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LAND USE HISTORY PROMOTES SHIFTS IN COMPOSITION AND INCREASES THE FUNCTIONAL VULNERABILITY OF URBAN FORESTS

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ABSTRACT

Urbanisation is rapidly transforming our world and threatening the maintenance of ecosystem functions as biodiversity and primary production. This study aimed to understand how different land-use histories affect functional composition and diversity of urban forests and how functionally vulnerable are these forests to future disturbances. We used data from nine urban forests with different land-use histories (LUH) grouped in three intensity categories with three forests in each: soil denudation (high intensity LUH), cropland (medium intensity LUH) and without land use history (low intensity LUH) and from three non-urban mature forests (control), for comparison purposes, all situated in the Brazilian Atlantic forest. We addressed two questions: (i) to what extent do urban forests with different land-use histories differ in functional composition and diversity metrics?; and (ii) how functionally vulnerable are these forests to future disturbances? The first was answered from the species categorization into functional groups and by the functional richness and dispersion indices; and the second through a resistance analysis based on functional redundancy and a resilience analysis based on species response diversity. As we predict, urban forests showed differences in functional composition, regardless of the land use history. However, negative effects on the amount and diversity of functions were only related to the more intense previous land use (cropland and denudation LUH). Only urban forests with some land use history had significant reductions in functional redundancy and species response diversity. Surprisingly, urban forests without land use history are able to maintain high levels of functional diversity and safety, similar to those found in non-urban forests. We conclude that, although urban forests can still serve as reservoirs of functional diversity and may present some safety in the provision of their functions in the face of future disturbances, the intensity of land use history is determinant for the functional reduction, homogenization and vulnerability of these urban forests.

Keywords: urban forests, functional composition, functional diversity, functional vulnerability, functional resistance and resilience, land use history

RESUMO

A urbanização está transformando rapidamente nosso mundo e ameaçando a manutenção das funções do ecossistema, como biodiversidade e produção primária. Este estudo teve como objetivo compreender como diferentes histórias de uso da terra afetam a composição funcional e a diversidade das florestas urbanas e quão funcionalmente vulneráveis são essas florestas a futuros distúrbios. Utilizamos dados de nove florestas urbanas com diferentes históricos de uso da terra (HUT), agrupadas em três categorias de intensidade com três florestas em cada: desnudamento do solo (alta intensidade de HUT), cultivo (intensidade média de HUT) e sem histórico de uso da terra (baixa intensidade de HUT) e de três florestas maduras não urbanas (controle), para fins de comparação, todas situadas na Floresta Atlântica Brasileira. Abordamos duas questões: (i) em que medida as florestas urbanas com diferentes históricos de uso da terra diferem na composição e diversidade funcional e (ii) qual é a consequência do histórico de uso da terra na resistência e resiliência funcional das florestas urbanas? A primeira pergunta foi respondida através da categorização de espécies em grupos funcionais e pelos índices de riqueza funcional e dispersão; e a segunda através de uma análise de resistência, baseada em redundância funcional, e uma análise de resiliência, baseada na diversidade de resposta de espécies. Como prevemos, as florestas urbanas mostraram alterações na composição funcional, independente do histórico de uso. No entanto, efeitos negativos sobre a quantidade e diversidade funcional foram apenas encontrados em florestas com uso prévio da terra mais intenso (desnudamento do solo e cultivo). Apenas as florestas urbanas com histórico de uso da terra tiveram reduções significativas na redundância funcional e na diversidade de respostas das espécies. Surpreendentemente, as florestas urbanas sem histórico de uso da terra são capazes de manter altos níveis de diversidade e segurança funcional, semelhantes aos encontrados nas florestas não urbanas. Concluímos que, embora as florestas urbanas ainda possam servir como reservatórios de diversidade funcional e apresentar alguma segurança no fornecimento de suas funções diante de futuros distúrbios, a intensidade o uso prévio da terra é determinante para a redução, homogeneização e vulnerabilidade funcional dessas florestas.

Palavras-chave: Florestas urbanas, composição funcional, diversidade funcional, vulnerabilidade funcional, resistência funcional, resiliência, histórico de uso da terra.

SUMMARY

INTRODUCTION

Human actions are rapidly transforming the world through land use changes. In particular, urbanization (Even with less than 5% of the Earth's surface – see McKinney 2002) causes profound transformations at the landscape level and is considered a major threat to global biodiversity (Hansen et al. 2005). Currently, urban areas are expanding on average twice as fast as their populations (Angel et al. 2011; Seto et al. 2012), leading to massive destruction of high conservation value habitats inside and outside cities (Mcdonald et al. 2008) and highlighting the urgency for tools that support such transformation along sustainable paths (Pickett et al. 2014).

When not completely cleared by urban expansion, the cities remaining vegetation is restricted to smaller patches, limiting the survival and dispersion of native species (Bierwagen 2007),and subjected to changes in environmental conditions, such as higher levels of air pollution and temperature (Williams et al. 2009). In this process, many species are lost, whereas new anthropogenic environmental conditions are created, providing habitats for new species and new plant communities (Godefroid and Koedam 2007). Thus, the biodiversity of urban forests is commonly marked by the decline of native specialist species (Bierwagen 2007; Schleicher et al. 2011) and by a large influx of exotic local species due the proximity to diverse socioeconomic activities, in particular, gardening and agricultural and forestry production (Essl et al. 2011; Kowarik 2011). This species replacement may lead to species extinction and to a biotic homogenization of urban forests remaining (i.e. the gradual replacement of specialist species to generalist species) (McKinney and Lockwood 1999; McKinney 2006), which can be triggered by human preferences and environmental filtering (McKinney 2006; Williams et al. 2009). The human demands may increase the propagation pressure of planted species (Williams et al. 2015) and the urban environment may filter the species according to the characteristics that make them more or less tolerant of the present conditions (Mouillot et al. 2013). In both cases, the flora and fauna of cities tend to be increasingly similar to each other, leading to negative genetic, evolutionary, and functional consequences for the community (Olden et al. 2004).

In this context of species changes, a functional approach can be extremely useful in assessing the performance of species in face of the various disturbances inherent to urbanization and for suggesting the functional homogenization of these communities. Functional traits are morphological and physiological characteristics that define the ecological role of each species within the ecosystem (Villéger et al. 2008). Their interaction with environmental conditions determines where, when, and to what extent a species can occur within a habitat (Tilman et al. 1997; Hough-Snee et al. 2015) and help elucidate mechanisms underlying the ecological strategies of plants (Westoby et al. 2002). Through a trait-based approach, it is possible to infer about community assembly rules and dynamic changes over time (Uriarte et al. 2010; Bhaskar et al. 2014) and also to predict successional trajectories (Webb et al. 2010). For instance, forest degradation may promote a gradual shift from dominance by late-successional species, with conservative trait values and high biomass storage potential (e.g. high wood density, high stature, and large seed size), toward dominance by early-successional species, with acquisitive trait values and lower biomass storage potential (e.g. low wood density, lower stature, and small seed size) (Carreño-Rocabado et al. 2012). In response to the conditions imposed by urbanization, traits such as seed mass and maximum height tend to increase (Duncan et al. 2011), suggesting stress resistance strategies and, possibly, a great potential for carbon storage in urban forests (Osuri & Sankaran 2016).

Besides to functional composition and assembly rules, through functional diversity, it is possible to infer about the community resistance and resilience (Nyström and Folke 2001; Laliberté et al. 2010),and so, about functional vulnerability. According to Elmqvist et al. (2003), the presence of functionally similar species that respond differently to environmental changes provides security to the maintenance of the ecosystem processes in case of local species extinction. Thus, the functional resistance is achieved by the presence of species that overlap in their traits being functionally redundant in their effects on ecosystem (Díaz and Cabido 2001), and the high diversity of responses within these set of redundant species ensures the renewal and reorganization of the ecosystem, promoting a functional resilience (Elmqvist et al. 2003). As in urban forests, the pressure for land use change is constant (Colding 2007) and the risk of species extinction is high (Hansen et al. 2005), the knowledge about the forest responses to future disturbances is especially important (Pickett et al. 2016) because can prevent loss of important traits and functional diversity, thus guarantying the permanence of ecosystem functions and services in these novel ecosystems (Oliver et al. 2015).

Here, we investigate how functional composition and diversity metrics, as well as functional resistance and resilience, are affected by urbanization though land use history (LUH) of urban forests (without LUH, cropland LUH, and denudation LUH). The Brazilian Atlantic Forest offers one of the most dramatic examples related to the effect of urbanization on ecosystems. Owing to five centuries of intense human occupation and approximately 70% of the Brazilian population, more than 80% of its forests are smaller than 50 ha and about 50% of them are less than 100 m from a forest edge (Ribeiro et al. 2009). We addressed two questions: (i) to what extent do urban forests with different land-use histories differ in functional composition and diversity metrics, and (ii) how functionally vulnerable are these forests? We hypothesized that forests within urban matrix would exhibit shifts in functional composition toward an increase in the abundance of species with highly acquisitive traits and a decrease in the functional diversity indices, leading to greater functional homogenization. Moreover, we predict that under stronger land-use history, the resistance and resilience of urban forests would decrease, making such forests more functionally vulnerable.

MATERIAL AND METHODS

Study sites and data sampling

This study was conducted in twelve forest fragments located in state of Minas Gerais, South-eastern of Brazil, in the municipalities of Juiz de Fora, Lima Duarte, Rio Preto and Santos Dumont (21°24'- 22°1'S and 43°18' – 43°55'W) (Fig. 1). The region experiences a mesothermic climate, characterized by dry winters and temperate summers (Cwb – Köppen Classification) (Alvares et al. 2013). The annual mean precipitation ranges from 1497 to 1585 mm and mean annual temperature ranges from 17.6 to 18.9°C. The original vegetation of region is classified as Mountaine Semideciduous Seasonal Forests (IBGE 2012), belonging to the

Brazilian Atlantic Forest domain with latosols (Oxisoils) as predominant soils in the region (CETEC et al. 2010).

The land use conversion is the major impact experienced by the Atlantic Forest, which currently has most of its forests in small and isolated fragments, with different land-use histories (Calmon et al. 2011). According with SOSMA and INPE (2014), the intense expansion of urbanization and agricultural lands reduced in 89% the natural forest cover in the region studied. Thus, in this study, we sought to encompass the main land-use changes experienced by the Brazilian Atlantic Forest: urban expansion, conversion of forest areas into agricultural areas and total deforestation. The forests studied here have different land use histories and are contained within (N=9) and outside (N=3) of the urban matrix in private areas, legal reserves or conservation units. The land use histories were determined through satellite images, photos and interviews with residents (Table S1).

The urban forests were classified into three forest classes according to the land-use history before their conservation status (Table S1). Urban forests with: a) no land-use history, forests that had partial suppression or selective logging of original vegetation (> 100 years), mainly promoted by the urban areas expansion, but without any known history of land use (N=3); b) cropland history, forests that had total suppression of original vegetation to be replaced by agricultural crops (coffee and /or pasture) before being abandoned (~70 to 80 years) (N=3); and c) denudation history, those forests which emerged after complete vegetation and soil removal (~50 to 60 years) (N=3). The forests outside the urban matrix, even though they also have a fragmentation history and some very light selective logging (maximum one or two trees per hectare) in the past, the forest structure (e.g. high basal area) and the presence of high species diversity, allowed to classify them as control forests for this study (N=3). All plots were established in the core areas where there was no logging signal.

