## **UNIVERSIDADE FEDERAL DE JUIZ DE FORA** PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

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### **BAMBOO DOMINANCE IN AN ATLANTIC FOREST COMMUNITY: A STRUCTURAL, FUNCTIONAL AND TAXONOMIC APPROACH**

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Dissertação apresentada ao Programa de Pós-Graduação em Ecologia, da Universidade Federal de Juiz de Fora, como parte dos requisitos à obtenção do Título de Mestre em Ecologia Aplicada ao Manejo e Conservação dos Recursos Naturais.

**Orientador:** Prof. Dr. Fabrício Alvim Carvalho **Coorientador:** Dr. Jamir Afonso do Prado Júnior

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#### ABSTRACT

Native species also have the potential to spread and proliferate disproportionally, causing considerable damage as much as exotic species. The increase in native species dominance is called as overabundance and it has affected communities and ecosystems in many different ways. In Brazil, many woody bamboos are typical examples of invasive native species. Their high dominance usually alters the structure and composition of forests, reducing tree density, total basal area, richness, as well as taxonomic and functional diversity of trees. Merostachys sp. is a common native bamboo genus in the Atlantic Forest and in certain disturbed conditions can become overabundant in forest communities. In order to understand the relationship between bamboo dominance and forest parameters we allocated 30 plots of 10x20 m in a Atlantic forest fragment, we marked and identified all the trees individuals with DAB  $\geq$ 5cm and we measured the basal area of all bamboo clumps within the plots. We evaluated the relationships between bamboo basal area and structural, taxonomic and functional diversity metrics in a tropical forest community, and how these relationships change among the underlying diameter classes of the community. We found that plots with higher bamboo dominance have lower tree density and higher basal area of dead trees, whereas those plots have higher functional and taxonomic diversity, considering that the *niche-filling hypothesis* plays an important role in invaded communities at local scale. In addition, we found that bamboo dominance was positively related to high dominance of acquisitive traits species and that those relationships were stronger for small trees than larger trees. Even though we have found strong evidence of the effects of the bamboo overdominance, we cannot affirm that those changes within community were the cause or consequence of invasion. In overall, this study was import to highlight the native bamboo interactions with forest parameters, also bringing new contributions for invasion studies at local scale.

**Keywords:** Overabundance; invasion; niche-filling hypothesis; community-weighted mean (CWM); functional diversity; average taxonomic distinctness.

#### RESUMO

Espécies nativas também tem o potencial de se espalhar e proliferar desproporcionalmente, causando danos consideráveis tanto quanto espécies exóticas. O aumento na dominância dessas espécies nativas é chamado de superabundância e tem afetado comunidades e ecossistemas de diferentes formas. No Brasil, muitas espécies de bambu lenhosos são típicos exemplos de espécies invasoras nativas. Sua alta dominância geralmente altera a estrutura e composição de florestas, reduzindo a densidade, área basal total, riqueza de espécies, assim como a diversidade taxonômica e funcional de árvores. Merostachys é um gênero comum de bambu nativo encontrado em fragmentos de Floresta Atlântica que sofreram algum tipo de perturbação, tornando-se superdominante nesses ambientes. De forma a entender as relações entre dominância de bambu e parâmetros florestais, nós alocamos 30 parcelas de 10x20 m em um fragmento de Floresta Atlântica; marcamos e identificamos todas as espécies arbóreas com DAP ≥5cm e medimos a área basal de todas as touceiras de bambu por parcela. Nós avaliamos as relações entre a área basal do bambu e os parâmetros estruturais, e as métricas de diversidade taxonômica e funcional em uma comunidade de floresta tropical, e como essas relações variam entre as classes de diâmetro subjacentes da comunidade. Encontramos que parcelas com maior dominância de bambu possuem menor densidade de árvores e maior área basal de árvores mortas, enquanto que essas mesmas parcelas apresentam maior diversidade funcional e taxonômica, considerando que a hipótese de preenchimento de nicho desempenha um papel importante na comunidade invadida em escala local. Além disso, encontramos que a dominância de bambu estava positivamente relacionada à alta dominância de espécies com traços funcionais aquisitivos e que essas relações são mais fortes para árvores pequenas do que árvores maiores. Embora tenhamos encontrado fortes evidências dos efeitos da superabundância do bambu, não podemos afirmar que essas mudanças dentro da comunidade tenham sido a causa ou consequência da invasão. No geral, este estudo foi importante para destacar as interações da espécies de bambu nativo com outros parâmetros florestais, trazendo também novas contribuições para estudos de invasão em escala local.

**Palavras-chave:** Superabundância; invasão; hipótese de preenchimento de nicho; CWM; diversidade funcional; distinção taxonômica média.

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#### **INTRODUCTION**

Biological invasions have directly affected the worldwide biodiversity in different scales (Tilman 1999). Most of our knowledge of invasion ecology is based on studies evaluating the effect of alien species in native communities (Simberloff *et al.* 2003). These alien species are usually introduced by man into a new environment, and for many reasons, such as the lack of predators or competitors, they can become dominant (Vitousek *et al.* 1987). A central but yet understudied question is whether native species can also become invasive species. Some of them have the potential to spread and proliferate disproportionally, causing considerable damage as much as alien species (Garrott *et al.* 1993). The overabundance of native species in natural communities (Garrot *et al.* 1993) is associated to several human impacts such as land use intensification (Wiens 2009) and climate change (Pivello *et al.* 2018). When these disturbances overcome the thresholds that limit the community resilience, these superperformers species (that usually combine high growth and reproduction rates) can outcompete other species and leads to reduced productivity and to changes in ecosystem functions (Pivello *et al.* 2018).

Most studies evaluating the effect of "native invader species" in natural communities indicates that they are stronger competitors than the resident species (other native species in a community besides the invader one), and leads to a strong decrease in species richness and diversity (Hejda et al. 2009). Nevertheless, other studies have shown that the impacts of plant invasions are context-dependent, and not necessarily influences species diversity. In some cases, especially when the life form of the alien species is different from the other resident species most species are able to coexist with the invader (Tecco et al. 2009). The lack of concern among the studies is probably due to the use of species richness as the main metric to evaluate the invasion resistance of communities. Especially in high-diverse tropical forests, the number of coexisting species does not necessarily reflect the ecosystem structure, because they do not inform about species relatedness and function (Diaz & Cabido 2001). Therefore, to understand the invasive potential of a native species, and the capacity of natural communities to deal with invasion, we must evaluate the whole community diversity, including functional and phylogenetic parameters, and then infer more precisely about the differences in the niche occupation and in the competitive capacity of species (McGill et al. 2006; Kunstler et al. 2012; Kraft, Godoy, & Levine 2015).

