al., 2011). Thus, in tree communities from human-modified tropical landscapes there is a well-known pattern characterized by hyperproliferation of pioneer species along with a decrease in number of shade-tolerant species from old-growth forests, consisting in the dynamic substitution of a wide range of native "losers" by a few native "winners" (Tabarelli et al., 2008; Tabarelli et al., 2012). These changes in community structure can also modify the relative importance of species in terms of their contribution to ecosystem processes (e.g., biomass and carbon stock, Poorter et al., 2017). On the other hand, the importance of hyperdominant species has been recently reported to Amazonia, where the dominance of forest functions is even more concentrated by a few species, with only as much as 1% of Amazonian tree species accounting for 50% of all carbon storage and productivity that takes place on the regional scale (Fauset et al., 2015). However, there is still limited research on the influence of different environmental drivers (e.g., climate, soil, and topography) on tree community assembly, with only few studies having analyzed the relative contribution of species to ecosystem functioning.

The Brazilian Atlantic forest is considered one of the most important global centers of diversity and endemism of vascular plants (Myers et al., 2000; Murray-Smith et al., 2009) as well as one of the most threatened tropical forest regions in the world (Myers et al., 2000; Scarano and Ceotto, 2015). Anthropogenic drivers in fragmented landscapes undergoing human modification in the Atlantic forest induce loss of not only biodiversity but also ecosystem functions such as biomass production and carbon storage (Magnago et al., 2015; Pütz et al., 2014). However, little is known on the heterogeneity-diversity-hyperdominance relationship in the Atlantic forest, and thus comprehending these processes is of major importance to better comprehend the structure of tree communities and the functioning of ecosystems, as well as to establish effective management and conservation practices.

We evaluated the effect of topographic heterogeneity on the relationship between species richness and the distribution of hyperdominant species in an Atlantic forest fragment, aiming to identify the relative contribution of stem and biomass hyperdominants in areas with contrasting topographic conditions. For that, 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. We wished to address the following questions: i) Does higher topographic heterogeneity determine the occurrence of higher species richness? ii) Does higher tree species richness determine the occurrence of a higher number of stem and biomass hyperdominant species? iii) Are stem hyperdominant species also biomass hyperdominant? These questions are essential to understand the functioning of tropical forests as well as to develop monitoring and conservation strategies.

3. MATERIAL AND METHODS

3.1. 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 area 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 (Paula et al., 2002). 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 (Golfari, 1975). The mean annual relative humidity is ca. 80%, mean annual air temperature is 19 oC and mean annual precipitation is 1340 mm (Castro et al., 1973). The study area is located between 620 and 820 m elevation and the relief varies from strongly undulating to mountainous (Valverde, 1958). 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 (Resende et al., 1988; EMBRAPA, 1997).

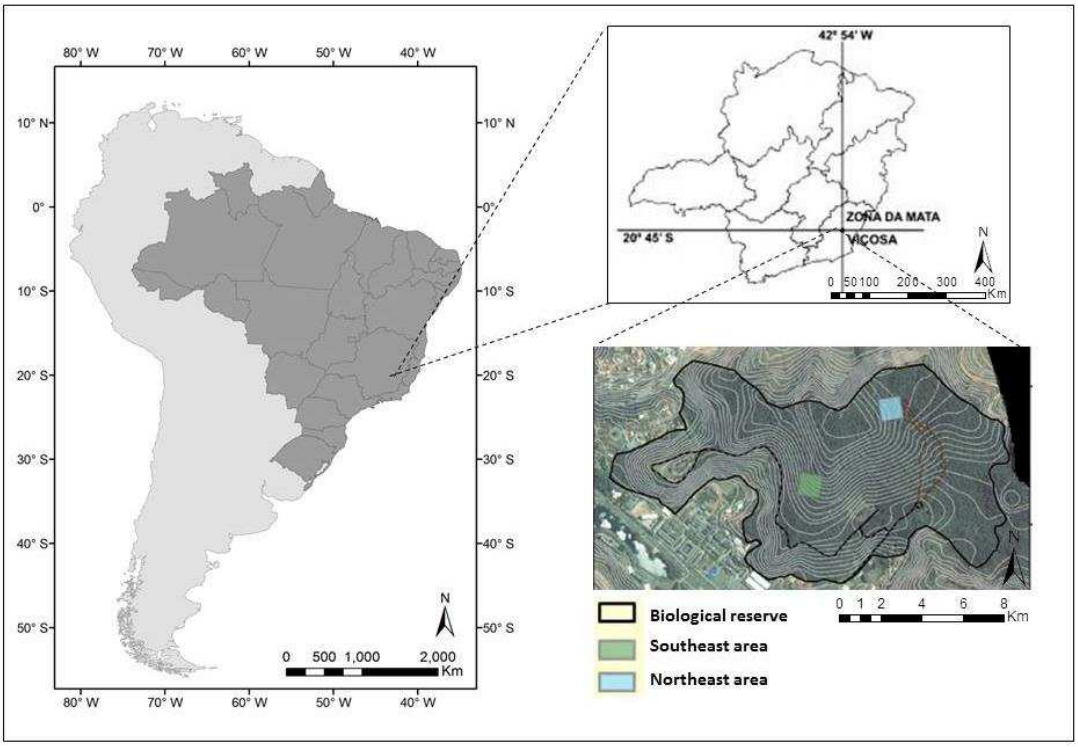

Figure 1: Map showing the location of the study area. Adapted from Ferreira-Júnior, et al., (2007) and Del Peloso, (2012).

3.2. Forest inventory and data collection

We selected two sampling areas with contrasting topographic conditions: a Southeast area (UTM 23K 722758/7703626) and a Northeast area one (UTM 23K 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) ≥ 3.2 cm were identified to the species level and tagged for measurement. All individuals were identified using specialized 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. Species nomenclature and the respective abbreviations of their authors were checked against the Tropicos.org list databases (MOBOT, 2015).

3.3. 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, 2011). 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, 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 et al., 1988). This data was then transferred to a computer and analyzed with software AutoCAD® for further procedures (Autodesk Inc., San Rafael, CA, USA).

3.4. 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 (Zanne et al., 2009; 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.

3.5. Data analyses

To address the first question, “does a higher topographic heterogeneity determine a higher species richness?”, we performed a multivariate regression tree

(MRT) analysis (De’ath, 2002; Larsen & Speckman, 2004) to classify habitat types according to topographic variables and species composition (Guo et al., 2016; Wang et al., 2016), and rarefaction and extrapolation curves of species richness were constructed for both sampled areas (Chao et al., 2014). MRT is a method of constrained clustering that identifies clusters (group of plots) that are most similar to 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 & Speckman, 2004). MRT analysis was performed using the “rpart” package (Therneau et al., 2017). The two study areas showed marked differences in the spatial distribution of topographic variables, mainly elevation and slope (Fig. S1). 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. S2, MRT).

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), being higher than thrice the sample size (Colwell et al., 2012). These estimates were obtained using the “iNEXT” package (Hsieh et al., 2016). 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., 2013). 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., 2013), and to test for significant clustering of areas across the AGB gradient (Solar et al., 2016).

To address the second question, “does a 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 as follows:

Ab = total number of individuals per species / total number of plots that contain that species.

Ar = Ab of the species × 100 / Total abundance of that species.

The most important species were those with the highest numbers of individuals per unit area; therefore, the proportional analysis of IVI 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., 2015).

4. RESULTS

4.1. Species richness and composition

Species richness differed significantly between areas (Fig. 2). 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. 3). The NMDS ordination distribution separated the two study areas along the second axis.

4.2. Phytosociology and stem hyperdominants species

The number of stem hyperdominants varied significantly between areas. In the Southeast area, only two species out of the 85 recorded (i.e., 2.38%) accounted for 50% of the number of stems hyperdominants, while in the Northeast area 10 species (s.d. 7.94%) accounted for 50% of stems hyperdominants (Fig. 4). The Top 20 highest stem dominant species are given in Table 1. Data on all species is found in appendix S1.

4.3. 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. S3 boxplot). In the Southeast area, only two species (s.d. 2.38%) were classified as biomass hyperdominants, i.e., accounting for more than 50% of the biomass (Fig. 4). In the Northeast area, on the other hand, five species (i.e., 3.97% of all identified species in the data set) accumulated 50% of the AGB (Fig. 4). The 20 most dominant species by AGB are given in Table 2. Data on all species is found in appendix S2.