The inventories data were collected from 2013 to 2016 by several authors (Almeida, 2016; Pessoa, 2016; Rubioli, T 2016.; In each forest, 10 permanent plots (20 m × 20 m) were randomly assigned, yielding a total of 120 sample plots (4.8 ha in total). During the sampling (which was carried out at different time periods), all live trees with a diameter at breast height (DBH) ≥ 5 cm were tagged, identified to species level, with their diameters measured and height estimated. Our database comprised 7202 trees, belonging to 383 species and 68 botanical families.

Functional traits

The functional traits considered in the study are related to two processes of successional trajectory, the resource availability and primary productivity (Van Der Sande et al. 2016). We evaluated six traits: maximum height, wood density, leaf deciduousness, leaf compoundness, seed size and dispersal mode. The species maximum height (Hmax, m) is an indicator of the adult stature species, potentially related to the species longevity and life-history strategy (King et al. 2006), and was calculated as the 95th-percentile height of all trees of the species. Maximum height across species ranged from 3 to 35 m, with an average of 13.7 m. Species wood density (WD, g.cm^{-3}) is an indicator of stem construction costs, resistance and hydraulic conductivity (Poorter et al. 2010) and was obtained from the Global Wood Density database (filtered by Tropical South America, Zanne et al. 2009). For the species with WD not available (~64% of species), we used the genera or family WD mean values. Wood density species ranged from 0.18 to 1.18 g.cm^{-3}, with an average of 0.64 g.cm^{-3}. Leaf deciduousness (Dec, %) reflects species growth length period and drought tolerance and was calculated as the percentage of individuals that belonged to deciduous species per plot (Van Der Sande et al. 2016).This trait was evaluated for only 279 species (~73%) rather than for all species due to lack of information about some species in the reference literature. The leaf leaf compoundness (Comp, %) reflects the species heat balance and was also calculated as the percentage of individuals with compound leaves per plot. Seed size (SS, categorical data), although usually related to the competitive vigour of the seedlings (Kitagima, 2007), is also an important life history trait for trees, correlated to a suite of morphological and physiological traits of pioneer species (small seeds) and shade-tolerant species (large seeds) (Poorter and Rose 2005; Osuri & Sankaran 2016). Qualitative data for species SS were obtained from herbarium specimens, and the species were classified as small seeds species (seed length ≤1.5 cm) and large seeds species (length between ≥ 1.6 cm), following Tabarelli and Peres (2002) and Santos et al. (2008). Dispersal mode (DM, categorical data) is an indicator of the ability of plants to colonize habitats and is especially important in fragmented urban landscapes because they can improve predictions of dispersal probability and seed bank composition (Kraft et al. 2015). All species were categorized: biotic dispersion and abiotic dispersion. Details about species functional traits can be found in supplementary material (Table S5).

Functional composition and functional diversity

Functional composition was assessed and discussed through functional groups, which are sets of species with similar functional trait values (Díaz and Cabido 2001). This approach is important because ecosystem functions are determined by the trait values of the most dominant species in the community (Grime 1998). The species classification into groups was done using the ‘FD’ package in R (Laliberté et al. 2015) through a dendrogram of Ward’s clustering method (Fig S1). To calculate the dissimilarity matrix, we used a generalization of Gower’s distance that allows mixed traits types (e.g continuous, ordinal and categorical, Pavoine et al. 2009).

To analyse functional diversity we used two indices: Functional richness (FRic) and Functional dispersion (FDis). Functional richness is an indicator of the species volume occupying the niche space of a community (Villéger et al. 2008). Functional dispersion is an indicator of species distribution in the niche space and was calculated with the species basal area as a weighting factor (Laliberte et al. 2010). The basal area was chosen as a weighting factor because it better reflects plant performance and adaptation to local conditions than abundance (Lohbeck et al. 2015). These indices are complementary: While FRic measures the extent to which the trait space is filled, FDis measures how this space is filled while giving a more conservative measure of its size (Liebergesell et al. 2016). Both were obtained for each sampling site.

Community resistance and resilience

To assess the resistance and resilience of communities two measures were used: Functional redundancy (FR) and Response diversity (RD) (Mumme et al. 2015). Functional redundancy is an indicator of species numbers that contribute similarly to an ecosystem function or process (Laliberté et al. 2010) and response diversity is an indicator of how species belonging to the same functional group (redundant species) present different responses to disturbances and environmental changes (Elmqvist et al. 2003). An important step for such approach is to define which function or process will be investigate and which functional traits and species are relevant for it (Suding et al. 2008). Here, we investigated the process-related to natural successional trajectories of forests (increase of resource availability and primary productivity, Van Der Sande et al. 2016). So, we re-classified the functional traits into effect traits, that directly affect the availability of resources and the productivity and into response traits, that respond to these changes in environmental conditions (Lavorel and Garnier 2002; Cornelissen et al. 2003, Table S2).

The functional redundancy was calculated as ratio between the species richness (S) and the amount of functional effect groups found in the plot (Laliberté et al. 2010). The functional effect groups were established by Ward´s clustering method based on the effect-trait dissimilarity matrix, also estimated by Gower dissimilarity index (Fig. S2). The response diversity was calculated by the functional dispersion sum of functional effect groups of each sampled site (Fig S3). Functional dispersion is indicated to represent the response diversity by reflecting the functional differences between species in a community (Craven et al. 2016). Thus, through dispersion variation between species belonging to the same functional group, we can access how different are these species in terms of functional response (characteristics), even if they play the same role in the ecosystem.

Statistical analysis

Generalized linear mixed model analysis were carried out, with site as a random factor (to account for the possible lack of independence of plots within the sites), to evaluate how functional diversity indices differ among forest categories (control, without LUH, cropland LUH and denudation LUH). A Gaussian error distribution with identity link function was used for response variables (normality was tested and confirmed by the Shapiro–Wilk test) and, to assess the differences among the forests, Tukey's post-hoc test was used, considering statistical differences for P-values higher than 0.05.We also calculated marginal (m) and conditional (c) R^2 of GLMM. The R^2m is the variance explained by fixed factors alone; and R^2c is the variance explained by fixed and random factors combined (Nakagawa and Schielzeth 2013).

Relationships between functional traits were assessed using Spearman correlation coefficient (not all traits showed normal distribution, Table S3). To test for differences in basal area proportion of functional groups and for functional dispersion of functional effect groups, we used Kruskal-Wallis' test ($p < 0.05$) (none of these variables showed normal distribution). All analyses, figures and graphs were performed using the platform R (R-Core-Team, 2015) and the following packages: multcomp (Bretz et al. 2015), lme4 (Bates et al. 2014), lmerTest (Kuznetsova et al. 2016), MuMIn (Barton 2016), and ggplot2 (Wickham and Chang 2016).

RESULTS

Functional composition and diversity

A total of 383 woody species were recorded and classified into eleven functional groups (FGs) (Table.1 and Fig.1). Urban forests without LUH, when compared to the control forests, presented an increase of basal area in seven functional groups but only in FG6, the difference was statistical. The urban forests with cropland and denudation LUH showed a significant increase of basal area in two functional groups: FG3 and FG6 in forests with cropland LUH and FG6 and FG10 in denudation LUH forests. The FG6 was the only group that had a significant increase of basal area in urban forests regardless of its history of land use.The main characteristics (traits) shared between these groups (FG3,FG6 and FG10) are species with higher than average stature and small seeds. FG6 also presents species with deciduous and compound leaves and abiotic dispersion and is likely to be a group formed by Fabaceae species family. With 30 species (~7% of total sampled), the FG10 represents almost 70% of the total basal area of urban forests with denudation history, suggesting that these forests are dominated by species with similar characteristics: height and wood density higher than average, evergreen and simple leaves, abiotic dispersion and small seeds. Likewise, the forests with cropland LUH have approximately 40% of basal area allocated in FG3, which differs from FG10 only in relation to the predominant dispersion mode. In areas that regenerated from croplands, the biotic dispersion prevailed.

On the other hand, three groups had their basal area decreased in urban forests: FG5, FG8 and FG9 (Fig 1 and Table S4 and S7). Among them, FG8 and FG9 are the only two groups that present statistical difference between the control and all urban forests that present the predominance of large seeds.

Table 1: Functional group description based on distinctive functional traits

FG	S	Hmax	WD	LD	LC	DM	SS
FG1	15	-0.4	0.01	Evergreen	Compound	Abiotic	Small
FG2	30	-2.29	-0.03	Deciduous	Simple	Biotic	Small
FG3	58	3.04	-0.13	Evergreen	Simple	Biotic	Small
FG4	44	0.66	-0.08	Evergreen	Compound	Biotic	Small
FG5	66	-5.44	-0.01	Evergreen	Simple	Biotic	Small
FG6	25	0.27	0.05	Deciduous	Compound	Abiotic	Small
FG7	20	-0.41	0.04	Evergreen or deciduous	Compound	Abiotic	Large
FG8	30	-0.01	0.07	Evergreen	Simple	Biotic	Large
FG9	14	7.45	0.07	Evergreen or deciduous	Simple	Abiotic	Large
FG10	30	0.64	-0.02	Evergreen	Simple	Abiotic	Small
FG11	51	2.14	0.16	Evergreen	Simple	Biotic	Small

FG: Functional groups and S: species richness. Continuous traits shown according to the difference between the mean values found within each group and the mean value found for all traits. Hmax mean = 13.70 (m) and WD mean = 0.64 (gcm^{-3}).

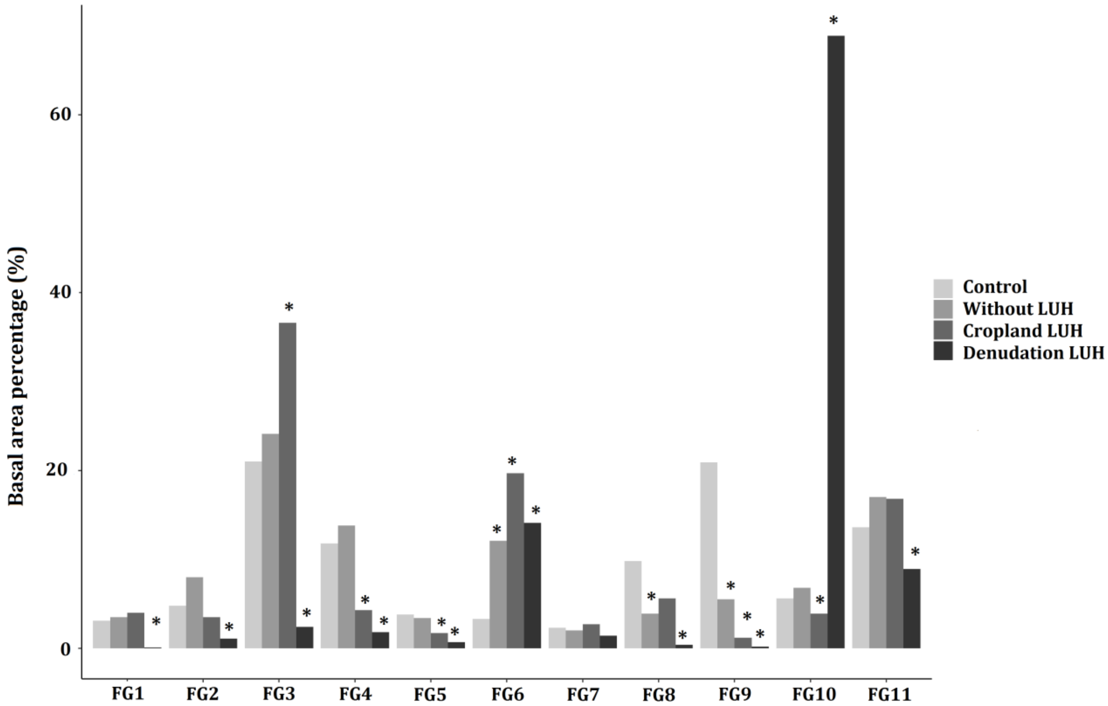

Fig 1: Histogram of functional groups basal area by forest category in percentage."*" p-value<0.05.