Two long-standing contrasting hypotheses based on the ecological dissimilarity between resident species have been put forward to understand how alien

species influence community's attributes, and to predict the susceptibility of communities to invasion (Thuiller et al. 2010; Blonder 2016; Loiola et al. 2018). The environmental filtering hypothesis (Kembel & Hubbell 2006) assumes that there is a similar supply of resources for resident and alien species, and then, communities with large functional and phylogenetic diversity should use available resources more completely (Gerhold et al. 2011; Hejda & de Bello 2013) and be more resistant to invasion (Levine, Adler, & Yelenik 2004) than communities with low functional and phylogenetic diversity. In this sense, the impacts of invasion would be relatated to the competitive exclusion between alien and resident species, promote the dominance of certain groups of similar species related to greater competitive abilities against the alien species, that have higher performance under the available resources, possibly leading to decreased in functional and taxonomic diversity. Conversely, the nichefilling hypothesis (Thuiller et al. 2010) predicts that communities of native species with large functional and phylogenetic diversity would be more susceptible to invasion (Gurvich, Tecco & Díaz 2005), since high dissimilarity between species could lead to empty gaps within the phylogenetic and functional space of a community (Blonder 2016). These niches could be used by aliens to establish and enhance invasion in communities with higher functional and phylogenetic diversity. The contrasting predictions among the effects of environmental filtering hypothesis and niche-filling hypothesis seem to be scale-dependent (Götzenberger et al. 2012). While environmental filtering hypothesis is expected to be the most important driver of invasion among habitats, *niche-filling hypothesis* is expected to be more important at local scales within habitats. Evaluating how invasion change the overall diversity metrics among the resident species in invaded communities are still rare (Bennett et al. 2016).

In Brazil, many woody bamboos (Poaceae: Bambusoideae) are typical examples of invasive native species that have many characteristics of successful invaders (Lima *et al.* 2012). The Brazilian Atlantic forest, one of the conservation hotspots in the world, is one of the richness spots of Neotropical bamboos distribution (Clark 1991; Bystriakova *et al.* 2004). This extends to the genus *Merostachys* that has the center of endemism and diversity spot in the Atlantic domain (Judziewicz *et al.* 1999). *Merostachys* species generally inhabit both wet and shaded understories as well as forest gaps and edges of forests formations (Judziewicz *et al.* 1999; Filgueiras and Santos Goncalves 2004). Species from *Merostachys* genus are characterized by having a long life cycle (around 30 years) (Judziewicz *et al.* 1999; Guilherme *et al.* 

2004), enabling the growth of their populations by great production of seeds that provides food for rodents and birds (Jaksic and Lima 2003; Cestari & Bernardi 2011; Kaminski *et al.* 2016). Flowering in *Merostachys* species is generally gregarious and the death of individuals allows the opening of clearings in the areas where they are established, which interferes in floristic composition and diversity of forests (Filgueiras 1988).

Many studies using bamboo species as model have shown that bamboos dominance alter the structure and composition of tropical forest communities, reducing tree density, total basal area, richness, seedling establishment, functional groups and functional diversity of plants (Griscom & Ashton, 2006; Rother 2006; Griscom et al. 2007; D'Oliveira et al. 2013; Montti et al. 2014). Furthermore, some studies with Merostachys species in semideciduous dry forests in southeastern Brazil found that clumps of the genus generally are associated with low density of tree species, constraining the recruitment, growth and survival of trees (Oliveira-Filho et al. 1994; Guilherme et al. 2004). However, these studies have focused on the relationships between bamboo dominance and the overall forests attributes, neglecting that the influence of bamboo can be size-dependent, e.g., the influence of bamboo on small trees can be different from the larger trees. As a species that usually occupies the understory (rarely higher than 8 m), the influence of Merostachys sp. should be stronger on small trees than in larger trees. Yet, to better understand the relationships between bamboo dominance and forests attributes, we need to disentangle the forest communities in its underlying vertical strata, and such a size-dependent approach is needed if we better want to understand the impacts of bamboo species in tropical forests.

Considering *Merostachys sp.* (Figure 1) as an overdominant species in the studied tropical forest community, the aim of this study was to evaluate the relationships between bamboo dominance and the resident native tree species, including the underlying different diameter classes which species belongs. Considering that the *niche-filling hypothesis* may be the stronger driver of local patterns of diversity, we addressed the two following questions: (1) How the invasive bamboo species is related to the tree community structural (e. g. species richness, basal area, species density) and diversity metrics? We hypothesize that plots with high bamboo dominance have lower tree density, but higher species richness, functional and phylogenetic diversity, since high dissimilarity between species could lead to empty gaps within the phylogenetic and functional space of a community. Moreover,

species dominance will change from conservative to acquisitive traits (e.g., species with lower wood density, higher specific leaf area, abiotic dispersal syndrome, deciduousness and with smaller seed size) with increasing bamboo dominance. 2) Do the relationships between bamboo dominance and the resident tree species differ between size (diameter) classes? We hypothesized that the relationship of bamboo (rarely higher than 8 m) and the native tree community is size-dependent, being stronger for the small trees than larger trees.



Figure 1: Clumps of the bamboo species Merostachys sp.

#### **METHODS**

#### Study area and vegetation sampling

This study was conducted in a secondary semideciduous tropical forest (21°33'9.94"S, 43°15'10.09"O; 80 ha) located in the experimental field of Embrapa Gado de Leite, southeastern region of the state of Minas Gerais, Brazil (Figure 2). The predominant climate of the region is characterized by hot and rainy summers (October to March) and cold and dry winters (April to September). Mean annual rainfall is 1501 mm (290 mm in the wettest month and 19 mm in driest month), and the mean annual temperature is 21.9 °C (Oliveira-Filho 2017). The predominant soil type is classified as red-yellow latosol (Paciullo *et al.* 2008). The study area has a historical of selective logging, where the main species extracted were *Apuleia leiocarpa*, *Ocotea* sp. and *Plathymenia* sp. No extraction of wood has been made in the last 50 years.



**Figure 2:** Study area located in the experimental field of Embrapa Gado de Leite, southeastern region of the state of Minas Gerais, Brazil.

We established 30 permanent sample plots  $(20 \times 10 \text{ m})$  in the forest, totaling 0.6 ha. All living and standing dead trees with diameter at breast height (DBH)  $\geq$  5 cm (DBH, measured at 1.3 m from the ground or above the buttresses) were tagged, identified to species level and their DBH and height were measured. The samples of botanical material were collected and identified by specialists and through herbarium consultation. The species classification followed the APG IV system (2016).

#### Bamboo dominance estimation and tree community metrics

To quantify the bamboo dominance, we identify all the clumps inside the sample plots and we measure the diameter at the ground level of each clump to calculate the basal area of bamboo (BA). We used the basal area (BA) because this parameter may reflect the real size of the clumps, also considering the space between the culms, which arboreal individuals usually are not able to occupy.

To evaluate how the relationships between bamboo dominance and the overall vegetation metrics are related to the community underlying diameter classes, we split the community data into three diameter: small trees (DHB  $\leq$  10 cm), medium trees (10 cm < DBH < 20 cm), and large trees (DBH > 20 cm). All vegetation metrics

explained below were calculated for the overall community (i.e. all resident trees) and for the three diameter classes separately. Per plot for the overall community and for each diameter class (trees with DBH  $\leq$  10 cm, DBH between 10 and 20 cm, and DBH > 20 cm), we described structural metrics as tree density (number of individuals), stand basal area of trees (m<sup>2</sup>) and basal area of dead trees (m<sup>2</sup>). We described the floristic diversity using the species richness and Shannon diversity index (H<sup>2</sup>).