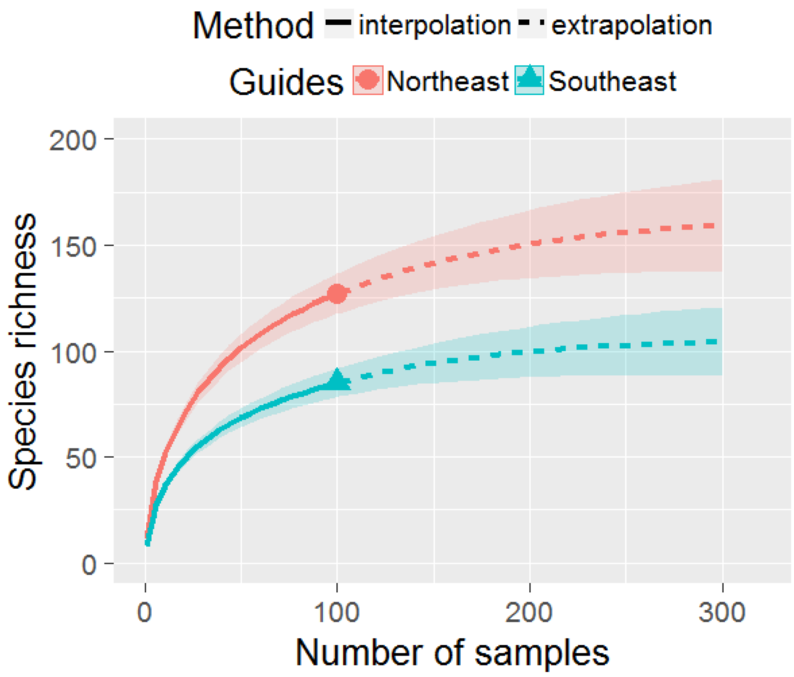

Figure 2. Sample-based rarefaction (solid line) and extrapolation (dashed lines) curves of tree richness of the two study areas.

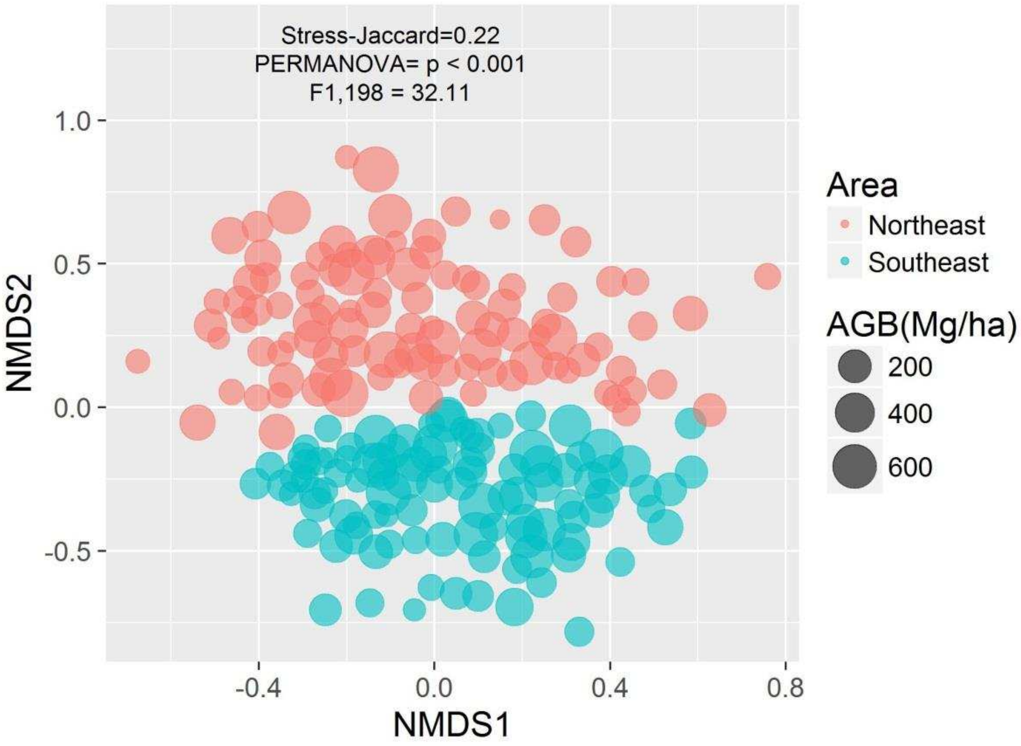

Figure 3. Non-metric multidimensional scaling based on species composition according to aboveground biomass gradient (circle sizes) and study areas (point colors).

Table 1. The 20 most abundant tree species in study site.

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

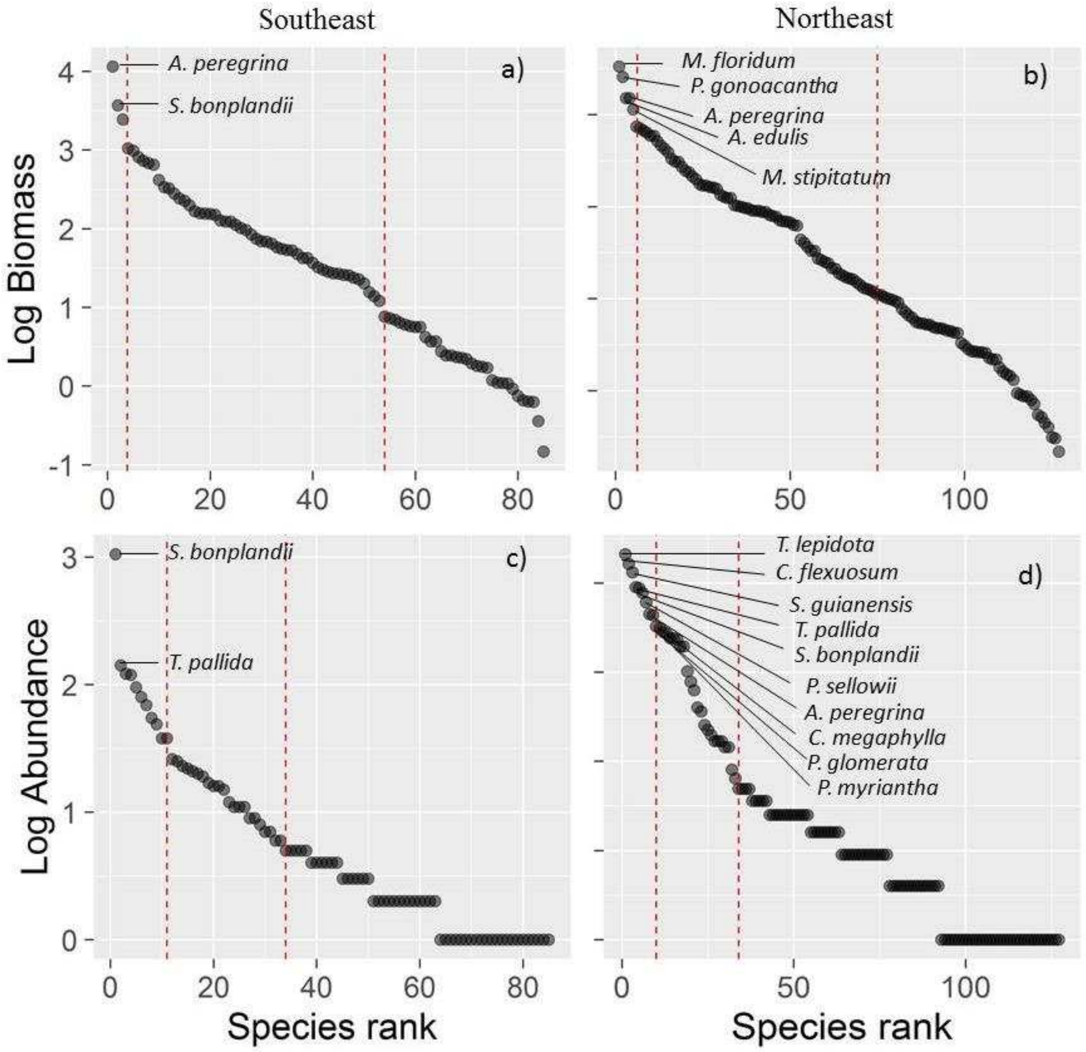

Figure 4. Species abundance distribution in the two study areas separated by stem and biomass hyperdominant species.

Table 2. Top 20 most dominat species in aboveground biomass in Biological Reserve.