The GLMMs showed that functional richness is negatively affected to land use history of urban forests (Fig 2a, R^2m= 0.46, R^2c=0.54). Forests with denudation history differed significantly from others, presenting extremely low functional richness values. The cropland history also presented significant negative effects on forest functional richness, but less than the latter. Interestingly, urban forests without land use history did not present significant differences in functional richness indices when compared with control forests (Table S6). The functional dispersion was also sensitive to the land use history (Fig 2b, R^2m= 0.21, R^2c=0.44), but less than the functional richness. Urban forests presented lower values of functional dispersion than control forests, but only forests with denudation land use history were statistically different (Table S6). These results indicate that the decrease of urban forest functional diversity is more related to the intensity of its land-use history than to the presence of urban matrix.

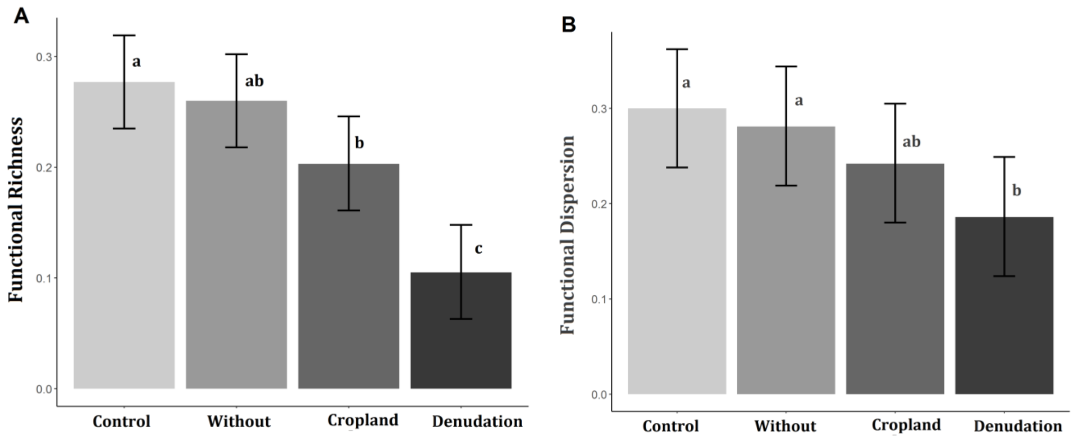

Fig 2: Histograms show the functional richness (A) and functional dispersion (B) across forest categories. Different letters represent significant differences (P < 0.05) of pairwise comparisons in GLMM models. Error bars represent the 95% of confidence intervals with n = 30.

Community resistance and resilience

The clustering method shaped six different functional effect groups (Fig. S2), which differed substantially in the number of species and in basal area ratio between forests categories (Table S7 and Fig. S3). The land-use history had negative effects on functional redundancy of urban forests (Fig. 3a, R^2m= 0.61, R^2c= 0.67). Forests with cropland and denudation histories presented functional redundancy significantly lowers than control forests. Conversely, the urban forests without land-use history did not differ from control forest in relation to this index (Table S6), suggesting that the land use history promotes a reduction in the number of species per function and, differently from the functional richness and dispersion indices, the functional redundancy of urban forests without land-use history was not statistically equal to functional redundancy found in forests with cropland history.

Different patterns of functional dispersion into functional effect groups were found among forests categories (Fig. S3 and Table S7), resulting in statistical differences between response diversity indices (Fig 3b. R^2m= 0.49, R^2c= 0.51). Response diversity showed higher values in the control forests and urban forests without land-use history. On the other hand, this index showed significantly lower values in urban forests with a cropland history followed by urban forests with denudation history. This result indicates that in urban forests with some previous land-use, species tend to present more similar functional responses.

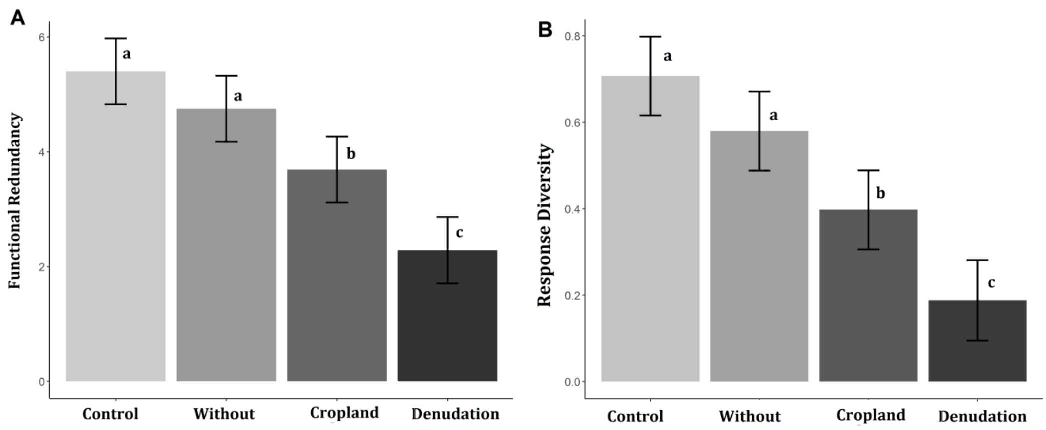

Fig 3: Histograms show the functional redundancy (A) and response diversity (B) across forest categories. Different letters represent significant differences ($P < 0.05$) of pairwise comparisons in GLMM models. Error bars represent the 95% of confidence intervals with $n = 30$.

DISCUSSION

We examined how urban matrix and previous land-use affect the functional composition and diversity of urban forests, and to what extent these forests can maintain functional resistance and be functionally resilient to future disturbances. We found that land-use history is the determinant for negative effects on functionality, through shifts in functional composition and diversity, translating into greater functional vulnerability of these urban forests, due decrease in functional resistance and resilience. Conversely, when there is no land-use history, urban forests may maintain high levels of functional diversity and resistance, although they differ from control forests in terms of species assembly composition. Taken together, our results suggest that urban forests still serve as reservoirs of functional diversity and may present some safety in the provision of their functions in the face of future disturbances. However, the abandonment after land-use profoundly reduces the amount of ecosystem functions provided and increases the vulnerability of forests in an anthropogenic landscape.

Shifts in functional composition and diversity in urban forests

The distribution of species biomass (basal area) among functional groups is less uniformly dispersed in urban forests with denudation land-use history than in others. This might be related to a strong environmental filtering process (Lohbeck et al. 2014), in which, the abandonment of post-use areas (abiotic filters, i.e. high light incidence, exposed soil), associated with the presence of an urban matrix (dispersion filters, i.e. large distance between forest fragments), establishes adverse environmental conditions, restricting the forest regeneration to individuals with specific and similar traits (Lebrija-trejos et al. 2010). The reduction of functional richness and dispersion also reinforces the species filtering hypothesis in these forests (Cornwell et al. 2006; Flynn et al. 2009). Environmental conditions can selectively remove species (Naeem and Wright 2003) and alter their occurrence probabilities and abundances according to functional traits (Mason et al. 2013). This scenario is typical of early-successional forests (Lohbeck et al. 2014) and the persistence of dominant functional groups with low functional diversity, even after 50 years of regeneration, might be indicative of alternative successional pathways associated with prior land use (Longworth et al. 2014).

The cropland history also promoted loss of functional richness, as expected, due of land-use conversion (Tscharntke et al. 2005). However, the species basal area distribution in this case is more uniformly spread compared with denudation history forests. In accordance with functional dispersion index, the most abundant species are as functionally divergent as those found in the control forests. This is likely to be a result of the distinct initial composition of croplands LUH forests, since each area had different species being cultivated (e.g. *Coffea arabica*, *Brachiaria* spp.) and the spatial pattern of landscape (urban matrix) that may limit the exchange of seeds (and species) among forests (Arroyo-Rodríguez et al. 2013). Differences in cultivated species may lead to compositional divergence in species assemblages and different successional pathways among forest fragments (Arroyo-Rodríguez et al. 2013). Nevertheless, this result should be interpreted with some caution. The effects of biotic similarity are strongly scale-dependent (Sax and Gaines 2003). Previous taxonomic studies showed that, although there is a large pool of species in the studied urban matrix (high beta diversity), the species richness and diversity were low within forests with cropland history (Fonseca 2017). Thus, at the community scale, where species interact, such functional similarity may be high.

Contrary to our hypothesis, urban forests without land-use history did not present a decrease in functional diversity when compared with control forests; thus, the 80 years of urbanization around the forests does not appear to alter the volume occupied or the distribution of species within the community. In fact, the direct impacts of urbanization on species diversity, such as habitat loss, habitat fragmentation and the introduction of new species (Kowarik 2011) do not occur visibly in the studied forests since they achieved a conservation status.

Three functional groups were distinguished by their increased proportion in urban forests with a land-use history. It was expected that acquisitive-trait species prevailed in forests with more intense disturbance history (Carreño-Rocabado et al. 2012), but the only acquisitive trait shared by them was seed size. While small-seeded species incur an advantage because they can persist longer in the soil seed bank and germinate under favourable conditions (Poorter and Rose 2005), the higher values of maximum height could be taken as an unexpected tree investment in disturbed areas, because with shorter and more open canopy, light is a non-limiting resource (Ruiz-Jaen and Potvin 2011). However, this seems to be a trend for species success in urban habitats (Williams et al. 2015), which may be related to the likely possibility involving local extinction of short plants (Duncan et al. 2011).Functional groups negatively affected by urban matrix and land-use history did not share any specific trait. However, the only two groups with large-seeded species sensitive to land-use history had their biomass decreased with increasing intensity of the land-use history. This result is consistent with several other studies that show a greater vulnerability of the large-seeded species to habitat loss (Santos et al. 2008; Santo-Silva et al. 2015; Rocha-Santos et al. 2017) and land use changes (Castro et al. 2010). The dispersion of large-seeded plants is deeply affected by local or functional extinction of large-bodied frugivores, commonly seen in urban matrices (Er et al. 2005; Francis et al. 2011). In addition, the presence of a more open canopy, typical of disturbed areas, reduces the survival of these species, which have a greater success in shaded habitats (Westoby et al. 2002; Baraloto et al. 2005).