#### Functional traits

We collected functional traits that are important for forest succession and competition, once bamboo invasion influences the forest establishment and compete with trees for space and resource. We sampled/compiled four vegetative traits (wood density, leaf specific area, species maximum stem diameter and deciduousness), and two reproductive traits (dispersal syndrome and seed size) (Table S1). Wood density, leaf specific area and maximum diameter were collected from species comprising at least 80% of all individuals and basal area sampled, following the methodology proposed by Perez-Harguindeguy et al. (2013). We collected traits for five individuals of each selected species. Wood density is an important functional trait related to the stability, defense, architecture, hydraulics, carbon accumulation, and growth potential of plants (Chave et al. 2009; Perez-Harguindeguy et al. 2013). Low wood density is related to fast growth and high hydraulic capacities, while a high wood density indicates slow growth, but high survival investments (Chave et al. 2009). Wood density was determined using the water-displacement method, and calculated by the ratio of dry mass of wood (g) and sample volume (cm<sup>3</sup>). Specific leaf area is positively correlated with photosynthetic rate and leaf nitrogen concentration, and negatively with leaf longevity and carbon investment in quantitatively important secondary compounds (Perez-Harguindeguy et al. 2013). To calculate the specific leaf area (SLA) we selected 10 leafs for individual, obtaining the ratio of the leaf area (mm<sup>2</sup>, obtained with the ImageJ program after leaf scanning) and leaf dry mass (mg). Maximum diameter plays a structural and architectural role within communities; large sizes may realize faster growth rates (Hérault et al. 2011). The maximum diameter of the species (cm) was obtained by the 95th percentile of all the diameters of the individuals of the species sampled. Deciduousness is a trait that confers drought avoidance (Borchert 1994), and is also related to the species growth length period (Poorter & Markesteijn 2008). We classified the deciduousness of species evergreen or deciduous. Dispersal syndrome is an indicator of the distance that propagules can cover, the routes it can travel and its final destination, this trait can also be important to understand the

species separation in space and reduction on competitive exclusion (Seidler & Plotkin 2006; Perez-Harguindeguy *et al.* 2013). The dispersal syndrome was divided in biotic (zoochory) and abiotic (anemochory, barochory) categories. Seed size is an indicator of seeding survivor and trade-offs that affect forest performance; small seeds are related to colonization ability whereas fewer larger seeds enable survival under a variety of hazards (Westoby *et al.* 2002, Muller-Landau 2010; Wright *et al.* 2010). We classified the seed of the species into smaller, medium and large size. The information about dispersal syndrome, deciduousness and seed size was compiled by consulting the literature (Borges & De Assis 2014; Pyles *et al.* 2018).

#### Functional dominance and diversity

We used the species that comprised at least 80% of all individuals to calculate functional dominance and diversity. The functional dominance was calculated by the community-weighted mean (CWM) for each plot. The CWM was calculated for each trait, using the relative abundance of the species as weighting factor. We used species abundance rather than species basal area to equally weight small trees and big trees. Functional diversity was evaluated using functional richness (Fric) and functional dispersion (Fdis) indices, and was calculated for each plot (Villéger *et al.* 2008). Functional richness (Fric) represents the multivariate range of traits that is filled by the community and considers only species presence/absence data and their respective traits values; and the functional dispersion (Fdis) indicates how the relative abundance of the species is distributed in the multivariate space covered by the functional traits (Laliberté & Legendre 2010). The CWM values and the functional diversity indices were calculated using the "FD" package in the R (Laliberté *et al.* 2014).

#### Taxonomic diversity and average taxonomic distinctness

To evaluate the phylogenetic relatedness between the sampled species, we created a taxonomic matrix, classifying all the species identified from genus to class level (Table S2), and we calculated the taxonomic diversity (delta and delta\*) and the average taxonomic distinctness (delta+ or AvTD, Clarke & Warwick 1998, 2001) for each plot. These indices combine species richness and taxonomic structure to estimate the community phylogenetic diversity (Leira *et al.* 2009; Gwali *et al.* 2010). The taxonomic diversity and distinctness equations were calculated using trees abundance data, and the average taxonomic distinctness were based on presence/absence data (less sensitive to dominant species) and it is calculated as the sum of all branch lengths connecting two species averaged across all species, thus representing the

mean distance between two randomly chosen species (Warwick & Clarke 1995; Gallardo *et al.* 2011). High values of these indices indicate that species in a plot are more distinct phylogenetically (i.e., a plot with one species of Myrtaceae and one of Lauraceae have higher AvTD than a plot with one species of Myrtaceae and one of Asteraceae, see APG IV (2016). The taxonomic diversity and the average taxonomic distinctness index were calculated using the "Vegan" package in the R (Oksanen *et al.* 2010).

#### Statistical analysis

All the parameters compiled for the community were evaluated in relation to bamboo dominance using mixed linear models. We used bamboo basal area as fixed factor and all the parameters as response variables. Before analysis, we transformed data using log10 or square root when necessary, in order to find the assumptions of normality and homoscedasticity.

To test the spatial autocorrelation of the samples, when our variables are not independent, we used a Moran's I test. A p-value <0.05 indicates that the model residuals show spatial autocorrelation. When we found spatial correlation in our linear mixed model residuals, we used simultaneous autoregressive (SAR) models (Kissling & Carl 2008), based on the geographical coordinates of the plots. In SAR models, we need to define a minimum-weighted neighborhood structure to fit the spatial structure of the models residuals (Raymundo *et al.* 2019). We used a neighborhood distance of 10 meters because our plots are very close and it seems the smallest distance between two plots.

All analyses were performed using the software R (R-Core-Team, 2015) and the following packages: lme4 (Bates *et al.* 2014), lmerTest (Kuznetsova *et al.* 2016), MuMIn (Barton 2016), spdep (Bivand *et al.* 2005), ncf (Van Etten 2017), nlme (Pinheiro *et al.* 2014) and gstat (Pebesma 2004)

#### RESULTS

We sampled a total of 763 individuals, belonging to 101 species, 64 genus and 34 families (**Table S3**). The most abundant species were *Siparuna guianensis* Aubl., *Mabea fistulifera* Mart. and *Brosimum guianense* (Aubl.) Huber. We found a total basal area of 7.57 m<sup>2</sup> for bamboo and 16.45 m<sup>2</sup> for the live standing trees.

For the overall community metrics, we found that bamboo basal area was significantly negative related to tree density and CWM wood density, and positively related to basal area of dead trees, functional dispersion and taxonomic diversity (Table 1; Figure 3). These results indicates that the dominance of bamboo is higher when plots have less trees and more dead trees, when dominant species have lower wood density, and when resident species are more diverse functionally and phylogenetically. We found no relationships between bamboo basal area and community stand basal area, species richness and diversity (H'), CWM<sub>SLA</sub>, CWM<sub>Dmax</sub>, CWM<sub>Dec</sub>, CWM <sub>DS</sub>, CWM <sub>SS</sub> and functional richness, taxonomic diversity (Table 1).

When considering the three diameter classes separately (trees with DBH  $\leq 10$  cm, DBH between 10 and 20 cm, and DBH > 20 cm), we found significant relationships between bamboo basal area and the evaluated community metrics for the first diameter class (DBH  $\leq 10$  cm), and the results become non-significant for the medium and larger diameter classes (Table 1; Figure 4). Considering the first diameter class, bamboo basal area was significantly negatively related to tree density and CWM<sub>WD</sub>, and positively related to CWM<sub>SLA</sub>, functional dispersion, taxonomic diversity and taxonomic relatedness (Table 1). These results indicate that the relationships between bamboo basal area and the overall community metrics are size-dependent, and are more markedly for the small trees.



**Figure 3:** Bivariate relationships between bamboo basal area and number of trees (A), basal area of dead trees (B), functional diversity (FDis; C), community - weighted mean of wood density (CWM WD; D), and the average taxonomic distinctness (Delta<sup>+</sup>; E) for the overall community. Continuous lines represent significant relationships, and blue areas represent the 95% confidence intervals.