Species / Southeast	**AGB (Mg ha^{-1})**	**Cumulative AGB (Mg ha^{-1})**	**% AGB/ species**	**% cumulative AGB**
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})**	**Cumulative AGB (Mg ha^{-1})**	**% AGB/ species**	**% cumulative AGB**
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

5. DISCUSSION

5.1. Topography heterogeneity and species richness

Our results revealed 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 pattern 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 (Douda, et al., 2012). Higher habitat heterogeneity is associated with heterogeneous resource distribution, which in turn results in higher variation in woody plant structural diversity (Lippok et al., 2014). 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 (Warren et al., 2008). 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/indirect effects of topography (Grubb, 1977).

In our study, the Southeast area not only had a lower number of species but also had one species with high dominance, *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 (Kneitel & Chase, 2004; Leigh et al., 2004). Strong environmental contrasts among microhabitats enable the coexistence of a large number of plant species with different life histories (Loehle, 2000). Conversely, a limited number of species may coexist in a homogeneous environment, as the best competitors overgrow the area and reduce the number of other species (Huston 1979; Tilman & Pacala, 1993). From a practical point of view, we consider fundamental to understand how environmental drivers (e.g., topography) determine richness patterns on a local scale, and how environmental conditions can limit or favor tropical forest management and conservation activities.

5.2. Relationship between species richness and hyperdominance

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 local 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 (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). Reports with this type of analysis are quite scarce for tropical forests, mainly on a local 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., 2016). However, our results shed a first light on how a local-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.

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 (Fig. 4). For instance, *Sorocea bonplandii*, the most dominant species in our dataset, accounted for 46% of the total stem abundance. 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 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 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 (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; Püzt et al., 2014; Fauset et al., 2015; Poorter 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 & 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 replacement dynamics may be responsible for up to a 50% reduction in the AGB of fragmented habitats and tropical forests (Laurance et al., 1997; 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. Therefore, we consider local-scale hyperdominance analyses to be necessary for devising management and conservation actions on that same scale, on which forest fragments may have specific environmental conditions.

5.3. 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 Steeg et al., 2013). Analogously, a recent study conducted in the 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 and 2). Despite that, these species may still contribute to forest biomass stocks (Table S2).

Our results showed that *Myroxylon peruiferum* (with only 2 stems) and *Copaifera langsdorffii* (8 stems) altogether in the Southeast area and *Machaerium floridum* (8 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 S1), they all contributed considerably to biomass production. *Myroxylon peruiferum* and *Copaifera 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 *Myroxylon peruiferum*, *Copaifera langsdorffii* and *Machaerium 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 & Malmqvist, 2004; Kirwan et al., 2007; 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).

5.4. *Implications for forest management and conservation*

Our results present a first approximation on how the ecosystem functioning of fragmented landscapes can be evaluated through stem and biomass hyperdominant species in areas with different topographic heterogeneities. This approach is of major importance for analyzing the impacts of tropical forests on a global scale (Fauset et al., 2015). However, we consider this approach to be of high relevance also to fragmented landscapes of the Atlantic forest. Forest ecosystem services are highly suppressed by fragmented habitats, which themselves are dominated by pioneer species and invade typically mature forests conditions (Pütz et al., 2011; Pütz et al., 2014), impacting biomass production and carbon storage thereat. Nonetheless, Atlantic forest fragments 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 those regions, which itself may be leading to an important reduction of the current carbon stock in the highly diverse Atlantic forest.

On the other hand, we consider important to understand the implications of this approach when analyzing different forest types (e.g., primary and secondary forests). For that reason, we presume that assessing hyperdominance in mature forests, specifically by analyzing species with higher functional contributions (e.g., 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 primary 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 (Poorter et al., 2016). Forests undergoing regeneration should thus become the focus of conservation practices (Gilroy et al., 2014), as they play a key role in increasing biomass resilience, carbon sequestration and storage, and biodiversity restoration on a local scale (Pan et al., 2011; Chazdon et al., 2016; Poorter et al., 2016).

6. CONCLUSIONS

Our results showed that high topographic heterogeneity induces high species richness in the Atlantic Forest. 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, with similar patterns of aboveground biomass being observed among plots. Our results also showed that the number of stem and biomass hyperdominant species increase along with richness on a local 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 revealed that higher tree species richness can influence the number of biomass or stem hyperdominant species. Moreover, in our local-scale study we observed similar patterns between areas, with 35% of the main biomass hyperdominant species in the Southeast area not is 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 topographic heterogeneity can strongly influence biomass and stem hyperdominance and forest ecosystem functioning on a local scale.

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8. APPENDICES

Figura S1: 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 (LIP).

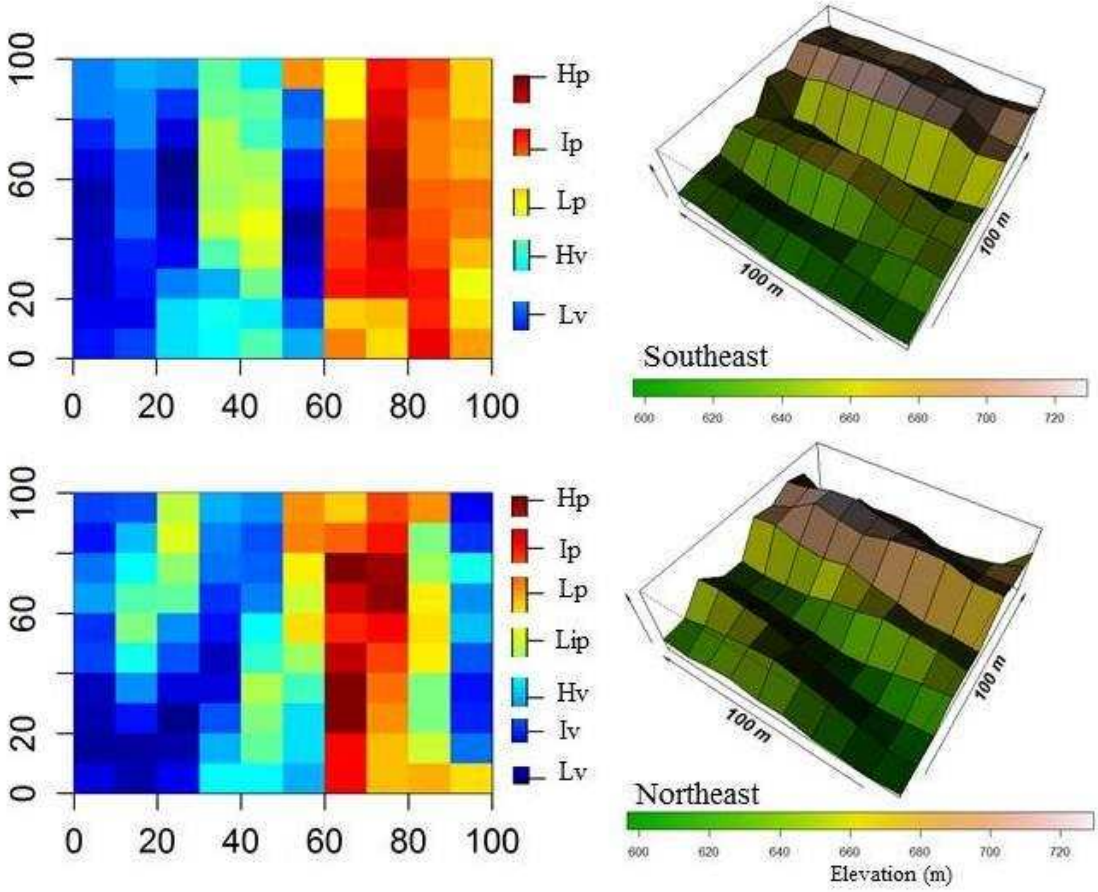


Table S1: Data on all species for stem abundance.