Functional resistance and resilience

As observed for the functional diversity, only the urban forests with land-use history had significant reductions in functional redundancy and in response diversity. Urban forests without land-use history did not show changes in these indices. Ours findings are similar to those observed in previous studies where functional resistance and resilience decreased along land-use intensification gradients (Laliberté et al. 2010), which is possibly related to the simplification of ecosystem structure (Fig 1 and 2, Pimm and Raven 2000; Sala et al. 2000). The relatively low functional resistance and richness of urban forests with cropland and denudation histories is typical of species-poor assemblages (Díaz and Cabido 2001; Petchey et al. 2007) and may have dramatic consequences for ecosystem functioning, especially when the range of species reactions to environmental change is low (i.e. low response diversity, Elmqvist et al. (2003)). When species with similar functional effect traits respond similarly to environmental conditions and changes, even small disturbances could result in a major loss and complete extinguishment of certain ecosystem functions (Elmqvist et al. 2003). Conversely, the random loss of one species may not affect the ecosystem functioning in communities with greater functional redundancy, as its function can be compensated by others within the same functional effect group (Fonseca and Ganade 2001; Bruno et al. 2016).

Contrary to our hypothesis, there were no significant differences in the functional redundancy and response diversity between control and urban forests without land-use history, suggesting that these last forests could resist changes in environmental conditions and maintain functions through internal reorganization alone (Gunderson et al. 2010). However, this result might still represent a real concern for conservation. Urbanization is considered a ‘press’ disturbance and tends to persist or increase in its intensity through time (Nimmo et al. 2015). The shifts in functional composition (Fig 1 and Tables S4 and S7), and species reduction by function and lower species response diversity (Fig S3), even without significant differences, reinforce the importance of identifying determinants and thresholds of resistance in the face of persistent disturbances (Funk et al. 2008).

CONCLUDING REMARKS

For a long time, conservation efforts were directed almost exclusively to areas where biodiversity was not threatened by human activities (Brandon and Wells 1992; Scott et al. 2001). However, we show that even in a fully anthropogenic matrix, forests can maintain high levels of biodiversity, functional resistance and resilience. This finding highlights the need to expand the protection of intact forests against any anthropogenic land-use change activity, which may lead to shifts in the functions provided by the urban forest even several years after the disturbance has ceased. In addition, our results did not find evidence that urbanization causes greater functional homogenization among its forests. It is likely that this process is driven by intensive land-use changes (e.g. denudation history). Finally, future studies should include measurements of abiotic conditions, which would help elucidate the role of functional traits in the organization and composition of plant communities (McGill et al. 2006) and expand the use of functional traits, especially the leaf traits, which are strongly linked to species responses to disturbance (Lienin and Kleyer 2011; Van Der Sande et al. 2016).

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SUPPLEMENTARY MATERIAL

Land-use history promotes shifts in composition and increases the functional vulnerability of urban forests

This Supplementary material includes:

Table S1: Characterization of forest fragments sampled in this study

Table S2: Effect and response traits considered to characterize the woody species

Table S3: Spearman correlations between functional traits.

Table S4: Distribution of basal area by functional group in percentage.

Table S5: Overview of the 383 forest tree species included in the study.

Table S6: Tukey test from generalized mixed models testing effects of land-use history on functional index.

Table S7: The results from a nonparametric analysis of variance (Kruskal-Wallis test) for species basal area among each functional group

Fig S1: Dendrogram resulting from classifying species according to their similarity in the functional traits.

Fig S2: Dendrogram resulting from classifying species according to their similarity in the effects functional traits.

Fig S3: Species and functional dispersion of the 6 functional effects groups (FG) based in their response traits.

Table S1: Characterization of forest fragments sampled in this study

Forest name	Category	Urban matrix	Size (ha)	Coordinates	
Brejo Novo [1]	Control	Out	45	21°24'45.920"S	43°34'25.268"W
Fazenda da Serra[1]	Control	Out	50	21°48'14.975"S	43°55'52.273"W
Fazenda Mato Limpo[1]	Control	Out	20	22°1'58.163"S	43°52'37.389"W
Parque da Lajinha[2]	Without LUH	Within	88	21°47'29.778"S	43°22'33.908"W
Parque Poço D'Antas[3]	Without LUH	Within	277	21°45'13.625"S	43°18'58.251"W
Mata da Ed. Física[4]	Without LUH	Within	5	21°46'46.628"S	43°22'17.162"W
Mata da Embrapa[4]	Cropland LUH	Within	4.5	21°46'52.902"S	43°22'3.828"W
Mata Urbanizada[8]	Cropland LUH	Within	15	21°44'5.915"S	43°22'7.350"W
Mata Secundarizada[7]	Cropland LUH	Within	25	21°44'3.715"S	43°22'12.840"W
Mata do ICB[4]	Denudation LUH	Within	1.5	21°46'35.419"S	43°22'18.089"W
Mata do Pinus[5]	Denudation LUH	Within	2	21°46'33.741"S	43°22'6.168"W
Candeal[6]	Denudation LUH	Within	1.6	21°46'37.380"S	43°22'2.646"W

[1]Almeida, 2016 [2]Pessoa, 2016, [3]Fonseca,. 2017. [4]Rubioli, 2017; [5]Carvalho et al. 2014; [6]Santana et al.2018; [7]Brito et al. 2014; [8]Fonsecaet al. 2012

Table S2: Effect and response traits considered to characterize the woody species

Trait	Effect/ Response	Type	Units/Categories
Wood density	E/R	C	$g\ cm^{-3}$
Maximum plant height	E/R	C	m
Leaf deciduousness	E/R	%	Deciduous
Leaf compoundness	E/R	%	Compound
Seed size	R	CAT	cm
Dispersal mode	R	CAT	Biotic / Abiotic

C: continuous traits; % percentage traits and CAT: categorical traits. $g\ cm^{-3}$: grams per cubic centimeter; m: meters; cm: centimeter

Table S3: Spearman correlations between functional traits: Dispersal mode (DM), seed size (SS), compoundness (Comp, simple S or compound C), deciduousness (Dec, deciduous D, or evergreen E), wood density (WD, g.cm-3), and maximum height (Hmax, m)

P-value	DM	SS	Comp	Dec	WD	Hmax
DM	-					
SS	0.001	-				
Comp	0	0.421	-			
Dec	0	0.492	0	-		
WD	0.323	0.001	0.362	0.957	-	
Hmax	0.023	0.02	0.708	0.582	0.469	-

Table S4: Distribution of basal area by functional group in percentage

Forest category	FG1	FG2	FG3	FG4	FG5	FG6	FG7	FG8	FG9	FG10	FG11
Control	3.1%	4.80%	21%	11.8%	3.8%	3.3%	2.3%	9.8%	20.9%	5.6%	13.6%
Without LUH	3.5%	8%	24.1%	13.8%	3.4%	12.1%	2.0%	3.9%	5.5%	6.8%	17.0%
Cropland LUH	4%	3.5%	36.6%	4.3%	1.7%	19.7%	2.7%	5.6%	1.2%	3.9%	16.8%
Denudation LUH	0.1%	1.1%	2.40%	1.8%	0.7%	14.1%	1.4%	0.4%	0.2%	68.9%	8.9%

Table S5: Overview of the 383 forest tree species included in the study. Scientific name, family, dispersal mode (DM), seed size (SS), compoundness (Comp, simple S or compound C), deciduousness (Dec, deciduous D, or evergreen E), wood density (WD, g.cm^{-3}), and maximum height (Hmax, m) are given.

Species	**Family**	**DM**	**SS**	**Comp**	**Dec**	**WD**	**Hmax**
Abarema langsdorffii (Benth.) Barneby & J.W.Grimes	Fabaceae	Abiotic	Small	C	E	0.585	17.4
Aegiphila integrifolia (Jacq.) Moldenke	Lamiaceae	Biotic	Small	S	D	0.86	17.3
Alchornea glandulosa Poepp. & Endl.	Euphorbiaceae	Biotic	Small	S	E	0.378	17.3
Alchornea triplinervia (Spreng.) Muell. Arg.	Euphorbiaceae	Biotic	Small	S	E	0.467	20
Allophylus edulis (A.St.-Hil. et al.) Hieron.	Sapindaceae	Biotic	Small	C	D	0.651	16.65
Allophylus petiolulatus Radlk.	Sapindaceae	Biotic	Small	C	E	0.7	16
Allophylus racemosus Sw.	Sapindaceae	Biotic	Small	C	E	0.435	16.9
Amaioua guianensis Aubl.	Rubiaceae	Biotic	Small	S	E	0.625	8.6
Amaioua intermedia Mart. ex Schult. & Schult.f.	Rubiaceae	Biotic	Small	S	E	0.625	13.55
Anadenanthera colubrina (Vell). Brenan	Fabaceae	Abiotic	Small	C	D	0.866	22.8
Anadenanthera peregrina (L.) Speg.	Fabaceae	Abiotic	Small	C	D	1.08	15.35
Andira anthelmia (Vell.) Benth.	Fabaceae	Biotic	Large	C	D	0.736	8.7
Andira fraxinifolia Benth.	Fabaceae	Biotic	Large	C	D	0.788	18.1
Annona cacans Warm.	Annonaceae	Biotic	Small	S	D	0.424	20
Annona dolabripetala Raddi	Annonaceae	Biotic	Small	S	D	0.424	14
Annona emarginata (Schltdl.) H.Rainer	Annonaceae	Biotic	Small	S	D	0.413	8
Annona glabra L.	Annonaceae	Biotic	Large	S	E	0.59	12.4
Annona mucosa Jacq.	Annonaceae	Biotic	Small	S	D	0.413	14.6
Annona sylvatica (A.St.-Hil.)	Annonaceae	Biotic	Small	S	E	0.373	11.6
Aparisthmium cordatum	Euphorbiaceae	Biotic	Small	S	D	0.52	12