**Figure 4:** Bivariate relationships between community - weighted mean of wood density (CWM WD; A), community - weighted mean of specific leaf area (CWM SLA; B), taxonomic diversity (Delta; C), and the average taxonomic distinctness (Delta<sup>+</sup>; D) for the first diameter class (DBH  $\leq$  10 cm). Continuous lines represent significant relationships, and blue areas represent the 95% confidence intervals.

**Table 1:** Results of the mixed linear models between bamboo basal area and all the parameters analysed for the overall community, small trees (DHB  $\leq$  10 cm), medium trees (10 cm < DBH < 20 cm), and large trees (DBH > 20 cm). CWM WD (community weithghed mean of wood density), CWM SLA (community weithghed mean specific leaf area), CWM Dmax (community weithghed mean of maximum diameter), CWM AD (community weithghed mean of abiotic dispersion), CWM BD (community weithghed mean of biotic dispersion), CWM SS (community weithghed mean of small seeds), CWM MS (community weithghed mean of medium seeds), CWM LS (community weithghed mean of large seeds), CWM Dec (community weithghed mean of deciduous species), Fdis (functional dispersion), Delta and Delta\* (taxonomic diversity) and Delta+ (average taxonomic distinctness). BA dead trees 31.4973 0.1982 1.3550 0.0056

Parameter	Intercept	<b>R</b> <sup>2</sup>	β	p-value
Overall communiy				
Individuals number	50.7988	0.2036	-1.1229	*0.003
<b>BA dead trees</b> Species richness (S)	31.4973 41.6851	0.1982 0.0755	1.3550 -1.0495	*0.005 0.1084
Diversity (H')	46.9599	0.0265	-8.4100	0.355
CWM WD	180.3410	0.2168	-324.9600	*0.003
CWM SLA	-47.3854	0.0845	4.4771	0.095
CWM Dmax	-6.8160	0.0707	1.2171	0.130
CWM AD	25.8084	0.0012	-3.7771	0.883
CWM BD	22.0313	0.0012	3.7771	0.883
CWM SS	38.3889	0.0531	-35.2836	0.164
CWM MS	25.2638	0.0005	-0.0010	1.000
CWM LS	19.3775	0.1154	79.6825	0.061
CWM Dec	24.5060	0.0010	1.9596	0.899
CWM Eve	26.4656	0.0010	-1.9596	0.899
Fric	23.9785	0.0017	2.7604	0.850
Fdis	4.6202	0.1582	5.6755	*0.017
Delta	-87.3068	0.0898	1.3968	0.075
Delta*	-88.7496	0.0692	1.3416	0.134
Delta+	-131.8630	0.1766	1.8697	*0.009
$DBH \le 10$				
Individuals number	35.1635	0.0948	-0.9473	0.065
Species richenss (S)	35.1595	0.0541	-1.1910	0.173

Diversity (H')	37.6072	0.0177	-6.1894	0.4440	
CWM WD	116.3370	0.2606	-183.2790	*0.0011	
CWM SLA	-27.8444	0.1083	3.2844	*0.0535	
CWM Dmax	25.6070	0.0005	-0.0146	0.9771	
CWM AD	25.6488	0.0016	-2.4601	0.8579	
CWM BD	23.1887	0.0016	2.4601	0.8579	
CWM SS	33.2026	0.0698	-18.3543	0.1017	
CWM MS	19.9011	0.0279	10.7499	0.3144	
CWM LS	23.6364	0.0290 24.0786		0.3484	
CWM Dec	26.0013	0.0015	-2.3594	0.8621	
CWM Eve	23.6419	0.0015	2.3594	0.8621	
Fric	24.4723	0.0025	3.2690	0.8051	
Fdis	21.2985	0.0160	1.3550	0.4837	
Delta	-32.7904	0.1302	0.7302	*0.0343	
Delta*	-19.9554	0.0816	0.5395	0.0998	
Delta+	-34.2136	0.1254	0.7183	*0.0357	
10 cm < DBH < 20 cm					
Individuals number	30.9607	0.0338	-0.7528	0.3092	
Species richenss (S)	31.4973	0.0345	-0.9740	0.3035	
Diversity (H')	41.2994	0.0891	-9.2781	0.0876	
CWM WD	55.3910	0.0438	-64.3760	0.2348	
CWM SLA	-17.1900	0.0903	2.6755	0.0847	
CWM Dmax	-16.0267	0.2305	1.6938	0.0965	
CWM AD	26.2583	0.0081	-7.8455	0.6294	
CWM BD	18.4128	0.0081	7.8455	0.6294	
CWM SS	29.1386	0.0277	-9.1570	0.3596	
CWM MS	19.8614	0.0402	10.2878	0.2588	
CWM LS	25.9825	0.0127	-13.8353	0.5105	
CWM Dec	19.1324	0.0766	15.0048	0.1156	
CWM Eve	34.1372	0.0766	-15.0048	0.1156	
Fric	18.9394	0.0081	8.8535	0.8204	
Fdis	13.6382	0.1270	4.1551	*0.0220	
Delta	62.9713	0.0750	-0.4552	0.0911	
Delta*	63.1266	0.0467			
Delta+	48.3451	0.0194	-0.2674	0.4350	
$DBH > 20 \ cm$					
Individuals number	29.8515	0.0267	-1.0369	0.3658	
Species richenss (S)	29.5281	0.0274	-1.1597	0.3535	
Diversity (H')	28.3697	0.0130	-2.8736	0.5227	
CWM WD	30.2680	0.0022	-12.2980	0.8034	
CWM SLA	13.1287	0.0075	0.6761	0.6249	

CWM Dmax	18.2254	0.0050	0.1920	0.7016
CWM AD	29.4356	0.0790	-29.1805	0.0849
CWM BD	0.2551	0.0790	29.1805	0.0749
CWM SS	24.1917	0.0020	3.0308	0.8122
CWM MS	29.4838	0.0143	-6.4875	0.5061
CWM LS	23.6553	0.0221	14.1532	0.4113
CWM Dec	25.9034	0.0024	-1.9309	0.8003
CWM Eve	23.9725	0.0024	1.9309	0.8003
Fric	27.4350	0.0022	12.4680	0.8034
Fdis	26.1136	0.0033	-0.5053	0.7383
Delta	30.5964	0.0071	-0.0710	0.6414
Delta*	37.6691	0.0182	-0.1518	0.4558
Delta+	40.3433	0.0242	-0.1841	0.3804
Those is a significantly	valationahim at m	~ ^ ^ 5		

There is a significantly relationship at p < 0.05

#### DISCUSSION

We evaluated the relationships between bamboo basal area and structural, taxonomic and functional diversity metrics in a tropical forest community, and how these relationships change among the underlying diameter classes of the community. We found that plots with higher bamboo dominance have lower tree density and higher basal area of dead trees, whereas those plots have higher functional and taxonomic diversity. In addition, we found that bamboo dominance was positively related to high dominance of acquisitive traits species (lower wood density and higher specific leaf area), and that those relationships were stronger for small trees than larger trees.

#### Relationships between bamboo basal area and the resident species

We hypothesize that bamboo dominance would be negatively related to structural forests attributes, considering that *Merostachys sp.* has been related as a potential invasive native species. We indeed found lower tree density and higher basal area of dead trees in plots with higher dominance of bamboo. These results could be related to the competition for space and resources. Although this pattern is commonly found in natural forests (i.e., if a given species is abundant in a plot, that the rest of the species are less abundant) (Magurran 1988), we do not found the same results when considering the relationships between other two most abundant species (*Siparuna guianensis* and *Mabea fistulifera*) and the other resident species. These results highlight that bamboo competition is by far stronger than its ability to facilitate most of other resident species in our study area.