Espécie / Oeste	**Família**	**Ni**	**DenR**	**AbuR**	**FreR**	**IVI**	**IVI (%)**
Sorocea bonplandii (Baill.) W.C. Burger. Lanj. & Wess. Boer	Moraceae	1053	45.88	8.79	12.32	66.99	22.33
Anadenanthera peregrina (L.) Speg.	Fabaceae	53	2.31	1.16	4.68	8.15	2.72
Casearia ulmifolia Cambess.	Salicaceae	95	4.14	1.65	5.91	11.70	3.90
Trichilia pallida Sw.	Meliaceae	142	6.19	2.16	6.77	15.12	5.04
Protium warmingiana March.L.	Burseraceae	122	5.32	2.61	4.80	12.73	4.24
Siparuna guianensis Aubl.	Siparunaceae	119	5.19	2.92	4.19	12.29	4.10
Machaerium nyctitans (Vell.) Benth.	Fabaceae	69	3.01	1.44	4.93	9.37	3.12
Apuleia leiocarpa (Vogel) J.F. Macbr.	Fabaceae	55	2.40	1.31	4.31	8.02	2.67
Plinia glomerata (O.Berg) Amshoff	Myrtaceae	80	3.49	1.71	4.80	10.00	3.33
Rollinia sylvatica (A. St.-Hil.) Martius	Annonaceae	38	1.66	1.13	3.45	6.24	2.08
Coutarea hexandra (Jacq.) K. Schum.	Rubiaceae	38	1.66	1.59	2.46	5.71	1.90
Allophylus edulis (A. St.-Hil.. A. Juss. & Cambess.) Hieron. ex Niederl.	Sapindaceae	22	0.96	1.53	1.48	3.97	1.32
Luehea grandiflora Mart.	Malvaceae	17	0.74	1.01	1.72	3.48	1.16
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Sapotaceae	26	1.13	1.09	2.46	4.68	1.56
Anadenanthera colubrina (Vell.)Brenan	Fabaceae	6	0.26	0.83	0.74	1.84	0.61
Copaifera langsdorffii Desf.	Fabaceae	8	0.35	0.83	0.99	2.17	0.72
Brosimum guianense (Aubl.) Huber	Moraceae	23	1.00	1.28	1.85	4.13	1.38
Ocotea odorifera Rohwer	Lauraceae	16	0.70	1.03	1.60	3.33	1.11
Amaioua guianensis Hemsl.	Rubiaceae	19	0.83	0.99	1.97	3.79	1.26
Piptadenia gonoacantha (Mart.) J.F. Macbr.	Fabaceae	20	0.87	1.19	1.72	3.79	1.26
Ceiba speciosa (A. St.-Hil.) Ravenna	Malvaceae	11	0.48	0.92	1.23	2.63	0.88
Trichilia lepidota Mart.	Meliaceae	20	0.87	1.11	1.85	3.83	1.28
Eugenia leptoclada O. Berg	Myrtaceae	25	1.09	1.90	1.35	4.34	1.45
Casearia decandra Jacq.	Salicaceae	12	0.52	1.00	1.23	2.76	0.92
Myrciaria axillaris O. Berg	Myrtaceae	16	0.70	1.03	1.60	3.33	1.11
Dalbergia nigra (Vell.) Allemão ex Benth.	Fabaceae	11	0.48	0.92	1.23	2.63	0.88
Myroxylon peruiferum L. f.	Fabaceae	2	0.09	0.83	0.25	1.17	0.39
Casearia arborea (Rich.) Urb.	Salicaceae	11	0.48	1.15	0.99	2.61	0.87
Ocotea dispersa (Nees & Mart.) Mez	Lauraceae	15	0.65	1.39	1.11	3.15	1.05
Sparattosperma leucanthum (Vell.) K. Schum.	Bignoniaceae	7	0.31	0.97	0.74	2.02	0.67
Pterocarpus rohrii Vahl	Fabaceae	5	0.22	1.04	0.49	1.75	0.58
Eugenia strictopetala DC.	Myrtaceae	9	0.39	1.07	0.86	2.33	0.78
Cordia sellowiana Cham.	Boraginaceae	3	0.13	0.83	0.37	1.34	0.45
Astronium fraxinifolium Schott	Anacardiaceae	6	0.26	0.83	0.74	1.84	0.61
Clarisia ilicifolia (Spreng.) Lanj. & Rossberg	Moraceae	6	0.26	1.25	0.49	2.01	0.67
Jacaranda micrantha Cham.	Bignoniaceae	7	0.31	0.97	0.74	2.02	0.67
Seguieria americana L.	Phytolaccaceae	5	0.22	1.04	0.49	1.75	0.58
Carpotroche brasiliensis (Raddi) A. Gray	Achariaceae	5	0.22	0.83	0.62	1.67	0.56
Picramnia regnelli Engl.	Picramniaceae	8	0.35	1.67	0.49	2.51	0.84
Endlicheria paniculata (Spreng.) J.F. Macbr.	Lauraceae	2	0.09	0.83	0.25	1.17	0.39
Licania spicata Hook. f.	Chrysobalanaceae	4	0.17	0.83	0.49	1.50	0.50

Trichilia elegans A. Juss.	Meliaceae	4	0.17	0.83	0.49	1.50	0.50
Eriotheca candolleana (K. Schum.) A. Robyns	Malvaceae	5	0.22	1.04	0.49	1.75	0.58
Prunus sellowii Koehne	Rosaceae	4	0.17	0.83	0.49	1.50	0.50
Aspidosperma olivaceum Müll. Arg.	Apocynaceae	4	0.17	1.11	0.37	1.66	0.55
Zanthoxylum rhoifolium Lam.	Rutaceae	3	0.13	0.83	0.37	1.34	0.45
Cariniana legalis (Mart.) Kuntze	Lecythidaceae	3	0.13	1.25	0.25	1.63	0.54
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Sapotaceae	2	0.09	0.83	0.25	1.17	0.39
Cordia silvestres Fresen.	Boraginaceae	3	0.13	0.83	0.37	1.34	0.45
Guarea kunthiana A. Juss.	Meliaceae	4	0.17	1.11	0.37	1.66	0.55
Simira sampaioana (Standl.) Steyerm.	Rubiaceae	3	0.13	0.83	0.37	1.34	0.45
Garcinia gardneriana (Planch. & Triana) Zappi	Clusiaceae	3	0.13	0.83	0.37	1.34	0.45
Peltophorum dubium (Spreng.) Taub.	Fabaceae	2	0.09	0.83	0.25	1.17	0.39
Zeyheria tuberculosa (Vell.) Bureau	Bignoniaceae	2	0.09	0.83	0.25	1.17	0.39
Vitex megapotamica (Spreng.) Moldenke	Lamiaceae	2	0.09	0.83	0.25	1.17	0.39
Qualea jundiahy Warm.	Vochysiaceae	2	0.09	0.83	0.25	1.17	0.39
Zollernia ilicifolia (Brongn.) Vogel	Fabaceae	2	0.09	0.83	0.25	1.17	0.39
Guettarda scabra (L.) Lam.	Rubiaceae	2	0.09	0.83	0.25	1.17	0.39
Cedrela fissilis Vell.	Meliaceae	5	0.22	4.17	0.12	4.52	1.51
Ocotea pulchella Mart.	Lauraceae	1	0.04	0.83	0.12	1.00	0.33
Myrcia sphaerocarpa DC.	Myrtaceae	2	0.09	0.83	0.25	1.17	0.39
Cybistax antisyphilitica (Mart.) Mart. ex A. DC.	Bignoniaceae	2	0.09	0.83	0.25	1.17	0.39
Swartzia myrtifolia Sm.	Fabaceae	2	0.09	0.83	0.25	1.17	0.39
Casearia obliqua Spreng.	Salicaceae	1	0.04	0.83	0.12	1.00	0.33
Matayba elaeagnoides Radlk.	Sapindaceae	2	0.09	1.67	0.12	1.88	0.63
Maytenus aquifolium Mart.	Celastraceae	1	0.04	0.83	0.12	1.00	0.33
Aniba firmula (Nees & Mart.) Mez	Lauraceae	1	0.04	0.83	0.12	1.00	0.33
Cariniana estrellensis (Raddi) Kuntze	Lecythidaceae	1	0.04	0.83	0.12	1.00	0.33
Inga striata Benth.	Fabaceae	1	0.04	0.83	0.12	1.00	0.33
Nectandra lanceolata Nees & Mart.	Lauraceae	1	0.04	0.83	0.12	1.00	0.33
Syagrus romanzoffiana (Cham.) Glassman	Arecaceae	1	0.04	0.83	0.12	1.00	0.33
Campomanesia xanthocarpa Mart. ex O. Berg	Myrtaceae	1	0.04	0.83	0.12	1.00	0.33
Platymiscium pubescens Micheli	Fabaceae	1	0.04	0.83	0.12	1.00	0.33
Mollinedia argyrogyna Perkins	monimiaceae	1	0.04	0.83	0.12	1.00	0.33
Matayba guianensis Aubl.	Sapindaceae	1	0.04	0.83	0.12	1.00	0.33
Pouteria sp.	Sapotaceae	1	0.04	0.83	0.12	1.00	0.33
Andira fraxinifolia Benth.	Fabaceae	1	0.04	0.83	0.12	1.00	0.33
Cupania ludowigii Somner & Ferrucci	Sapindaceae	1	0.04	0.83	0.12	1.00	0.33
Eugenia sp.	Myrtaceae	1	0.04	0.83	0.12	1.00	0.33
Psychotria carthagenensis Jacq.	Rubiaceae	1	0.04	0.83	0.12	1.00	0.33
Machaerium brasiliense Vogel	Fabaceae	1	0.04	0.83	0.12	1.00	0.33
Myrciaria cauliflora (Mart.) O. Berg	Myrtaceae	1	0.04	0.83	0.12	1.00	0.33
Maytenus ilicifolia Mart. ex Reissek	Celanstraceae	1	0.04	0.83	0.12	1.00	0.33
Guapira opposita (Vell.) Reitz	Nyctaginaceae	1	0.04	0.83	0.12	1.00	0.33