(A.Juss.) Baill.							
Apuleia leiocarpa (Vogel) J.F.Macbr.	Fabaceae	Abiotic	Small	C	D	0.83	18
Araucaria angustifolia (Bertol.) Kuntze	Araucariaceae	Biotic	Large	S	E	0.55	14.9
Aspidosperma olivaceum Müll.Arg	Apocynaceae	Abiotic	Large	S	D	0.793	9
Aspidosperma parvifolium A. DC.	Apocynaceae	Abiotic	Large	S	D	0.79	16.65
Aspidosperma polyneuron Müll.Arg.	Apocynaceae	Abiotic	Large	S	E	0.79	22.3
Aspidosperma ramiflorum Müll.Arg.	Apocynaceae	Abiotic	Large	S	D	0.79	10
Aspidosperma spruceanum Benth. ex Müll.Arg.	Apocynaceae	Abiotic	Large	S	E	0.753	15.4
Austrocritonia angulicaulis R.M.King & H.Rob.	Asteraceae	Abiotic	Small	S	D	0.505	11.9
Bathysa australis (A.St.-Hil.) K.Schum.	Rubiaceae	Abiotic	Small	S	E	0.64	15
Bathysa cuspidata (A.St.-Hil.) Hook.f.	Rubiaceae	Abiotic	Small	S	E	0.64	13.5
Bathysa nicholsonii K.Schum.	Rubiaceae	Abiotic	Small	S	E	0.637	17.55
Bauhinia pulchella Benth.	Fabaceae	Abiotic	Small	C	D	0.6	6.9
Bauhinia ungulata L.	Fabaceae	Abiotic	Small	C	E	0.94	8.7
Beilschmiedia emarginata (Meisn.) Kosterm.	Lauraceae	Biotic	Large	S	E	0.61	34.7
Beilschmiedia taubertiana (Schwacke & Mez) Kosterm.	Lauraceae	Biotic	Large	S	E	0.563	11
Brosimum guianense (Aubl.) Huber	Moraceae	Biotic	Small	S	E	0.88	18
Buchenavia hoehneana N.F.Mattos	Combretaceae	Biotic	Small	S		0.705	18
Buchenavia tomentosa Eichler	Combretaceae	Biotic	Large	S	E	0.705	8
Cabralea canjerana (Vell.) Mart.	Meliaceae	Biotic	Small	C	D	0.69	18
Calyptranthes clusiifolia O.Berg	Myrtaceae	Biotic	Small	S	E	0.72	7.95
Calyptranthes widgreniana O.Berg	Myrtaceae	Biotic	Small	S	E	0.82	12.6
Campomanesia guaviroba (DC.) Kiaersk.	Myrtaceae	Biotic	Small	S	D	0.76	19.75
Campomanesia guazumifolia (Cambess.) O.Berg	Myrtaceae	Biotic	Small	S	E	0.73	9.85
Campomanesia laurifolia Gardner	Myrtaceae	Biotic	Small	S	E	0.76	10.85
Campomanesia pubescens (Mart. ex DC.) O.Berg	Myrtaceae	Biotic	Small	S	E	0.73	12
Cariniana estrellensis (raddi) kuntze	Lecythidaceae	Abiotic	Large	S	D	0.78	34.75
Casearia arborea (Rich.)	Salicaceae	Biotic	Small	S	E	0.574	17.4

Urb.							
Casearia decandra Jacq.	Salicaceae	Biotic	Small	S	D	0.664	18.5
Casearia lasiophylla Eichler	Salicaceae	Biotic	Small	S	D	0.664	12
Casearia obliqua Spreng.	Salicaceae	Biotic	Small	S	E	0.678	8
Casearia selloana Eichler	Salicaceae	Biotic	Small	S		0.664	12.4
Casearia sylvestris Sw.	Salicaceae	Biotic	Small	S	E	0.84	15.4
Casearia ulmifolia Vahl ex Vent.	Salicaceae	Biotic	Small	S		0.574	15.7
Cassia ferruginea (Schrad.) Schrad. ex DC.	Fabaceae	Abiotic	Small	C	D	0.5	4
Casuarina equisetifolia L.	Casuarinaceae	Abiotic	Small	S	E	0.809	13.95
Cecropia glaziovii Snethl.	Urticaceae	Biotic	Small	S	E	0.41	17.7
Cecropia hololeuca Miq.	Urticaceae	Biotic	Large	S	E	0.43	23.6
Cecropia pachystachya Trécul	Urticaceae	Biotic	Small	S	E	0.41	16.1
Cedrela fissilis Vell.	Meliaceae	Abiotic	Large	C	D	0.55	19.3
Cedrela odorata L.	Meliaceae	Abiotic	Large	C	D	0.66	19.4
Ceiba speciosa (A.St.-Hil.) Ravenna	Malvaceae	Abiotic	Small	C	D	0.392	15.8
Cheiloclinium cognatum (Miers) A.C.Sm.	Celastraceae	Biotic	Large	S	E	0.732	7
Cheiloclinium serratum (Cambess.) A.C.Sm.	Celastraceae	Biotic	Large	S	E	0.732	15.85
Chionanthus filiformis (Vell.) P.S.Green	Oleaceae	Biotic	Large	S	E	0.855	9.85
Chomelia brasiliana A.Rich.	Rubiaceae	Biotic	Small	S	E	0.57	3
Citharexylum myrianthum Cham.	Verbenaceae	Biotic	Small	S	D	0.643	11.4
Citronella paniculata (Mart.) Howard	Cardiopteridacea e	Biotic	Small	S	E	0.47	10
Clethra scabra Pers.	Clethraceae	Abiotic	Small	S	E	0.53	14.55
Coccoloba declinata (Vell.) Mart.	Polygonaceae	Biotic	Small	S		0.568	5
Coccoloba warmingii Meisn	Polygonaceae	Biotic	Small	S		0.568	13.4
Copaifera langsdorffii Desf.	Fabaceae	Biotic	Small	C	E	0.7	11.6
Copaifera trapezifolia Hayne	Fabaceae	Biotic	Small	C	E	0.615	25
Cordia aberrans I.M.Johnst.	Boraginaceae	Biotic	Small	S		0.485	13.4
Cordia ecalyculata Vell.	Boraginaceae	Biotic	Small	S	E	0.485	8
Cordia magnoliifolia Cham.	Boraginaceae	Biotic	Small	S		0.52	19.2
Cordia sellowiana Cham.	Boraginaceae	Biotic	Small	S	E	0.485	24.8
Cordia toqueve Aubl.	Boraginaceae	Biotic	Small	S		0.485	19.55
Cordia trichotoma (Vell.) Arráb. ex Steud.	Boraginaceae	Abiotic	Small	S	D	0.78	21
Cordiera elliptica (Cham.) Kuntze	Rubiaceae	Biotic	Small	S		0.637	6.5

Coussapoa microcarpa (Schott) Rizzini	Urticaceae	Biotic	Small	S	E	0.59	27.6
Coussarea nodosa (Benth.) Müll.Arg.	Rubiaceae	Biotic	Small	S	E	0.61	8
Crepidospermum atlanticum Daly	Burseraceae	Biotic	Small	S		0.578	10.6
Croton celtidifolius Baill.	Euphorbiaceae	Abiotic	Small	S		0.459	10
Croton floribundus Spreng.	Euphorbiaceae	Abiotic	Small	S	D	0.6	12.5
Croton salutaris Casar.	Euphorbiaceae	Abiotic	Small	S		0.408	13
Croton urucurana Baill.	Euphorbiaceae	Abiotic	Small	S	D	0.83	14.4
Cryptocarya aschersoniana Mez	Lauraceae	Biotic	Large	S	E	0.57	5
Cryptocarya micrantha Meisn.	Lauraceae	Biotic	Large	S	E	0.563	18
Cupania emarginata Cambess.	Sapindaceae	Biotic	Small	C	E	0.65	13.8
*Cupania ludowigi*i Sommer & Ferrucci	Sapindaceae	Biotic	Large	C		0.619	19.3
Cupania oblongifolia Mart.	Sapindaceae	Biotic	Small	C	E	0.67	12
Cupania racemosa (Vell.) Radlk.	Sapindaceae	Biotic	Small	C	E	0.622	18.4
Cupania vernalis Cambess.	Sapindaceae	Biotic	Small	C	E	0.65	18.4
Cybistax antisyphilitica (Mart.) Mart.	Bignoniaceae	Abiotic	Large	C	D	0.59	13.4
Dalbergia foliolosa Benth.	Fabaceae	Abiotic	Small	C		0.8	16.4
Dalbergia frutescens (Vell.) Britton	Fabaceae	Abiotic	Large	C		0.69	5.85
Dalbergia nigra (Vell.) Alemao ex Benth.	Fabaceae	Abiotic	Small	C	D	0.87	10.6
Dalbergia villosa (Benth.) Benth.	Fabaceae	Abiotic	Small	C	E	0.808	9.7
Daphnopsis brasiliensis Mart.	Thymelaeaceae	Biotic	Small	S	E	0.52	5
Daphnopsis fasciculata (Meisn.) Nevling	Thymelaeaceae	Biotic	Small	S	E	0.47	9
Dictyoloma vandellianum A.Juss	Rutaceae	Abiotic	Small	C	E	0.639	15.3
Duguetia lanceolata A.St-Hil	Annonaceae	Biotic	Large	S	E	0.92	15.05
Ecclinusa ramiflora Mart.	Sapotaceae	Biotic	Small	S	E	0.961	20
Endlicheria glomerata Mez	Lauraceae	Biotic	Large	S	E	0.496	7
Endlicheria paniculata (Spreng.) J.F. Macbr.	Lauraceae	Biotic	Large	S	E	0.58	14
Enterolobium contortisiliquum (Vell.) Morong	Fabaceae	Biotic	Small	C	D	0.54	21.3
Eremanthus erythropappus (DC.) MacLeish	Asteracea	Abiotic	Small	S	D	0.59	10
Eriobotrya japonica (Thunb.) Lindl.	Rosaceae	Biotic	Large	S	E	0.88	5.5
Eriotheca candolleana (K. Schum.) A. Robyns	Malvaceae	Abiotic	Small	C	E	0.43	15.75

Erythroxylum citrifolium A.St.-Hil.	Erythroxylaceae	Biotic	Small	S		0.71	7
Erythroxylum deciduum A.St.-Hil.	Erythroxylaceae	Biotic	Small	S	D	0.81	14.5
Erythroxylum pelleterianum A.St.-Hil.	Erythroxylaceae	Biotic	Small	S		0.808	19.25
Eugenia brasiliensis Lam.	Myrtaceae	Biotic	Small	S	E	0.761	8.9
Eugenia candolleana DC.	Myrtaceae	Biotic	Small	S	E	0.91	15.5
Eugenia capparidifolia DC.	Myrtaceae	Biotic	Small	S		0.726	16.25
Eugenia cerasiflora Miq.	Myrtaceae	Biotic	Small	S	E	0.65	16.6
Eugenia dodonaeifolia Cambess.	Myrtaceae	Biotic	Small	S		0.761	8
Eugenia handroana D.Legrand	Myrtaceae	Biotic	Large	S		0.726	11
Eugenia handroi (Mattos) Mattos	Myrtaceae	Biotic	Large	S		0.726	15.25
Eugenia hiemalis Cambess.	Myrtaceae	Biotic	Small	S	D	0.726	19.85
Eugenia involucrata DC.	Myrtaceae	Biotic	Small	S	E	0.726	15.4
Eugenia longipedunculata Nied.	Myrtaceae	Biotic	Small	S	D	0.726	11
Eugenia moonioides O.Berg	Myrtaceae	Biotic	Small	S		0.726	9
Eugenia pisiformis Cambess.	Myrtaceae	Biotic	Small	S		0.726	13.2
Eugenia sphenophylla O.Berg	Myrtaceae	Biotic	Small	S		0.726	7
Eugenia subundulata Kiaersk.	Myrtaceae	Biotic	Small	S		0.722	13.75
Eugenia vattimoana Mattos	Myrtaceae	Biotic	Small	S		0.726	8.9
Eugenia widgrenii Sond. ex O.Berg	Myrtaceae	Biotic	Small	S		0.726	7
Euphorbia cotinifolia L.	Myrtaceae	Abiotic	Small	S	E	0.731	7.85
Euterpe edulis Mart.	Arecaceae	Biotic	Small	C	E	0.407	19
Faramea hyacinthina Mart.	Rubiaceae	Biotic	Small	S	E	0.637	17.75
Faramea multiflora A.Rich. ex DC.	Rubiaceae	Biotic	Small	S		1.137	5.875
Faramea nigrescens Mart.	Rubiaceae	Biotic	Small	S		0.637	5.95
Ficus citrifolia Mill.	Moraceae	Biotic	Small	S	E	0.618	13
Ficus elastica Roxb.	Moraceae	Biotic	Small	S	E	0.618	4
Ficus mexiae Standl	Moraceae	Biotic	Small	S	E	0.6	7
Garcinia gardneriana (Planch. & Triana) Zappi	Clusiaceae	Biotic	Large	S	E	0.87	20.3
Geonoma schottiana Mart.	Arecaceae	Biotic	Small	C	E	0.557	3.5
Guapira graciliflora (Mart. ex Schmidt) Lundell	Nyctaginaceae	Biotic	Small	S	D	0.492	12.4
Guapira hirsuta (Choisy) Lundell	Nyctaginaceae	Biotic	Small	S		0.492	11.35
Guapira opposita (Vell.) Reitz	Nyctaginaceae	Biotic	Small	S	E	0.83	12