Our results differ from others studies involving different species and life forms at different scales, where invasion generally decreases species richness and diversity (Griscom 2007; Gaertner *et al.* 2009; Hedja 2009). However, Hedja *et al.* (2009, 2017) and Gaertner *et al.* (2009) found that some invaded species exhibit low impact on species richness and diversity, and invader species identity is also an important characteristic to consider, once some types of growth form have advantages related to the potential of invasion compared to others (Gaertner *et al.* 2009). The significant negative relationship between the number of trees and not on species richness may be related to the capacity of higher bamboo dominance to reduce the density of individuals within plots, but not be capable to eliminate the species from the sample unit (Hedja 2013). Besides that, bamboo dominance can eliminate or promote the occurrence of some species, qualitatively altering species composition (Hedja 2013).

We hypothesize that bamboo dominance would be positively related to species, functional and phylogenetic diversity, considering that the niche-filling hypothesis plays an important role in invaded communities at local scale. We indeed found that plots with more bamboo basal area are functionally and phylogenetically more diverse than plots with lower bamboo basal area, though not relationships were found for species richness or diversity. Environmental filters are generally weaker in local communities assembly, thus it is believed that less related species are able to coexist due to niche difference than closely related species (Godoy et al. 2014; Loiola et al. 2018). Studies indicate that taxonomically and functionally closer species compete more intensely than more distant species, limiting their capacity to exist (Webb et al. 2002; Cahill et al. 2008; Cavender-Bares et al. 2009). Therefore, plots with higher bamboo basal area have less closely related species, so competitive exclusion may be playing a local structural role (Mayfield & Levine 2010). Furthermore, at small scales, the higher FD and AvTD values found in plots with higher bamboo basal area can be due to two different coexistence mechanisms, with the invader filling niche gaps or excluding resident species (Loiola et al. 2018). It is also possible to infer that the invader species contribute to create such a gap in the invaded communities, increasing phylogenetic and functional dissimilarity of native plant communities by replacing some specific native species. Based on our analyses, we cannot conclude whether such increase in dissimilarity between resident species is the cause or consequence of invasion. Future studies are necessary in order to evaluate the invader species traits and their relationships with the resident tree species in the community.

Higher bamboo dominance in plots dominated by species with acquisitive trait values Considering that high disturbance intensities shifts the CWM trait values from conservative to acquisitive traits in forests (Van der Sande *et al.* 2016; Lodge *et al.* 2018), we expected that plots with higher dominance of bamboo would increase density of species with higher specific leaf area, abiotic dispersion, deciduousness, and lower seed mass, wood density and maximum stem diameter. We indeed found that plots with higher bamboo dominance show lower values of CWM<sub>WD</sub> and higher CWM<sub>SLA</sub> (for small trees only). Invasive plants usually have acquisitive traits (Reich 2014), which allow them to take advantage in disturbed environments, occupying gaps and forest edges. Bamboo species, when under disturbed environments, usually become super-dominant, competing for light with species that possess acquisitive traits, growing rapidly and occupying the niche more efficiently than resident species (Richardson & Pysek 2006). A hypothesis to consider is that lower CWM<sub>WD</sub> values in plots with more bamboo basal area may be related to the need for resident species to coexist with the invasive species. Thus, resident species should invest more in growth to overcome the bamboo height barrier (rarely higher than 8 m), where light would no longer be a limiting factor. Species with low wood density and high specific leaf areas have typically high growth rates, and can quickly surpass bamboo clumps, reaching higher light conditions, and hence, increasing their abundance compared to the species with conservative traits (Raymundo *et al.* 2018). Another plausible explanation is that species having higher values of CWM<sub>WD</sub> and lower values of CWM<sub>SLA</sub> generally are those that are able to live under shaded conditions. Due to a relatively slow growth and under bamboo competition, those species may be not able to survive from bamboo-mass loading (Griscom *et al.* 2007). In these circumstances, having low values o WD and SLA would be a more efficient strategy.

The impacts of bamboo in increasing the abundance of species with low WD and high SLA may have multiple effects on forests productivity. For example, these species have inherent short lifespan and can lead to high biomass mortality and lower standing biomass stocks, reducing forests carbon stocks over time (Fukushima *et al.* 2015).

#### The size-dependent relationships between bamboo and forests communities

We hypothesized that the relationships between bamboo (rarely higher than 8 m) and the native community is size-dependent, being stronger for the small trees than larger trees. We indeed found that the relationships between bamboo and the overall community were stronger in the smallest diameter class and become non-significant for larger trees. It could be inferred once the light competition between bamboo and resident individuals probably would be high, reducing the density of tree within these diameter classes (Tabarelli & Montavani 2000; Guilherme *et al* 2004). Furthermore, we must highlight that the small trees in the first diameter class include not only the understory species, but also the young canopy trees. These results suggest that the relationships between bamboo and forests can lead to stronger and significant changes at longer timescales, even for the canopy composition, and that the impacts of bamboo are lasting and may become stronger over time.

#### **CONCLUDING REMARKS**

Our study can be summarized in three main results. First, dominance of the native bamboo species Merostachys sp. does not have significant relationships with species richness and diversity. However, higher bamboo dominance decreases the density of trees within plots, and increases functional and taxonomic diversity, considering that the niche-filling hypothesis plays an important role in invaded communities at local scale. Second, bamboo dominance only has significant relationship between wood density (CWM<sub>WD</sub>) and specific leaf area (CWM<sub>SLA</sub>), showing that the CWM trait values shift from conservative to acquisitive traits in plots with more bamboo basal area, Third, the relationships between bamboo population and the native trees community is size-dependent, being much stronger for the small trees than for medium and larger trees, due to competition habilities. Even though we have found strong evidence of the effects of the bamboo overdominance, we cannot affirm that those changes within community were the cause or consequence of invasion. In overall, this study was import to highlight the native bamboo interactions with forest parameter, also bringing new contributions for local invasion studies.

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# SUPPLEMENTARY MATERIAL

Table S1: Metrics of the 39 tree species included in the functional analysis.Table S2: Overview of the 91 tree species used in the taxonomic analyses.Table S3: Overview of the forest inventory parameters of 101 species.

**Table S1:** Metrics of the 39 tree species included in the functional analysis. Scientific name, wood density (WD, g.cm-3), specific leaf area (SLA), maximum diameter (Dmax), dispersion syndrome (DS; A= abiotic; B=biotic), seed size (SS; S=small; M=medium; L=large), and deciduousness (Dec; D=deciduous; E=evergreen) are given.