Espécie / Sul	**Família**	**Ni**	**DenR**	**AbuR**	**FreR**	**IVI**	**IVI (%)**

Anadenanthera peregrina (L.)Speg.	Fabaceae	81	4.40	1.08	4.21	9.69	3.23
Trichilia lepidota Mart.	Meliaceae	145	7.88	1.48	5.53	14.88	4.96
Piptadenia gonoacantha (Mart.) J.F. Macbr.	Fabaceae	44	2.39	0.81	3.07	6.27	2.09
Chrysophyllum flexuosum Mart.	Meliaceae	128	6.95	1.71	4.21	12.87	4.29
Siparuna guianensis Aubl.	Siparunaceae	115	6.25	1.57	4.12	11.94	3.98
Prunus sellowii Koehne	Rosaceae	88	4.78	1.13	4.39	10.29	3.43
Allophylus edulis (A. St.-Hil.. A. Juss. & Cambess.) Hieron. ex Niederl.	Sapindaceae	44	2.39	0.81	3.07	6.27	2.09
Trichilia pallida Sw.	Meliaceae	95	5.16	1.24	4.30	10.70	3.57
Sorocea bonplandii (Baill.) W.C. Burger. Lanj. & Wess. Boer	Moraceae	94	5.11	1.31	4.04	10.45	3.48
Machaerium stipitatum (DC.) Vogel	Fabaceae	52	2.82	1.15	2.54	6.52	2.17
Machaerium floridum (Mart. ex Benth.) Ducke	Fabaceae	8	0.43	0.86	0.53	1.82	0.61
Protium warmingiana March.L.	Burseraceae	53	2.88	0.87	3.42	7.17	2.39
Citronella megaphylla (Miers) R.A. Howard	Cardiopteridaceae	67	3.64	1.26	2.98	7.89	2.63
Xylosma prockia (Turcz.) Turcz.	Salicaceae	56	3.04	1.16	2.72	6.92	2.31
Luehea grandiflora Mart.	Malvaceae	32	1.74	0.79	2.28	4.81	1.60
Ocotea dispersa (Nees & Mart.) Mez	Lauraceae	48	2.61	0.79	3.42	6.82	2.27
Guapira opposita (Vell.) Reitz	Nyctaginaceae	49	2.66	0.85	3.25	6.76	2.25
Plinia glomerata (O.Berg) Amshoff	Myrtaceae	66	3.59	1.63	2.28	7.49	2.50
Nectandra lanceolata Nees & Mart.	Lauraceae	28	1.52	0.86	1.84	4.22	1.41
Dalbergia nigra (Vell.) Allemão ex Benth.	Fabaceae	49	2.66	1.75	1.58	5.99	2.00
Psychotria myriantha Müll. Arg.	Rubiaceae	57	3.10	1.26	2.54	6.90	2.30
Cedrela fissilis Vell.	Meliaceae	25	1.36	0.89	1.58	3.83	1.28
Cabralea canjerana (Vell.) Mart.	Meliaceae	20	1.09	0.86	1.32	3.26	1.09
Cariniana legalis (Mart.) Kuntze	Lecythidaceae	7	0.38	0.75	0.53	1.65	0.55
Coutarea hexandra (Jacq.) K. Schum.	Rubiaceae	15	0.81	0.64	1.32	2.77	0.92
Endlicheria paniculata (Spreng.) J.F. Macbr.	Lauraceae	14	0.76	0.82	0.96	2.54	0.85
Syagrus romanzoffiana (Cham.) Glassman	Arecaceae	13	0.71	0.69	1.05	2.45	0.82
Apuleia leiocarpa (Vogel) J.F. Macbr.	Fabaceae	10	0.54	0.80	0.70	2.05	0.68
Amaioua guianensis Hemsl.	Rubiaceae	19	1.03	0.87	1.23	3.13	1.04
Rollinia sylvatica (A. St.-Hil.) Martius	Annonaceae	13	0.71	0.76	0.96	2.43	0.81
Casearia decandra Jacq.	Salicaceae	16	0.87	0.86	1.05	2.78	0.93
Ficus enormis (Mart. ex Miq.) Mart.	Moraceae	1	0.05	0.64	0.09	0.78	0.26
Guarea kunthiana A. Juss.	Meliaceae	13	0.71	0.69	1.05	2.45	0.82
Cariniana estrellensis (Raddi) Kuntze	Lecythidaceae	5	0.27	0.64	0.44	1.35	0.45
Garcinia gardneriana (Planch. & Triana) Zappi	Clusiaceae	12	0.65	0.64	1.05	2.35	0.78
Guettarda viburnoides Cham. & Schltdl.	Rubiaceae	7	0.38	0.75	0.53	1.65	0.55
Cecropia glaziovii Snethl.	Urticaceae	9	0.49	0.82	0.61	1.93	0.64
Maytenus aquifolium Mart.	Celastraceae	1	0.05	0.64	0.09	0.78	0.26
Ceiba speciosa (A. St.-Hil.) Ravenna	Malvaceae	7	0.38	0.64	0.61	1.64	0.55
Persea pyrifolia (D. Don) Spreng.	Lauraceae	4	0.22	0.64	0.35	1.21	0.40
Nectandra rigida (Kunth) Nees	Lauraceae	6	0.33	0.77	0.44	1.53	0.51
Bauhinia forficata Link	Fabaceae	5	0.27	0.64	0.44	1.35	0.45
Annona cacans Warm.	Annonaceae	6	0.33	0.64	0.53	1.49	0.50
Casearia sylvestris Sw.	Salicaceae	3	0.16	0.64	0.26	1.07	0.36