Guarea kunthiana A. Juss	Meliaceae	Biotic	Small	C	E	0.82	8
Guarea macrophylla Vahl	Meliaceae	Biotic	Small	C	E	0.645	8.3
Guatteria australis A.St.-Hil.	Annonaceae	Biotic	Small	S	E	0.543	9.85
Guatteria pohliana Schltdl.	Annonaceae	Biotic	Small	S	E	1.09	12
Guatteria sellowiana Schltdl.	Annonaceae	Biotic	Small	S		0.55	18
Guatteria villosissima A.St.Hil.	Annonaceae	Biotic	Small	S		0.54	13.4
Guettarda viburnoides Cham. & Schltdl.	Rubiaceae	Biotic	Small	S	E	0.73	15.7
Handroanthus chrysotrichus (Mart. ex DC.) Mattos	Bignoniaceae	Abiotic	Large	C	D	0.615	13.5
Handroanthus impetiginosus (Mart. ex DC.) Mattos	Bignoniaceae	Abiotic	Large	C	D	0.96	8.5
Heisteria silvianii Schwacke	Olacaceae	Biotic	Small	S	E	0.7	20.7
Hirtella hebeclada Moric ex. DC.	Chrysobalanaceae	Biotic	Large	S	E	0.72	10.6
Holocalyx balansae Micheli	Fabaceae	Biotic	Large	C	E	0.859	8
Hortia brasiliana Vand. ex DC.	Rutaceae	Biotic	Small	S	E	0.842	10.95
Hyeronima alchorneoides Allemão	Euphorbiaceae	Biotic	Small	S	E	0.648	13
Hyeronima oblonga (Tul.) Müll.Arg.	Euphorbiaceae	Biotic	Small	S		0.603	22
Hymenolobium janeirense Kuhlm.	Fabaceae	Abiotic	Small	C		0.668	9.35
Hyptidendron asperrimum (Spreng.) Harley	Lamiaceae	Biotic	Small	S	E	0.43	12
Ilex cerasifolia Reissek	Aquifoliaceae	Biotic	Small	S	D	0.528	7
Ilex paraguariensis A.St.-Hil.	Aquifoliaceae	Biotic	Small	S	E	0.528	21.6
Ilex theezans Mart. ex Reissek	Aquifoliaceae	Biotic	Small	S	E	0.528	10.45
Inga barbata Benth.	Fabaceae	Biotic	Small	C		0.576	4
Inga capitata Desv.	Fabaceae	Biotic	Small	C		0.592	9.8
Inga cylindrica (Vell.) Mart.	Fabaceae	Biotic	Small	C	E	0.48	25
Inga edulis Mart.	Fabaceae	Biotic	Small	C	E	0.576	24.1
Inga flagelliformis (Vell.) Mart.	Fabaceae	Biotic	Small	C		0.576	13.5
Inga marginata Willd.	Fabaceae	Biotic	Small	C	E	0.547	8.85
Inga sessilis (Vell.) Mart.	Fabaceae	Biotic	Small	C	E	0.43	8
Inga striata Benth.	Fabaceae	Biotic	Small	C		0.576	11
Inga subnuda Salzm.	Fabaceae	Biotic	Small	C		0.576	17
Inga virescens Benth.	Fabaceae	Biotic	Small	C		0.576	20.35
Ixora brevifolia Benth.	Rubiaceae	Biotic	Small	S	E	0.88	8.7
Jacaranda macrantha Cham.	Bignoniaceae	Abiotic	Large	C	D	0.395	10.25

Jacaranda micrantha Cham.	Bignoniaceae	Abiotic	Small	C	D	0.482	14
Jacaranda puberula Cham.	Bignoniaceae	Abiotic	Large	C	D	0.58	20.1
Jacaratia spinosa (Aubl.) A. DC.	Caricaceae	Biotic	Small	C	E	0.265	12
Kielmeyera lathrophyton Saddi	Calophyllaceae	Abiotic	Large	S	E	0.67	4
Lacistema pubescens Mart.	Lacistemataceae	Biotic	Small	S		0.513	14
Lafoensia glyptocarpa Koehne	Lythraceae	Abiotic	Large	S	E	0.96	35
Lamanonia cuneata (Cambess.) Kuntze	Cunoniaceae	Abiotic	Small	C		0.513	8
Lamanonia ternata Vell.	Cunoniaceae	Abiotic	Small	C	E	0.513	19.9
Laplacea fruticosa (Schrad.) Kobuski	Theaceae	Abiotic	Small	S	E	0.66	22.5
Leucaena leucocephala (Lam.) de Wit	Fabaceae	Abiotic	Small	C	E	0.605	7.9
Licania kunthiana Hook. f.	Chrysobalanaceae	Biotic	Small	S	E	0.99	17.2
Licaria bahiana Kurz	Lauraceae	Biotic	Large	S	E	0.815	13.75
Lonchocarpus cultratus (Vell.) A.M.G.Azevedo & H.C.Lima	Fabaceae	Abiotic	Large	C	D	0.734	8
Luehea divaricata Mart.	Malvaceae	Abiotic	Small	S	D	0.64	13.4
Mabea fistulifera Mart.	Euphorbiaceae	Biotic	Small	S	D	0.616	7
Machaerium acutifolium Vogel	Fabaceae	Abiotic	Small	C	D	1.12	14
Machaerium brasiliensis Vogel	Fabaceae	Abiotic	Small	C	D	0.66	22.55
Machaerium hirtum (Vell.) Stellfeld	Fabaceae	Abiotic	Small	C	D	0.66	13.6
Machaerium nyctitans (Vell. Conc.) Benth.)	Fabaceae	Abiotic	Small	C	E	0.591	13
Machaerium ruddianum C.V.Mendonça & A.M.G.Azevedo	Fabaceae	Abiotic	Small	C		0.591	5
Machaerium stipitatum Vogel	Fabaceae	Abiotic	Small	C	E	0.84	5
Macropeplus schwackeanus (Perkins) I.Santos & Peixoto	Monimiaceae	Biotic	Small	S		0.665	13.65
Mangifera indica L.	Anacardiaceae	Biotic	Large	S	E	0.553	7.85
Maprounea guianensis Aubl.	Euphorbiaceae	Biotic	Small	S	E	0.72	18.65
Margaritopsis chaenotricha (DC.) C.M.Taylor	Rubiaceae	Biotic	Small	S	E	0.52	4
Marlierea eugenioides (Cambess.) D.Legrand	Myrtaceae	Biotic	Small	S		0.936	8
Marlierea excoriata Mart.	Myrtaceae	Biotic	Small	S		0.936	10
Marlierea laevigata (DC.) Kiaersk.	Myrtaceae	Biotic	Small	S		0.936	25
Marlierea obscura O.Berg	Myrtaceae	Biotic	Small	S		0.936	19
Matayba elaeagnoides Radlk.	Sapindaceae	Biotic	Small	S	E	0.771	11.95

Matayba guianensis Aubl.	Sapindaceae	Biotic	Small	S	E	0.84	7
Matayba marginata Radlk	Sapindaceae	Biotic	Small	S		0.75	13.6
Maytenus brasiliensis Mart.	Celastraceae	Biotic	Small	S		0.745	14.65
Maytenus communis Reissek	Celastraceae	Biotic	Small	S		0.745	10
Maytenus evonymoides Reissek	Celastraceae	Biotic	Small	S	E	0.745	13.1
Maytenus floribunda Reissek	Celastraceae	Biotic	Small	S	E	0.745	14
Maytenus gonoclada Mart.	Celastraceae	Biotic	Small	S	E	0.745	15.05
Maytenus salicifolia Reissek	Celastraceae	Biotic	Small	S		0.745	16.4
Melanoxylon brauna Schott	Fabaceae	Abiotic	Small	C	E	1.05	17
Meliosma itatiaiae Urb.	Sabiaceae	Biotic	Large	S	E	1.18	19.3
Miconia budlejoides Triana	Melastomataceae	Biotic	Small	S		0.613	8.6
Miconia chartacea Triana	Melastomataceae	Biotic	Small	S		0.618	13
Miconia cinnamomifolia (DC.) Naudin	Melastomataceae	Biotic	Small	S	E	0.73	20
Miconia inconspicua Miq.	Melastomataceae	Biotic	Small	S		0.613	9.5
Miconia latecrenata (DC.) Naudin	Melastomataceae	Biotic	Small	S	E	0.623	15.15
Miconia mellina DC.	Melastomataceae	Biotic	Small	S		0.624	7.75
Miconia pusilliflora (DC.) Naudin	Melastomataceae	Biotic	Small	S		0.613	8
Miconia pyrifolia Naudin	Melastomataceae	Biotic	Small	S		0.613	16.55
Miconia sellowiana Naudin	Melastomataceae	Biotic	Small	S	E	0.613	5
Miconia trianae Cogn.	Melastomataceae	Biotic	Small	S		0.624	16.65
Miconia tristis Spring	Melastomataceae	Biotic	Small	S		0.613	9
Miconia urophylla DC.	Melastomataceae	Biotic	Small	S	E	0.623	14
Miconia valtheri Naudin	Melastomataceae	Biotic	Small	S		0.613	6
Mimosa artemisiana Heringer & Paula	Fabaceae	Abiotic	Small	C	D	0.91	18
Mimosa bimucronata (DC.) Kuntze	Fabaceae	Abiotic	Small	C	D	0.61	8
Mollinedia argyrogyna Perkins	Monimiaceae	Biotic	Small	S		0.63	14.9
Mollinedia blumenaviana Perkins	Monimiaceae	Biotic	Small	S		0.665	6
Mollinedia schottiana (Spreng.) Perkins	Monimiaceae	Biotic	Small	S		0.63	9.85
Mollinedia triflora (Spreng.) Tul.	Monimiaceae	Biotic	Small	S		0.665	4
Mollinedia widgrenii A.DC.	Monimiaceae	Biotic	Small	S	E	0.63	10.45
Mouriri guianensis Aubl.	Memecylaceae	Biotic	Small	S	E	1.1	10.85
Myrceugenia miersiana D.Legrand & Kausel	Myrtaceae	Biotic	Small	S	E	0.65	11.4
Myrcia amazonica DC.	Myrtaceae	Biotic	Small	S	E	0.801	8