Species	WD	SLA	Dmax	DM	SS	Dec
Abarema cochliacarpos (Gomes) Barneby & J.W.Grimes	0.494	17.227	13.019	А	М	D
Amaioua intermedia Mart. ex Schult. & Schult.f.	0.536	16.959	19.487	В	S	E
Aniba firmula (Nees & Mart.) Mez	0.388	18.167	47.555	В	М	Е
Annona mucosa Jacq.	0.387	13.956	22.059	В	М	D
Aparisthmium cordatum (A.Juss.) Baill.	0.484	18.131	14.897	В	S	D
Apuleia leiocarpa (Vogel) J.F.Macbr.	0.610	12.402	37.059	А	S	D
Bathysa australis (A.StHil.) K.Schum.	0.414	20.891	12.693	А	S	Е
Brosimum guianense (Aubl.) Huber	0.504	15.949	20.690	В	М	E
Byrsonima ligustrifolia A.Juss.	0.467	15.724	39.630	В	М	D
Casearia sylvestris Sw.	0.505	20.990	19.130	В	S	E
Ecclinusa ramiflora Mart.	0.455	10.657	40.839	В	М	E
Eugenia florida DC.	0.648	14.026	15.557	В	М	E
Helicostylis tomentosa (Poepp. & Endl.) Rusby	0.378	12.934	18.605	В	S	Е
Himatanthus bracteatus (A. DC.) Woodson	0.367	15.379	16.409	А	L	D
Hortia brasiliana Vand. ex DC.	0.483	13.809	19.767	В	М	Е
Hymenolobium janeirense Kuhlm.	0.576	24.357	28.115	А	S	Е
Lacistema pubescens Mart.	0.480	25.916	42.550	В	М	Е
Licania kunthiana Hook.f.	0.689	17.058	29.603	В	М	Е
Mabea fistulifera Mart.	0.360	19.227	32.595	В	М	D
Matayba marginata Radlk.	0.602	12.155	14.332	В	М	Е
Melanoxylon brauna Schott	0.605	18.934	30.717	А	М	Е
Myrceugenia campestris (DC.) D.Legrand & Kausel	0.603	16.011	13.584	В	М	E
Myrcia anceps (Spreng.) O.Berg	0.538	12.179	16.425	В	S	E
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Myrcia splendens (Sw.) DC.	0.580	14.244	16.767	В	S	Е
Naucleopsis oblongifolia (Kuhlm.) Carauta	0.504	13.235	24.955	В	L	E
Nectandra oppositifolia Nees	0.432	12.142	19.006	В	Μ	Е
Ocotea odorifera (Vell.) Rohwer	0.563	12.739	24.949	В	М	Е
Ocotea sp.	0.429	12.078	20.690	В	М	Е
Pourouma guianensis Aubl.	0.320	12.173	19.568	В	Μ	Е
Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima	0.523	12.223	60.479	А	L	E
Siparuna guianensis Aubl.	0.444	19.001	22.138	В	S	D
Sloanea guianensis (Aubl.) Benth.	0.484	15.291	29.030	В	Μ	Е
Sorocea bonplandii (Baill.) W.C.Burger et al.	0.491	13.170	11.580	В	Μ	Е
Tachigali rugosa (Mart. ex Benth.) Zarucchi & Pipoly	0.599	10.550	36.049	А	Μ	Е
Tapirira guianensis Aubl.	0.437	11.916	40.680	В	Μ	Е
Trichilia emarginata (Turcz.) C.DC.	0.565	19.137	38.611	В	М	E
Virola bicuhyba (Schott ex Spreng.) Warb.	0.323	15.108	20.332	В	L	E
Xylopia brasiliensis Spreng.	0.528	19.821	35.587	В	S	E
Xylopia sericea A.StHil.	0.421	11.784	18.904	В	S	E

Table S2: Overview of the 91 tree species used in the taxonomic analyses. Scientific name, genus, family, order, superorder, subclass and class are given.

Species	Genus	Family	Order	Superorder	Subclass	Class
<i>Abarema cochliacarpos</i> (Gomes) Barneby & J.W.Grimes	Abarema	Fabaceae	Fabales	Rosanae	Magnoliidae	Equisetopsida
Amaioua intermedia Mart. ex Schult. & Schult.f.	Amaioua	Rubiaceae	Gentianales	Asteranae	Magnoliidae	Equisetopsida
Amaioua sp.	Amaioua	Rubiaceae	Gentianales	Asteranae	Magnoliidae	Equisetopsida
Aniba firmula (Nees & Mart.) Mez	Aniba	Lauraceae	Laurales	Magnolianae	Magnoliidae	Equisetopsida
Annona mucosa Jacq.	Annona	Annonaceae	Magnoliales	Magnolianae	Magnoliidae	Equisetopsida
Aparisthmium cordatum (A.Juss.) Baill.	Aparisthmium	Euphorbiaceae	Malpighiales	Rosanae	Magnoliidae	Equisetopsida
Apuleia leiocarpa (Vogel) J.F.Macbr.	Apuleia	Fabaceae	Fabales	Rosanae	Magnoliidae	Equisetopsida
Aspidosperma parvifolium A.DC.	Aspidosperma	Apocynaceae	Gentianales	Asteranae	Magnoliidae	Equisetopsida
Aspidosperma ramiflorum Müll.Arg.	Aspidosperma	Apocynaceae	Gentianales	Asteranae	Magnoliidae	Equisetopsida
Bathysa australis (A.StHil.) K.Schum.	Bathysa	Rubiaceae	Gentianales	Asteranae	Magnoliidae	Equisetopsida
Bathysa mendoncaei K.Schum.	Bathysa	Rubiaceae	Gentianales	Asteranae	Magnoliidae	Equisetopsida
Brosimum guianense (Aubl.) Huber	Brosimum	Moraceae	Rosales	Rosanae	Magnoliidae	Equisetopsida
Byrsonima ligustrifolia A.Juss.	Byrsonima	Malpighiaceae	Malpighiales	Rosanae	Magnoliidae	Equisetopsida
Campomanesia sp.	Campomanesia	Myrtaceae	Myrtales	Rosanae	Magnoliidae	Equisetopsida
Caryocar edule Casar.	Caryocar	Caryocaraceae	Malpighiales	Rosanae	Magnoliidae	Equisetopsida

Casearia decandra Jacq. Casearia sylvestris Sw. Copaifera langsdorffii Desf. *Cordia superba* Cham. Dalbergia nigra (Vell.) Allemão ex Benth. Ecclinusa ramiflora Mart. Endlicheria sp. Ervthroxylum sp. Eugenia florida DC. *Eugenia moraviana* O.Berg Eugenia spl. Eugenia sp2. Eugenia sp3. Garcinia gardneriana (Planch. & Triana) Zappi Guatteria sellowiana Schltdl. Handroanthus heptaphyllus (Vell.) Mattos Helicostylis tomentosa (Poepp. & Endl.) Rusby Himatanthus bracteatus (A. DC.) Woodson Hirtella hebeclada Moric. ex DC.

Casearia Casearia Copaifera Cordia Dalbergia Ecclinusa Endlicheria Erythroxylum Eugenia Eugenia Eugenia Eugenia Eugenia Garcinia Guatteria Handroanthus Helicostylis Himatanthus Hirtella

Salicaceae Salicaceae Fabaceae Boraginaceae Fabaceae Sapotaceae Lauraceae Erythroxylaceae Myrtaceae **M**vrtaceae Myrtaceae Myrtaceae Myrtaceae Clusiaceae Annonaceae Bignoniaceae Moraceae Apocynaceae Chrysobalanaceae

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Magnoliidae Equisetopsida Equisetopsida Magnoliidae Magnoliidae Equisetopsida Magnoliidae Equisetopsida

Hirtella sp.
Hortia brasiliana Vand. ex DC.
Hymenolobium janeirense Kuhlm.
Inga cylindrica (Vell.) Mart.
Inga sp1.
Inga sp2.
Jacaranda micrantha Cham.
Lacistema pubescens Mart.
Lauraceae sp.
Licania kunthiana Hook.f.
Licania nitida Hook.f.
Mabea fistulifera Mart.
Maprounea guianensis Aubl.
Matayba marginata Radlk.
Matayba sp.
Maytenus gonoclada Mart.
Melanoxylon brauna Schott
Miconia cinnamomifolia (DC.) Naudin
Miconia sp.