Rollinia laurifolia Schltdl.	Annonaceae	4	0.22	0.64	0.35	1.21	0.40
Aniba firmula (Nees & Mart.) Mez	Lauraceae	5	0.27	0.64	0.44	1.35	0.45
Tabernaemontana laeta Mart.	Apocynaceae	2	0.11	0.64	0.18	0.93	0.31
Citronella paniculata (Mart.) R.A. Howard	Cardiopteridaceae	8	0.43	0.86	0.53	1.82	0.61
Guarea macrophylla Vahl	Meliaceae	6	0.33	0.64	0.53	1.49	0.50
Campomanesia xanthocarpa Mart. ex O. Berg	Myrtaceae	5	0.27	0.64	0.44	1.35	0.45
Anadenanthera colubrina (Vell.)Brenan	Fabaceae	5	0.27	0.64	0.44	1.35	0.45
Croton floribundus Spreng.	Euphorbiaceae	5	0.27	0.64	0.44	1.35	0.45
Seguieria americana L.	Phytolaccaceae	2	0.11	0.64	0.18	0.93	0.31
Piptadenia paniculata Benth.	Fabaceae	5	0.27	0.64	0.44	1.35	0.45
Platypodium elegans Vogel	Fabaceae	3	0.16	0.64	0.26	1.07	0.36
Peltophorum dubium (Spreng.) Taub.	Fabaceae	4	0.22	0.86	0.26	1.34	0.45
Matayba elaeagnoides Radlk.	Sapindaceae	5	0.27	0.64	0.44	1.35	0.45
Guapira hirsuta (Choisy) Lundell	Nyctaginaceae	5	0.27	0.64	0.44	1.35	0.45
Myrcia fallax (Rich.) DC.	Myrtaceae	5	0.27	0.80	0.35	1.42	0.47
Jacaranda micrantha Cham.	Bignoniaceae	5	0.27	0.80	0.35	1.42	0.47
Pseudobombax grandiflorum (Cav.) A. Robyns	Malvaceae	4	0.22	0.64	0.35	1.21	0.40
Maclura tinctoria (L.) D. Don ex Steud.	Moraceae	3	0.16	0.64	0.26	1.07	0.36
Persea americana Mill.	Lauraceae	2	0.11	0.64	0.18	0.93	0.31
Miconia hymenonervia (Raddi) Cogn.	Melastomataceae	6	0.33	1.28	0.26	1.87	0.62
Cassia ferruginea (Schrad.) Schrader ex DC.	Fabaceae	3	0.16	0.64	0.26	1.07	0.36
Sapium glandulatum (Vell.) Pax	Euphorbiaceae	3	0.16	0.64	0.26	1.07	0.36
Marlierea teuscheriana (O. Berg) D. Legrand	Myrtaceae	7	0.38	2.24	0.18	2.80	0.93
Inga marginata Willd.	Fabaceae	4	0.22	0.64	0.35	1.21	0.40
Cryptocarya moschata Nees & Mart.	Lauraceae	2	0.11	0.64	0.18	0.93	0.31
Machaerium nyctitans (Vell.) Benth.	Fabaceae	4	0.22	0.64	0.35	1.21	0.40
Psychotria sessilis Vell.	Rubiaceae	4	0.22	0.64	0.35	1.21	0.40
Copaifera langsdorffii Desf.	Fabaceae	5	0.27	1.07	0.26	1.60	0.53
Trichilia elegans A. Juss.	Meliaceae	3	0.16	0.64	0.26	1.07	0.36
Eugenia strictopetala DC.	Myrtaceae	4	0.22	0.86	0.26	1.34	0.45
Rollinia sericea (R.E. Fr.) R.E. Fr.	Annonaceae	4	0.22	0.86	0.26	1.34	0.45
Newtonia contorta (DC.) Burkart	Fabaceae	3	0.16	0.64	0.26	1.07	0.36
Erythroxylum pelleterianum A. St.-Hil.	Erythroxylaceae	4	0.22	0.86	0.26	1.34	0.45
Sparattosperma leucanthum (Vell.) K. Schum.	Bignoniaceae	3	0.16	0.64	0.26	1.07	0.36
Senna multijuga (Rich.) H.S. Irwin & Barneby	Fabaceae	1	0.05	0.64	0.09	0.78	0.26
Guatteria nigrescens Mart.	Annonaceae	3	0.16	0.64	0.26	1.07	0.36
Picramnia regnelli Engl.	Picramniaceae	3	0.16	0.64	0.26	1.07	0.36
Cordia bullata (L.) Roem. & Schult.	Boraginaceae	3	0.16	0.96	0.18	1.30	0.43
Casearia gossypiosperma Briq.	Salicaceae	2	0.11	0.64	0.18	0.93	0.31
Mabea fistulifera Mart.	Euphorbiaceae	3	0.16	0.96	0.18	1.30	0.43
Himatanthus phagedaenicus (Mart.) Woodson	Apocynaceae	2	0.11	0.64	0.18	0.93	0.31
Clarisia ilicifolia (Spreng.) Lanj. & Rossberg	Moraceae	3	0.16	0.96	0.18	1.30	0.43
Carpotroche brasiliensis (Raddi) A. Gray	Achariaceae	2	0.11	0.64	0.18	0.93	0.31
Zanthoxylum rhoifolium Lam.	Rutaceae	2	0.11	0.64	0.18	0.93	0.31
Inga affinis DC.	Fabaceae	2	0.11	0.64	0.18	0.93	0.31

Pithecellobium langsdorffii Benth.	Fabaceae	2	0.11	0.64	0.18	0.93	0.31
Guatteria villosissima A. St.-Hil.	Annonaceae	2	0.11	0.64	0.18	0.93	0.31
Ocotea odorifera Rohwer	Lauraceae	2	0.11	0.64	0.18	0.93	0.31
Mollinedia chrysorrhachis Perkins	Monimiaceae	2	0.11	0.64	0.18	0.93	0.31
Solanum pseudoquina A. St.-Hil.	Solanaceae	1	0.05	0.64	0.09	0.78	0.26
Cryptocarya sp.	Lauraceae	1	0.05	0.64	0.09	0.78	0.26
Platymiscium pubescens Micheli	Fabaceae	1	0.05	0.64	0.09	0.78	0.26
Allophylus sericeus Radlk.	Sapindaceae	1	0.05	0.64	0.09	0.78	0.26
Seguieria langsdorffii Moq.	Phytolaccaceae	2	0.11	1.28	0.09	1.48	0.49
Randia armata (Sw.) DC.	Rubiaceae	2	0.11	1.28	0.09	1.48	0.49
Eugenia sp.1	Myrtaceae	1	0.05	0.64	0.09	0.78	0.26
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Sapotaceae	1	0.05	0.64	0.09	0.78	0.26
Randia spinosa (Thunb.) Poir.	Rubiaceae	1	0.05	0.64	0.09	0.78	0.26
Albizia polycephala (Benth.) Killip	Fabaceae	1	0.05	0.64	0.09	0.78	0.26
Allophylus semidentatus (Miq.) Radlk.	Sapindaceae	1	0.05	0.64	0.09	0.78	0.26
Alchornea glandulosa Poepp.	Euphorbiaceae	1	0.05	0.64	0.09	0.78	0.26
Zanthoxylum riedelianum Engl.	Rutaceae	1	0.05	0.64	0.09	0.78	0.26
Eugenia sp.2	Myrtaceae	1	0.05	0.64	0.09	0.78	0.26
Euterpe edulis Mart.	Arecaceae	1	0.05	0.64	0.09	0.78	0.26
Vernonia diffusa Less.	Asteraceae	1	0.05	0.64	0.09	0.78	0.26
Swartzia myrtifolia Sm.	Fabaceae	1	0.05	0.64	0.09	0.78	0.26
Lacistema pubescens Mart.	Lacistemataceae	1	0.05	0.64	0.09	0.78	0.26
Casearia arborea (Rich.) Urb.	Salicaceae	1	0.05	0.64	0.09	0.78	0.26
Bathysa cuspidata (A. St.-Hil.) Hook. f. ex K. Schum.	Rubiaceae	1	0.05	0.64	0.09	0.78	0.26
Tapirira guianensis Aubl.	Anacardiaceae	1	0.05	0.64	0.09	0.78	0.26
Psychotria vellosiana Benth.	Anacardiaceae	1	0.05	0.64	0.09	0.78	0.26
Machaerium brasiliense Vogel	Fabaceae	1	0.05	0.64	0.09	0.78	0.26
Eugenia leptoclada O. Berg	Myrtaceae	1	0.05	0.64	0.09	0.78	0.26
Mollinedia schottiana (Spreng.) Perkins	Monimiaceae	1	0.05	0.64	0.09	0.78	0.26
Ocotea pubescens Nees	Lauraceae	1	0.05	0.64	0.09	0.78	0.26
Ocotea teleiandra (Meisn.) Mez	Lauraceae	1	0.05	0.64	0.09	0.78	0.26
Brunfelsia uniflora (Pohl) D. Don	Solanaceae	1	0.05	0.64	0.09	0.78	0.26
Eriotheca candolleana (K. Schum.) A. Robyns	Malvaceae	1	0.05	0.64	0.09	0.78	0.26
Eugenia sp.3	Myrtaceae 2	1	0.05	0.64	0.09	0.78	0.26
Platycyamus regnellii Benth.	Fabaceae	1	0.05	0.64	0.09	0.78	0.26
Casearia ulmifolia Cambess.	Salicaceae	1	0.05	0.64	0.09	0.78	0.26
Miconia vernalis Ruiz & Pav.	Melastomataceae	1	0.05	0.64	0.09	0.78	0.26

Table S2: Data on all species for AGB.

Species / oeste	**AGB (Mg/ha)**	**AGB (Mg/ha) 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 odorífera	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
Endlicheria paniculata	1.50	213.05	0.65	92.08
Casearia arborea	1.28	214.33	0.55	92.64
Trichilia pallida	1.23	215.56	0.53	93.17
Coutarea hexandra	1.23	216.79	0.53	93.70
Clarisia ilicifolia	1.12	217.92	0.49	94.19
Sparattosperma leucanthum	1.01	218.93	0.44	94.62
Seguieria americana	0.96	219.89	0.41	95.04
Astronium fraxinifolium	0.85	220.74	0.37	95.41
Anadenanthera colubrina	0.74	221.48	0.32	95.73
Piptadenia gonoacantha	0.69	222.17	0.30	96.03
Chrysophyllum marginatum	0.68	222.86	0.30	96.32
Myrciaria axillaris	0.65	223.50	0.28	96.60
Eugenia leptoclada	0.58	224.09	0.25	96.85
Ocotea pulchella	0.56	224.64	0.24	97.09
Chrysophyllum gonocarpum	0.53	225.18	0.23	97.32
Cariniana legalis	0.53	225.70	0.23	97.55
Peltophorum dubium	0.48	226.18	0.21	97.76
Amaioua guianensis	0.42	226.60	0.18	97.94
Casearia obliqua	0.42	227.02	0.18	98.12
Zeyheria tuberculosa	0.37	227.39	0.16	98.28
Vitex megapotamica	0.32	227.71	0.14	98.42