Myrcia anceps (Spreng.) O.Berg	Myrtaceae	Biotic	Small	S		0.801	16.65
Myrcia crocea Kiaersk.	Myrtaceae	Biotic	Small	S	E	0.801	6
Myrcia hebepetala DC.	Myrtaceae	Biotic	Small	S	E	0.801	5.85
Myrcia multiflora (O. Berg) D. Legrand	Myrtaceae	Biotic	Small	S	E	0.801	13
Myrcia pubipetala Miq.	Myrtaceae	Biotic	Small	S		0.801	16.7
Myrcia splendens (Sw.) DC.	Myrtaceae	Biotic	Small	S	E	0.8	16
Myrciaria floribunda (H. West. Ex. Wild.) O. Berg.	Myrtaceae	Biotic	Small	S	E	0.89	12
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	Primulaceae	Biotic	Small	S	E	0.647	11.1
Myrsine gardneriana A.DC.	Primulaceae	Biotic	Small	S	E	0.563	9
Myrsine lancifolia Mart.	Primulaceae	Biotic	Small	S	E	0.563	10.7
Myrsine umbellata Mart.	Primulaceae	Biotic	Small	S	E	0.86	18.2
Myrsine venosa A.DC.	Primulaceae	Biotic	Small	S	E	0.563	9
Nectandra lanceolata Ness	Lauraceae	Biotic	Small	S	E	0.583	11.05
Nectandra megapotamica (Spreng.) Mez	Lauraceae	Biotic	Small	S	E	0.583	14.1
Nectandra membranacea (Sw.) Griseb.	Lauraceae	Biotic	Small	S	E	0.583	9
Nectandra nitidula Nees	Lauraceae	Biotic	Small	S	E	0.77	18.7
Nectandra oppositifolia Nees	Lauraceae	Biotic	Small	S	E	0.521	17.1
Ocotea aciphylla (Nees & Mart.) Mez	Lauraceae	Biotic	Small	S		0.511	20
Ocotea bicolor Vattimo-Gil	Lauraceae	Biotic	Small	S		0.519	10
Ocotea brachybotrya (Meisn.) Mez	Lauraceae	Biotic	Small	S		0.525	3.5
Ocotea catharinensis Mez	Lauraceae	Biotic	Small	S	E	0.75	11
Ocotea corymbosa (Meisn.) Mez	Lauraceae	Biotic	Small	S	E	0.501	23.4
Ocotea cujumary Mart.	Lauraceae	Biotic	Small	S	E	0.501	8
Ocotea diospyrifolia (Meisn.) Mez	Lauraceae	Biotic	Small	S	E	0.519	18
Ocotea glaziovii Mez	Lauraceae	Biotic	Small	S	E	0.501	16.55
Ocotea indecora (Schott) Mez	Lauraceae	Biotic	Small	S		0.501	8.85
Ocotea lanata (Nees) Mez	Lauraceae	Biotic	Small	S		0.501	10.8
Ocotea lancifolia (Schott) Mez	Lauraceae	Biotic	Small	S		0.501	14.1
Ocotea laxa (Nees) Mez	Lauraceae	Biotic	Small	S		0.501	16.95
Ocotea longifolia Kunth	Lauraceae	Biotic	Small	S		0.501	12.85
Ocotea odorifera (Vell.) Rohwer	Lauraceae	Biotic	Small	S	E	0.76	20
Ocotea puberula (Rich.) Nees	Lauraceae	Biotic	Small	S	E	0.455	14.8
Ocotea vaccinioides	Lauraceae	Biotic	Small	S		0.501	13.9

(Meisn.) Mez							
Ocotea velloziana (Meisn.) Mez	Lauraceae	Biotic	Small	S		0.519	16.8
Ocotea villosa Kosterm.	Lauraceae	Biotic	Small	S		0.519	8.425
Ormosia altimontana Meireles & H.C.Lima	Fabaceae	Biotic	Large	S		0.621	15
Ouratea parviflora (A.DC.) Baill.	Ochnaceae	Biotic	Small	S		0.774	4.875
Ouratea semiserrata (Mart. & Nees) Engl.	Ochnaceae	Biotic	Small	S		0.774	9.625
Ouratea spectabilis (Mart. & Engl.) Engl.	Ochnaceae	Biotic	Small	S	D	0.64	6
Oxandra martiana (Schltdl.) R.E.Fr.	Annonaceae	Biotic	Small	S		0.748	25.8
Pachira endecaphylla (Vell.) Carv.-Sobr.	Malvaceae	Abiotic	Small	C		0.448	20.6
Pachira glabra Pasq.	Malvaceae	Abiotic	Large	C	E	0.448	7
Peltophorum dubium (Spreng.) Taub.	Fabaceae	Abiotic	Small	C	D	0.69	12
Pera glabrata (Schott) Poepp. ex Baill.	Euphorbiaceae	Biotic	Small	S	E	0.67	11.2
Persea americana Miller	Lauraceae	Biotic	Large	S	E	1.1	12.85
Persea willdenovii Kosterm.	Lauraceae	Biotic	Small	S	E	0.612	22.65
Picramnia glazioviana Engl.	Simaroubaceae	Biotic	Small	C		0.395	11
Picramnia ramiflora Planch.	Simaroubaceae	Biotic	Small	C		0.395	14.7
Pimenta pseudocaryophyllus (Gomes) Landrum	Myrtaceae	Biotic	Small	S	E	1	11.9
Pinus elliottii Engelm.	Pinaceae	Abiotic	Large	S	E	0.482	16
Piper cernuum Vell.	Piperaceae	Biotic	Small	S	E	0.33	4.95
Piptadenia gonoacantha (Mart.) J.F.Macbr.	Fabaceae	Abiotic	Small	C	D	0.75	20
Piptadenia paniculata Benth.	Fabaceae	Abiotic	Small	C	E	0.814	11.7
Piptocarpha macropoda (DC.) Baker	Asteraceae	Abiotic	Small	C	D	0.615	14
Platypodium elegans Vogel	Fabaceae	Abiotic	Small	C	D	0.82	16.8
Podocarpus sellowii Klotzsch ex Endl.	Podocarpeceae	Biotic	Small	S	E	0.474	13
Pogonophora schomburgkiana Miers ex Benth.	Peraceae	Abiotic	Small	S	E	0.833	8
Poincianella pluviosa (DC.) L.P.Queiroz	Fabaceae	Abiotic	Large	C	E	0.833	15.55
Posoqueria latifolia (Rudge) Schult.	Rubiaceae	Biotic	Small	S	E	0.582	13
Pourouma guianensis Aubl	Urticaceae	Biotic	Small	S	E	0.38	15
Pouteria caimito (Ruiz & Pav.) Radlk	Sapotaceae	Biotic	Large	S	E	0.95	15.75
Pouteria guianensis Aubl.	Sapotaceae	Biotic	Large	S	E	0.93	15
Protium heptaphyllum (Aubl.) Marchand	Burserácea	Biotic	Small	S	E	0.77	16.25

Protium spruceanum (Benth.) Engl.	Burserácea	Biotic	Small	S	E	0.56	8
Prunus myrtifolia (L.) Urb.	Rosaceae	Biotic	Small	S	E	0.741	15.2
Pseudobombax longiflorum (Mart. & Zucc.) A.Robyns	Malvaceae	Abiotic	Small	C	D	0.285	5
Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima	Fabaceae	Abiotic	Large	C	E	0.62	9.65
Pseudopiptadenia leptostachya (Benth.) Rauschert	Fabaceae	Abiotic	Small	C		0.664	22
Psychotria carthagenensis Jacq.	Rubiaceae	Biotic	Small	S	E	0.7	11.8
Psychotria cephalantha (Müll.Arg.) Standl.	Rubiaceae	Biotic	Small	S	E	0.52	7.8
Psychotria nuda (Cham. & Schltdl.) Wawra	Rubiaceae	Biotic	Small	S	E	0.52	18.35
Psychotria suterella Müll.Arg.	Rubiaceae	Biotic	Small	S	E	0.52	8
Psychotria vellosiana Benth.	Rubiaceae	Biotic	Small	S	E	0.52	12.6
Pterocarpus rohrii Vahl	Fabaceae	Abiotic	Small	C	E	0.427	13
Qualea gestasiana A.St.-Hil.	Vochysiaceae	Abiotic	Small	S		0.633	25.1
Qualea lundii (Warm.) Warm.	Vochysiaceae	Abiotic	Small	S		0.633	15.95
Roupala montana Aubl.	Proteaceae	Abiotic	Large	S	D	0.73	15
Sapium glandulatum (Vell.) Pax.	Euphorbiaceae	Biotic	Small	S	D	0.421	13.7
Schefflera angustissima (Marchal) Frodin	Araliaceae	Biotic	Small	C	E	0.45	14
Schefflera calva (Cham.) Frodin & Fiaschi	Araliaceae	Biotic	Small	C		0.45	17.5
Schefflera longipetiolata (Pohl ex DC.) Frodin & Fiaschi	Araliaceae	Biotic	Small	C		0.45	7.95
Schefflera morototoni (Aubl.) Maguire et al.	Araliaceae	Biotic	Small	C	E	0.62	22
Schefflera vinosa (Cham. & Schltdl.) Frodin & Fiaschi	Araliaceae	Biotic	Small	C		0.45	8.9
Schinus terebinthifolius Raddi	Anacardiaceae	Biotic	Small	C	E	0.82	8
Schizolobium parahyba (Vell.) S.F. Blake	Fabaceae	Abiotic	Large	C	E	0.32	15.5
Seguieria langsdorffii Moq.	Phytolaccaceae	Abiotic	Small	S	E	0.59	18
Senegalia polyphylla (DC.) Britton & Rose	Fabaceae	Abiotic	Small	C	D	0.79	11
Senna macranthera H.S.Irwin & Barneby	Fabaceae	Abiotic	Small	C	D	0.561	12
Senna multijuga (Rich.) H.S.Irwin & Barneby	Fabaceae	Abiotic	Small	C	D	0.582	22.2
Siparuna guianensis Aubl.	Siparunaceae	Biotic	Small	S	D	0.656	9.3
Sloanea guianensis (Aubl.) Benth.	Elaeocarpaceae	Biotic	Small	S	E	0.821	14.55
Sloanea hirsuta (Schott)	Elaeocarpaceae	Biotic	Small	S	E	0.809	15.7