Hirtella Hortia Hymenolobium Inga Inga Inga Jacaranda Lacistema Lauraceae Licania Licania Mabea Maprounea Matayba Matayba Maytenus Melanoxylon Miconia Miconia

Chrysobalanaceae Malpighiales Rosanae Rutaceae Sapindales Rosanae Fabaceae Fabales Rosanae Fabaceae Fabales Rosanae Fabaceae Fabales Rosanae Fabaceae Fabales Rosanae Bignoniaceae Lamiales Asteranae Rosanae Lacistemataceae Malpighiales Lauraceae Laurales Magnolianae Chrysobalanaceae Malpighiales Rosanae Chrysobalanaceae Malpighiales Rosanae Euphorbiaceae Malpighiales Rosanae Euphorbiaceae Malpighiales Rosanae Sapindaceae Sapindales Rosanae Sapindaceae Sapindales Rosanae Celastraceae Celastrales Rosanae Fabaceae Fabales Rosanae Melastomataceae Myrtales Rosanae Melastomataceae **Myrtales** Rosanae

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Myrceugenia campestris (DC.) D.Legrand & Kausel Myrcia anceps (Spreng.) O.Berg Myrcia splendens (Sw.) DC. Myrtaceae sp1. Myrtaceae sp2. Naucleopsis oblongifolia (Kuhlm.) Carauta Nectandra oppositifolia Nees Ocotea odorifera (Vell.) Rohwer Ocotea spl. Parinari brasiliensis (Schott) Hook.f. Pera glabrata (Schott) Baill. Pourouma guianensis Aubl. Pouteria caimito (Ruiz & Pav.) Radlk. Pouteria sp. Pouteria torta (Mart.) Radlk. Protium sp. Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima Quiina glaziovii Engl. Rubiaceae sp.

Myrceugenia Myrcia Myrcia Mvrtaceae Myrtaceae Naucleopsis Nectandra Ocotea Ocotea Parinari Pera Pourouma Pouteria Pouteria Pouteria Protium Pseudopiptadenia Fabaceae Ouina Rubiaceae

**M**vrtaceae Myrtaceae Myrtaceae **Mvrtaceae** Myrtaceae Moraceae Lauraceae Lauraceae Lauraceae Chrysobalanaceae Euphorbiaceae Urticaceae Sapotaceae Sapotaceae Sapotaceae Burseraceae Ouiinaceae Rubiaceae

**M**vrtales Rosanae Myrtales Rosanae Myrtales Rosanae Myrtales Rosanae Myrtales Rosanae Rosales Rosanae Laurales Magnolianae Magnolianae Laurales Laurales Magnolianae Malpighiales Rosanae Malpighiales Rosanae Rosales Rosanae Ericales Asteranae Ericales Asteranae Ericales Asteranae Sapindales Rosanae Fabales Rosanae Malpighiales Rosanae Gentianales Asteranae

Magnoliidae Equisetopsida Magnoliidae Equisetopsida Magnoliidae Equisetopsida Magnoliidae Equisetopsida Equisetopsida Magnoliidae Magnoliidae Equisetopsida Magnoliidae Equisetopsida

Sapotaceae sp.	Sapotaceae	Sapotaceae
Schefflera morototoni (Aubl.) Maguire et al.	Schefflera	Araliaceae
Siparuna guianensis Aubl.	Siparuna	Siparunaceae
Sloanea guianensis (Aubl.) Benth.	Sloanea	Elaeocarpaceae
Sloanea sp1.	Sloanea	Elaeocarpaceae
Sorocea bonplandii (Baill.) W.C.Burger et al.	Sorocea	Moraceae
Tachigali rugosa (Mart. ex Benth.) Zarucchi & Pipoly	Tachigali	Fabaceae
Tapirira guianensis Aubl.	Tapirira	Anacardiaceae
Terminalia fagifolia Mart.	Terminalia	Combretaceae
Tovomita sp.	Tovomita	Clusiaceae
Triatinichia sp.	Trattinnickia	Burseraceae
Trichilia emarginata (Turcz.) C.DC.	Trichilia	Meliaceae
Virola bicuhyba (Schott ex Spreng.) Warb.	Virola	Myristicaceae
Virola sp.	Virola	Myristicaceae
Vismia guianensis (Aubl.) Choisy	Vismia	Hypericaceae
Vochysia laurifolia Warm.	Vochysia	Vochysiaceae
Xylopia brasiliensis Spreng.	Xylopia	Annonaceae
Xylopia sericea A.StHil.	Xylopia	Annonaceae

Ericales Magnoliidae Equisetopsida Asteranae Apiales Magnoliidae Equisetopsida Asteranae Laurales Magnoliidae Equisetopsida Magnolianae Oxalidales Rosanae Magnoliidae Equisetopsida Oxalidales Magnoliidae Equisetopsida Rosanae Rosales Rosanae Magnoliidae Equisetopsida Fabales Rosanae Magnoliidae Equisetopsida Sapindales Magnoliidae Equisetopsida Rosanae Myrtales Rosanae Magnoliidae Equisetopsida Magnoliidae Equisetopsida Malpighiales Rosanae Sapindales Magnoliidae Equisetopsida Rosanae Magnoliidae Sapindales Equisetopsida Rosanae Magnoliales Magnolianae Magnoliidae Equisetopsida Magnoliales Magnolianae Magnoliidae Equisetopsida Malpighiales Rosanae Magnoliidae Equisetopsida Myrtales Rosanae Magnoliidae Equisetopsida Magnoliales Magnolianae Magnoliidae Equisetopsida Magnoliales Magnolianae Magnoliidae Equisetopsida

Species	AD	BA	AF	RD	RDo	RF
<i>Abarema cochliacarpos</i> (Gomes) Barneby & J.W.Grimes	9	651.96	9	1.181	0.396	1.557
Amaioua intermedia Mart. ex Schult. & Schult.f.	9	1296.81	6	1.181	0.788	1.038
Amaioua sp.	1	45.84	1	0.131	0.028	0.173
Aniba firmula (Nees & Mart.) Mez	15	7088.54	10	1.969	4.309	1.730
Aniba sp2.	5	824.26	5	0.656	0.501	0.865
Annona mucosa Jacq.	33	4198.31	26	4.331	2.552	4.498
Aparisthmium cordatum (A.Juss.) Baill.	5	467.40	4	0.656	0.284	0.692
Apuleia leiocarpa (Vogel) J.F.Macbr.	22	6811.20	18	2.887	4.140	3.114
Aspidosperma parvifolium A.DC.	1	38.52	1	0.131	0.023	0.173
Aspidosperma ramiflorum Müll.Arg.	4	1413.26	4	0.525	0.859	0.692
Bathysa australis (A.StHil.) K.Schum.	6	323.20	6	0.787	0.196	1.038
Bathysa mendoncaei K.Schum.	1	91.99	1	0.131	0.056	0.173
Brosimum guianense (Aubl.) Huber	41	4592.57	25	5.381	2.792	4.325
Byrsonima ligustrifolia A.Juss.	6	5376.11	6	0.787	3.268	1.038

**Table S3:** Forest inventory parameters of the 101 sampled species. Scientific name, absolute density (AD, 0,6 ha), basal area (BA, m<sup>2</sup>.ha<sup>-1</sup>), absolute frequency (AF), relative density (%), relative dominance (%), and relative frequency (%) are given