Prunus sellowii	0.30	228.01	0.13	98.55
Licania spicata	0.28	228.30	0.12	98.67
Aspidosperma olivaceum	0.27	228.57	0.12	98.79
Zanthoxylum rhoifolium	0.27	228.84	0.12	98.91
Eugenia strictopetala	0.26	229.10	0.11	99.02
Ocotea dispersa	0.25	229.35	0.11	99.13
Trichilia elegans	0.24	229.59	0.10	99.23
Carpotroche brasiliensis	0.23	229.82	0.10	99.33
Maytenus aquifolium	0.20	230.02	0.09	99.42
Zollernia ilicifolia	0.16	230.18	0.07	99.48
Qualea jundiahy	0.14	230.31	0.06	99.54
Matayba elaeagnoides	0.12	230.44	0.05	99.60
Cordia silvestres	0.08	230.51	0.03	99.63
Guettarda scabra	0.07	230.59	0.03	99.66
Cariniana estrellensis	0.07	230.65	0.03	99.69
Trichilia lepidota	0.06	230.72	0.03	99.72
Aniba firmula	0.06	230.78	0.03	99.75
Inga striata	0.06	230.84	0.02	99.77
Jacaranda micrantha	0.06	230.89	0.02	99.79
Eriotheca candolleana	0.06	230.95	0.02	99.82
Simira sampaioana	0.04	230.99	0.02	99.84
Picramnia regnelli	0.04	231.03	0.02	99.85
Myrcia sphaerocarpa	0.04	231.07	0.02	99.87
Campomanesia xanthocarpa	0.03	231.09	0.01	99.88
Platymiscium pubescens	0.02	231.12	0.01	99.89
Matayba guianensis	0.02	231.14	0.01	99.90
Nectandra lanceolata	0.02	231.17	0.01	99.91
Cybistax antisyphilitica	0.02	231.19	0.01	99.92
Swartzia myrtifolia	0.02	231.21	0.01	99.93
Pouteria sp	0.02	231.23	0.01	99.94
Mollinedia argyrogyna	0.02	231.25	0.01	99.95
Syagrus romanzoffiana	0.02	231.27	0.01	99.96
Andira fraxinifolia	0.02	231.28	0.01	99.96
Cedrela fissilis	0.01	231.29	0.01	99.97
Garcinia gardneriana	0.01	231.30	0.00	99.97
Guarea kunthiana	0.01	231.32	0.00	99.98
Cupania ludowigii	0.01	231.33	0.00	99.98
Eugenia sp.	0.01	231.34	0.00	99.99
Myrciaria cauliflora	0.01	231.34	0.00	99.99
Maytenus ilicifolia	0.01	231.35	0.00	99.99
Machaerium brasiliense	0.01	231.36	0.00	100.00
Psychotria carthagenensis	0.01	231.36	0.00	100.00
Guapira opposita	0.00	231.37	0.00	100.00
Species / sul	**AGB (Mg/ha)**	**AGB (Mg/ha) 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
Guettarda viburnoides	2.47	211.89	0.96	82.74
Tabernaemontana laeta	2.36	214.25	0.92	83.66
Protium warmingiana	2.13	216.38	0.83	84.49
Endlicheria paniculata	1.99	218.38	0.78	85.27
Bauhinia forficata	1.76	220.14	0.69	85.96
Seguieria americana	1.70	221.84	0.66	86.62
Trichilia pallida	1.69	223.52	0.66	87.28
Nectandra rígida	1.62	225.14	0.63	87.91
Guapira opposita	1.61	226.75	0.63	88.54
Platypodium elegans	1.57	228.33	0.61	89.15
Cabralea canjerana	1.35	229.68	0.53	89.68
Plinia glomerata	1.28	230.96	0.50	90.18
Siparuna guianensis	1.25	232.21	0.49	90.67
Syagrus romanzoffiana	1.24	233.45	0.49	91.15
Ocotea dispersa	1.04	234.49	0.41	91.56
Citronella megaphylla	1.02	235.51	0.40	91.96
Aniba firmula	1.00	236.50	0.39	92.35
Rollinia sylvatica	0.97	237.48	0.38	92.73
Persea americana	0.96	238.43	0.37	93.10
Peltophorum dubium	0.91	239.35	0.36	93.46
Casearia decandra	0.90	240.25	0.35	93.81
Senna multijuga	0.90	241.15	0.35	94.16
Ceiba speciosa	0.87	242.03	0.34	94.50
Rollinia laurifolia	0.87	242.90	0.34	94.84
Cecropia glaziovi	0.82	243.72	0.32	95.16

Coutarea hexandra	0.79	244.51	0.31	95.47
Campomanesia xanthocarpa	0.77	245.28	0.30	95.77
Cryptocarya moschata	0.71	245.99	0.28	96.05
Anadenanthera colubrina	0.70	246.69	0.27	96.32
Cassia ferruginea	0.69	247.38	0.27	96.59
Maclura tinctoria	0.68	248.05	0.26	96.86
Sorocea bonplandii	0.64	248.69	0.25	97.11
Annona cacans	0.62	249.31	0.24	97.35
Croton floribundus	0.44	249.75	0.17	97.52
Amaioua guianensis	0.40	250.15	0.16	97.68
Guarea macrophylla	0.37	250.52	0.14	97.82
Piptadenia paniculata	0.33	250.85	0.13	97.95
Myrcia fallax	0.33	251.18	0.13	98.08
Solanum pseudoquina	0.27	251.46	0.11	98.19
Casearia gossypiosperma	0.25	251.71	0.10	98.28
Sapium glandulatum	0.24	251.95	0.09	98.38
Trichilia elegans	0.22	252.16	0.08	98.46
Platymiscium pubescens	0.21	252.38	0.08	98.54
Citronella paniculata	0.19	252.56	0.07	98.62
Psychotria myriantha	0.18	252.74	0.07	98.69
Cryptocarya sp.	0.17	252.91	0.07	98.75
Guarea kunthiana	0.17	253.08	0.06	98.82
Newtonia contorta	0.16	253.24	0.06	98.88
Garcinia gardneriana	0.15	253.39	0.06	98.94
Eugenia sp. 1	0.14	253.53	0.05	99.00
Allophylus sericeus	0.13	253.66	0.05	99.05
Himatanthus phagedaenicus	0.13	253.79	0.05	99.10
Sparattosperma leucanthum	0.12	253.92	0.05	99.15
Pseudobombax grandiflorum	0.12	254.03	0.05	99.19
Cordia bullata	0.11	254.14	0.04	99.24
Matayba elaeagnoides	0.11	254.25	0.04	99.28
Randia spinosa	0.10	254.36	0.04	99.32
Chrysophyllum gonocarpum	0.10	254.46	0.04	99.36
Marlierea teuscheriana	0.10	254.56	0.04	99.40
Jacaranda micrantha	0.09	254.65	0.04	99.43
Eugenia strictopetala	0.09	254.74	0.04	99.47
Albizia polycephala	0.08	254.82	0.03	99.50
Allophylus semidentatus	0.07	254.89	0.03	99.53
Guapira hirsuta	0.07	254.96	0.03	99.55
Carpotroche brasiliensis	0.06	255.02	0.02	99.58
Zanthoxylum rhoifolium	0.06	255.08	0.02	99.60
Mabea fistulifera	0.05	255.13	0.02	99.62
Swartzia myrtifolia	0.05	255.18	0.02	99.64
Eugenia sp.2	0.05	255.24	0.02	99.66
Inga affinis	0.05	255.29	0.02	99.68