Campomanesia sp.	3	107.89	3	0.394	0.066	0.519
Caryocar edule Casar.	1	84.05	1	0.131	0.051	0.173
Casearia decandra Jacq.	3	650.98	3	0.394	0.396	0.519
Casearia sylvestris Sw.	15	1563.60	12	1.969	0.950	2.076
Copaifera langsdorffii Desf.	4	195.72	4	0.525	0.119	0.692
Cordia superba Cham.	1	69.25	1	0.131	0.042	0.173
Dalbergia nigra (Vell.) Allemão ex Benth.	2	99.63	2	0.262	0.061	0.346
Dead trees	78	13011.89	41	10.236	7.909	7.093
Ecclinusa ramiflora Mart.	5	2172.58	4	0.656	1.321	0.692
Endlicheria sp.	1	23.00	1	0.131	0.014	0.173
Erythroxylum sp.	2	48.74	2	0.262	0.030	0.346
Eugenia florida DC.	6	520.24	6	0.787	0.316	1.038
Eugenia moraviana O.Berg	3	205.01	3	0.394	0.125	0.519
Eugenia sp1.	3	564.30	3	0.394	0.343	0.519
Eugenia sp2.	2	95.99	2	0.262	0.058	0.346
Eugenia sp3.	1	35.09	1	0.131	0.021	0.173
Garcinia gardneriana (Planch. & Triana) Zappi	2	139.20	2	0.262	0.085	0.346

Guatteria sellowiana Schltdl.	1	31.83	1	0.131	0.019	0.173
Handroanthus heptaphyllus (Vell.) Mattos	1	91.99	1	0.131	0.056	0.173
Helicostylis tomentosa (Poepp. & Endl.) Rusby	7	961.61	6	0.919	0.585	1.038
Himatanthus bracteatus (A. DC.) Woodson	7	859.74	7	0.919	0.523	1.211
Hirtella hebeclada Moric. ex DC.	1	40.29	1	0.131	0.024	0.173
Hirtella sp.	1	320.88	1	0.131	0.195	0.173
Hortia brasiliana Vand. ex DC.	7	1113.13	7	0.919	0.677	1.211
Hymenolobium janeirense Kuhlm.	8	1449.28	8	1.050	0.881	1.384
Indet sp1	3	2791.90	3	0.394	1.697	0.519
Indet sp2	7	487.23	6	0.919	0.296	1.038
Indet sp3	1	95.27	1	0.131	0.058	0.173
Indet sp4	1	703.15	1	0.131	0.427	0.173
Indet sp5	1	447.62	1	0.131	0.272	0.173
Indet sp6	1	154.06	1	0.131	0.094	0.173
Indet sp7	1	435.77	1	0.131	0.265	0.173
Indet sp8	1	362.57	1	0.131	0.220	0.173
Indet sp9	1	91.99	1	0.131	0.056	0.173

Inga cylindrica (Vell.) Mart.	1	78.80	1	0.131	0.048	0.173
Inga sp1.	3	125.27	3	0.394	0.076	0.519
Inga sp2.	2	284.33	2	0.262	0.173	0.346
Jacaranda micrantha Cham.	7	1298.51	7	0.919	0.789	1.211
Lacistema pubescens Mart.	13	4525.39	11	1.706	2.751	1.903
Lauraceae sp.	1	25.78	1	0.131	0.016	0.173
Licania kunthiana Hook.f.	6	1337.64	6	0.787	0.813	1.038
Licania nitida Hook.f.	1	91.99	1	0.131	0.056	0.173
Mabea fistulifera Mart.	69	28199.74	41	9.055	17.141	7.093
Maprounea guianensis Aubl.	2	711.21	2	0.262	0.432	0.346
Matayba marginata Radlk.	10	773.73	9	1.312	0.470	1.557
Matayba sp.	1	147.14	1	0.131	0.089	0.173
Maytenus gonoclada Mart.	1	223.53	1	0.131	0.136	0.173
Melanoxylon brauna Schott	5	1457.18	5	0.656	0.886	0.865
Miconia cinnamomifolia (DC.) Naudin	1	522.11	1	0.131	0.317	0.173
Miconia sp.	1	51.75	1	0.131	0.031	0.173
Myrceugenia campestris (DC.) D.Legrand & Kausel	12	826.89	10	1.575	0.503	1.730

Myrcia anceps (Spreng.) O.Berg	19	1502.14	12	2.493	0.913	2.076
Myrcia splendens (Sw.) DC.	32	2778.47	21	4.199	1.689	3.633
Myrtaceae sp1.	1	389.93	1	0.131	0.237	0.173
Myrtaceae sp2.	2	150.32	2	0.262	0.091	0.346
Naucleopsis oblongifolia (Kuhlm.) Carauta	17	1949.69	14	2.231	1.185	2.422
Nectandra oppositifolia Nees	4	671.53	4	0.525	0.408	0.692
Ocotea odorifera (Vell.) Rohwer	13	2006.19	10	1.706	1.219	1.730
Ocotea sp.	3	175.50	3	0.394	0.107	0.519
Parinari brasiliensis (Schott) Hook.f.	2	377.69	2	0.262	0.230	0.346
Pera glabrata (Schott) Baill.	1	168.39	1	0.131	0.102	0.173
Pourouma guianensis Aubl.	10	1379.04	9	1.312	0.838	1.557
Pouteria caimito (Ruiz & Pav.) Radlk.	1	315.84	1	0.131	0.192	0.173
Pouteria sp.	5	2327.26	5	0.656	1.415	0.865
Pouteria torta (Mart.) Radlk.	2	155.91	2	0.262	0.095	0.346
Protium sp.	1	81.49	1	0.131	0.050	0.173
<i>Pseudopiptadenia contorta</i> (DC.) G.P.Lewis & M.P.Lima	16	15627.07	11	2.100	9.499	1.903
Quiina glaziovii Engl.	2	140.87	2	0.262	0.086	0.346

Rubiaceae sp.	1	25.78	1	0.131	0.016	0.173
Sapotaceae sp.	1	78.96	1	0.131	0.048	0.173
Schefflera morototoni (Aubl.) Maguire et al.	1	42.10	1	0.131	0.026	0.173
Siparuna guianensis Aubl.	70	7260.69	40	9.186	4.413	6.920
Sloanea guianensis (Aubl.) Benth.	17	4133.25	12	2.231	2.512	2.076
Sloanea sp1.	1	45.84	1	0.131	0.028	0.173
Sorocea bonplandii (Baill.) W.C.Burger et al.	9	397.44	8	1.181	0.242	1.384
Tachigali rugosa (Mart. ex Benth.) Zarucchi & Pipoly	11	3620.46	7	1.444	2.201	1.211
Tapirira guianensis Aubl.	5	2932.15	5	0.656	1.782	0.865
Terminalia fagifolia Mart.	1	38.52	1	0.131	0.023	0.173
Tovomita sp.	1	459.64	1	0.131	0.279	0.173
Triatinichia sp.	2	415.73	1	0.262	0.253	0.173
Trichilia emarginata (Turcz.) C.DC.	4	1768.23	4	0.525	1.075	0.692
Virola bicuhyba (Schott ex Spreng.) Warb.	6	705.59	6	0.787	0.429	1.038
Virola sp.	1	179.55	1	0.131	0.109	0.173
Vismia guianensis (Aubl.) Choisy	1	161.14	1	0.131	0.098	0.173
Vochysia laurifolia Warm.	2	1002.14	2	0.262	0.609	0.346

Xylopia brasiliensis Spreng.	13	5735.63	13	1.706	3.486	2.249
Xylopia sericea A.StHil.	8	1391.48	7	1.050	0.846	1.211