Rollinia sericea	0.05	255.34	0.02	99.70
Miconia hymenonervia	0.05	255.39	0.02	99.72
Alchornea glandulosa	0.05	255.43	0.02	99.74
Erythroxylum pelleterianum	0.05	255.48	0.02	99.76
Pithecellobium langsdorffii	0.05	255.53	0.02	99.77
Ocotea odorifera	0.04	255.57	0.02	99.79
Guatteria villosissima	0.04	255.61	0.02	99.81
Zanthoxylum riedelianum	0.04	255.66	0.02	99.83
Machaerium nyctitans	0.03	255.69	0.01	99.84
Guatteria nigrescens	0.03	255.72	0.01	99.85
Inga marginata	0.03	255.75	0.01	99.86
Lacistema pubescens	0.03	255.78	0.01	99.87
Euterpe edulis	0.03	255.80	0.01	99.88
Seguieria langsdorffii	0.03	255.83	0.01	99.89
Bathysa cuspidata	0.03	255.85	0.01	99.90
Casearia arborea	0.03	255.88	0.01	99.91
Copaifera langsdorffii	0.02	255.90	0.01	99.92
Clarisia ilicifolia	0.02	255.93	0.01	99.93
Vernonia diffusa	0.02	255.95	0.01	99.94
Machaerium brasiliense	0.02	255.96	0.01	99.95
Psychotria vellosiana	0.02	255.98	0.01	99.95
Eugenia leptoclada	0.02	256.00	0.01	99.96
Tapirira guianensis	0.01	256.01	0.01	99.96
Picramnia regnelli	0.01	256.02	0.01	99.97
Mollinedia schottiana	0.01	256.03	0.00	99.97
Randia armata	0.01	256.04	0.00	99.98
Ocotea pubescens	0.01	256.05	0.00	99.98
Ocotea teleiandra	0.01	256.06	0.00	99.98
Psychotria sessilis	0.01	256.07	0.00	99.99
Brunfelsia uniflora	0.01	256.08	0.00	99.99
Eugenia sp. 3	0.01	256.08	0.00	99.99
Platycyamus regnellii	0.01	256.09	0.00	99.99
Eriotheca candolleana	0.00	256.09	0.00	100.00
Mollinedia chrysorrhachis	0.00	256.09	0.00	100.00
Casearia ulmifolia	0.00	256.10	0.00	100.00
Miconia vernalis	0.00	256.10	0.00	100.00

Figure S2. Habitats types of the two study areas. 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 (LIP).

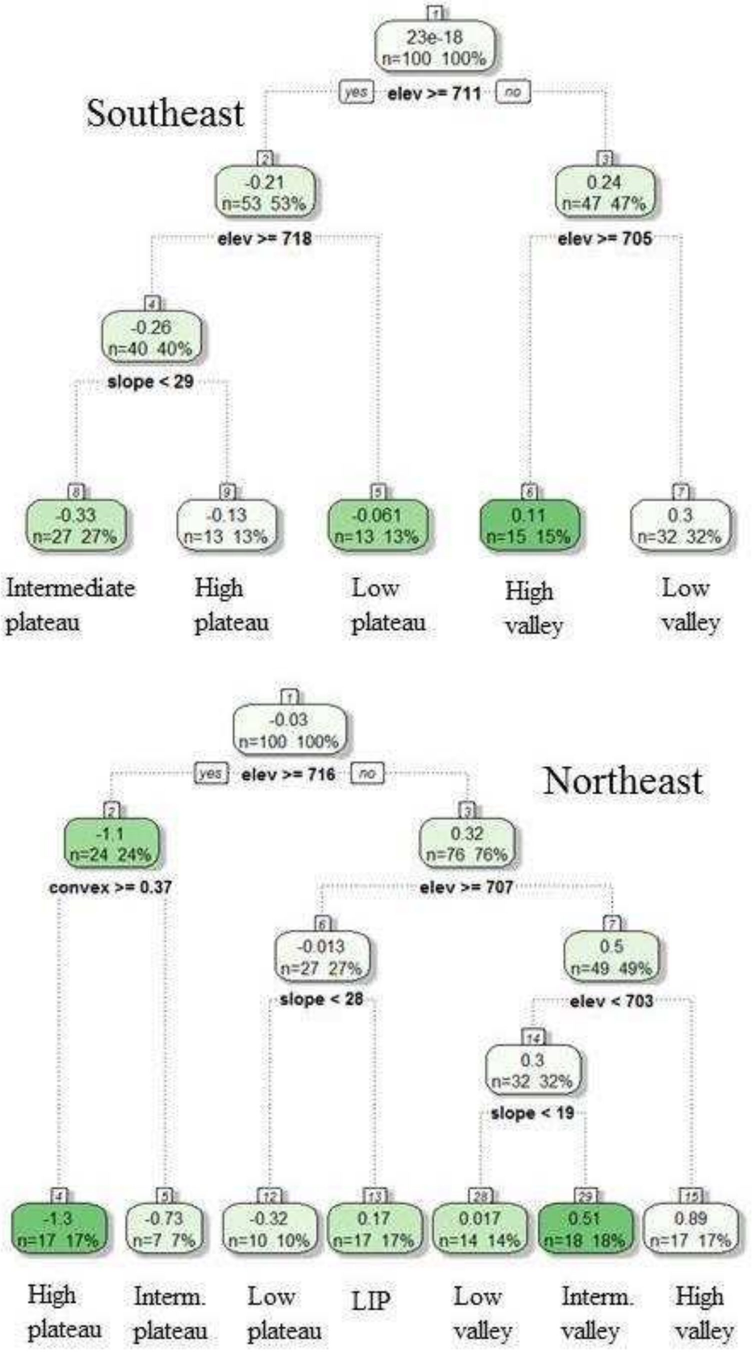
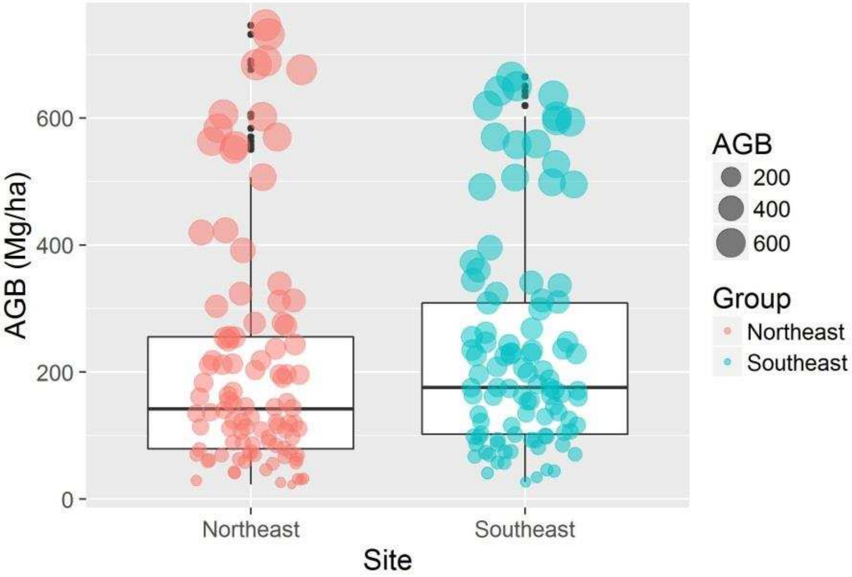


Figure S3. Aboveground biomass in sites with different topographical heterogeneity levels.



CONCLUSÕES GERAIS

Nossos resultados revelam que uma maior heterogeneidade topográfica promove uma maior riqueza de espécies, mas não implica mudanças significativas na estocagem de biomassa acima do solo. Encontramos também que o número de espécies hiperdominates em caule e biomassa aumenta com a riqueza. Nossas análises em escala de habitats indicam que na área menos heterogênea existe um padrão de distribuição de elevação mais uniforme, e sem variação na convexidade ao longo do gradiente, que induz mudanças nos atributos estruturais e taxonômicos ao longo do gradiente topográfico. Por outro lado, a área mais heterogênea não apresenta diferenças nos atributos estruturais entre habitats.

Encontramos uma forte relação dos *drivers* topográficos com a distribuição da composição florística em ambas as áreas estudadas, mas com a distribuição dos atributos estruturais e AGB só na área sudeste que foi menos heterogênea. Como mostrado em nossos resultados na área sudeste a maior disponibilidade de nutrientes se encontra em áreas mais baixas do gradiente e como consequência, nesses habitas há maiores árvores e maior quantidade de AGB. A riqueza e a composição das espécies em escala de área foram melhor explicadas pela elevação, mas sem nenhuma alteração significativa com os efeitos das principias propriedades fisicoquímicas do solo.

Nosso trabalho fornece as primeiras indicações sobre a importância relativa dos *drivers* topográficos sobre a composição, estrutura, distribuição de espécies hiperdominantes, e funcionamento ecossistêmico na Mata Atlântica. Assim, nossa abordagem representa uma primeira aproximação na análise da relação diversidade-função ecossistêmica ao longo de gradientes topográficos baseado em atributos taxonômicos e estruturais da floresta, o que pode favorecer o estabelecimento de critérios básicos de conservação e manejo. Com a análise de hiperdominância, é possível identificar a contribuição relativa das espécies nos processos ecossistêmicos; bem como as espécies que limitam o estabelecimento de outras espécies de florestas maduras com maior valor funcional. Desta forma, é possível controlar as trajetórias de sucessão com manejo direto das espécies com menor contribuição funcional, especialmente em paisagens sob modificação humana.