Planch. ex Benth.							
Sloanea monosperma Vell.	Elaeocarpaceae	Biotic	Small	S	E	0.806	19.95
Sloanea retusa Uittien	Elaeocarpaceae	Biotic	Small	S	E	0.93	14.6
Solanum argenteum Blanchet ex Dunal	Solanaceae	Biotic	Small	S		0.28	20.1
Solanum cernuum Vell.	Solanaceae	Biotic	Small	S		0.28	8.8
Solanum leucodendron Sendtn.	Solanaceae	Biotic	Small	S		0.24	15.85
Solanum pseudoquina A.St.-Hil.	Solanaceae	Biotic	Small	S	E	0.809	16.1
Solanum sellowianum Sendtn.	Solanaceae	Biotic	Small	S		0.28	16
Sorocea bonplandii (Baill.) W.C. Burger	Moraceae	Biotic	Small	S	E	0.67	9
Sorocea guilleminiana Gaudich.	Moraceae	Biotic	Small	S	E	0.578	12
Stryphnodendron polyphyllum Mart.	Fabaceae	Biotic	Small	C	E	0.619	16
Swartzia flaemingii Raddi	Fabaceae	Biotic	Large	C	E	0.834	21.55
Swartzia macrostachya Benth.	Fabaceae	Biotic	Large	C	E	0.92	6
Swartzia myrtifolia Sm.	Fabaceae	Biotic	Large	C	E	0.9	18.2
Syagrus romanzoffiana (Cham.) Glassman	Arecaceae	Biotic	Large	S	E	0.557	9.4
Symplocos pubescens Klotzsch ex Benth.	Symplocaceae	Biotic	Small	S	E	0.49	16
Syzygium jambos (L.) Alston	Myrtaceae	Biotic	Large	S	E	0.7	14
Syzygium cumin Bark	Myrtaceae	Biotic	Large	S	E	0.673	4
Tabernaemontana laeta Mart.	Bignoniaceae	Biotic	Small	S	E	0.462	17.6
Tachigali paratyensis (Vell.) H.C.Lima	Fabaceae	Abiotic	Small	S		0.559	14.85
Tachigali rugosa (Mart. ex Benth.) Zarucchi & Pipoly	Fabaceae	Abiotic	Small	S	E	0.69	15.75
Tachigali vulgaris L.G.Silva & H.C.Lima	Fabaceae	Abiotic	Large	S		0.56	29
Tapirira guianensis Aubl.	Anacardiaceae	Biotic	Small	S	E	0.51	22.4
*Tapirira obtusa (*Benth.) J.D.Mitch.	Anacardiaceae	Biotic	Small	S	E	0.293	20.75
Terminalia argentea Mart.	Combretaceae	Abiotic	Small	S	D	0.81	20.8
Tibouchina estrellensis (Raddi) Cogn.	Melastomataceae	Abiotic	Small	S	E	0.595	12
Tibouchina fissinervia (Schrank & Mart. ex DC.) Cogn.	Melastomataceae	Abiotic	Small	S	E	0.627	20
Tibouchina fothergillae (DC.) Cogn.	Melastomataceae	Abiotic	Small	S	E	0.627	8
Tibouchina mutabilis (Vell.) Cogn.	Melastomataceae	Abiotic	Small	S	E	0.66	12
Tovomita glazioviana Engl.	Clusiaceae	Biotic	Small	S		0.679	12
Tovomitopsis saldanhae Engl.	Clusiaceae	Biotic	Small	S		0.628	20.6

Trema micrantha (L.) Blume	Cannabaceae	Biotic	Small	S	D	0.267	10.8
Trichilia casarettoi C.DC.	Meliaceae	Biotic	Small	C	E	0.78	24.9
Trichilia catigua A.Juss.	Meliaceae	Abiotic	Small	C	E	0.688	13.55
Trichilia elegans A.Juss.	Meliaceae	Biotic	Small	C	E	0.651	12.55
Trichilia emarginata (Turcz.) C.DC.	Meliaceae	Biotic	Small	C	E	0.651	12
Trichilia hirta L.	Meliaceae	Biotic	Small	C	E	0.6	15
Trichilia lepidota Mart.	Meliaceae	Biotic	Small	C	E	0.635	23.65
Urera baccifera (L.) Gaudich. ex Wedd.	Urticaceae	Biotic	Small	C	E	0.18	3
Vernonanthura discolor (Spreng.) H.Rob.	Asteraceae	Abiotic	Small	S	E	0.54	6
Vernonanthura divaricata (Spreng.) H.Rob.	Meliaceae	Abiotic	Small	S		0.54	15
Vernonanthura phosphorica (Vell.) H.Rob.	Meliaceae	Abiotic	Small	S	E	0.54	11.75
Virola bicuhyba (Schott ex Spreng.) Warb.	Myristicaceae	Biotic	Large	S	E	0.61	25
Vismia guianensis (Aubl.) Choisy	Hypericaceae	Biotic	Small	S	E	0.475	12
Vismia magnoliifolia Schltdl. & Cham.	Hypericaceae	Biotic	Small	S		0.475	10.3
Vitex polygama Cham.	Lamiaceae	Biotic	Small	C	E	0.589	16.25
Vitex sellowiana Cham.	Lamiaceae	Biotic	Small	C	E	0.71	10
Vochysia bifalcata Warm.	Vochysiaceae	Abiotic	Large	S	E	0.75	30
Vochysia magnifica Warm.	Vochysiaceae	Abiotic	Large	S	E	0.78	24
Vochysia rectiflora Warm.	Vochysiaceae	Abiotic	Large	S		0.457	31.5
Vochysia tucanorum Mart.	Vochysiaceae	Abiotic	Large	S	D	0.457	19.6
Xylopia brasiliensis Spreng.	Annonaceae	Biotic	Small	S	E	0.7	23
Xylopia sericea A.St.-Hil.	Annonaceae	Biotic	Small	S	E	0.579	17.05
Xylosma ciliatifolia (Clos) Eichler	Salicaceae	Biotic	Small	S	E	0.82	8
Zanthoxylum rhoifolium Lam.	Rutaceae	Biotic	Small	C	D	0.493	14
Zollernia ilicifolia (Brongn.) Vogel	Fabaceae	Biotic	Small	S	D	1.05	7

Table S6: Tukey test from generalized mixed models testing effects of land-use history on functional index.

	Control-Without LUH		Control-Cropland LUH		Control-Denudation LUH	
	z-value	*p-value*	*z value*	*p-value*	*z value*	*p-value*
FRic	-0.634	0.921	-2.701	0.034*	-6.238	<0.001*
FDis	-0.456	0.968	-1.423	0.480	-2.790	0.026*
FR	-1.751	0.297	-4.604	<0.001*	-8.330	<0.001*
RD	-2.155	0.135	-5.234	<0.001*	-8.671	<0.001*

	Without-Cropland LUH		Without-Denudation LUH		Cropland-Denudation	
	z value	*p-value*	*z value*	*p-value*	*z value*	*p-value*
FRic	-2.067	0.163	-5.609	<0.001*	-3.557	0.001*
FDis	-0.967	0.768	-2.338	0.090	-1.38	0.520
FR	-2.854	0.022*	-6.589	<0.001*	-3.76	0.001*
RD	-3.078	0.011*	-6.543	<0.001 *	-3.505	0.002*

*are significantly different at p > 0 05

Table S7: The results from a nonparametric analysis of variance (Kruskal-Wallis test) for species basal area among each functional group

Functional Group	Chi-squared	p-value
FG1	14.489	0.0023*
FG2	32.422	<0.001*
FG3	59.707	<0.001*
FG4	53.101	<0.001*
FG5	26.846	<0.001*
FG6	24.317	<0.001*
FG7	8.1243	0.0435*
FG8	40.301	<0.001*
FG9	46.686	<0.001*
FG10	61.272	<0.001*
FG11	13.763	0.003*
Functional Effect Group		
EG1	35.283	<0.001*
EG2	21.288	<0.001*
EG3	51.017	<0.001*
EG4	11.296	0.01
EG5	30.412	<0.001*
EG6	40.825	<0.001*

*are significantly different at p < 0 05.

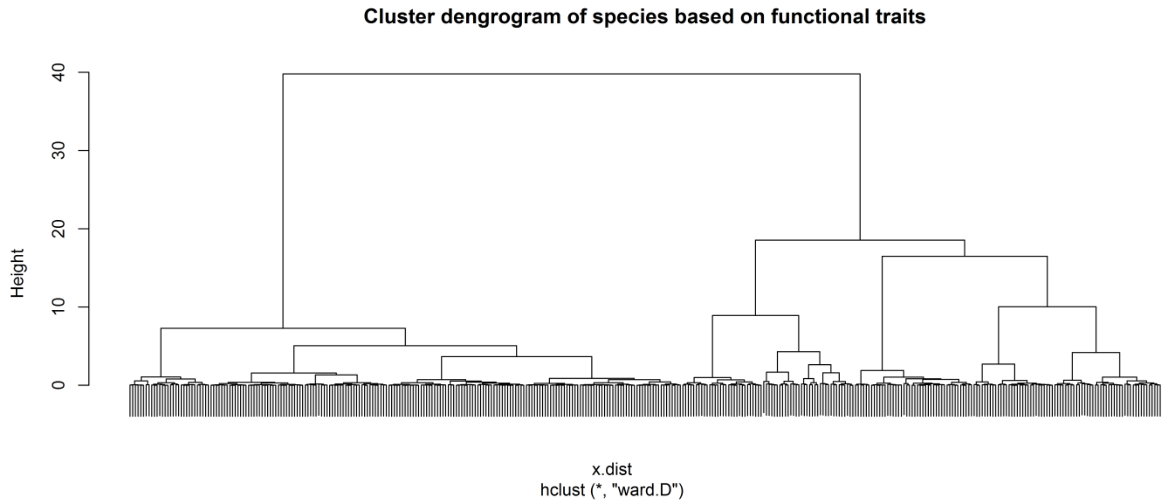

Fig S1: Dendrogram resulting from classifying species according to their similarity in the functional traits.

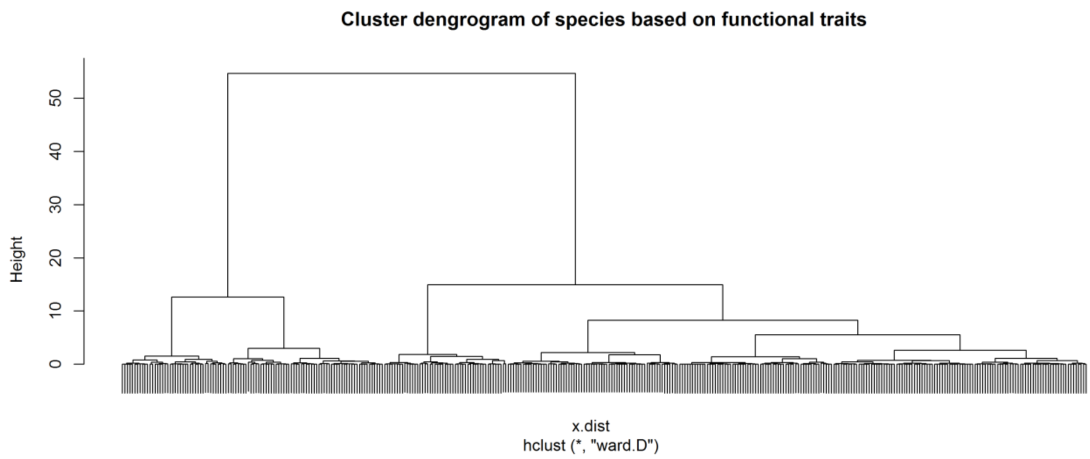

Fig S2: Dendrogram resulting from classifying species according to their similarity in the effects functional traits.

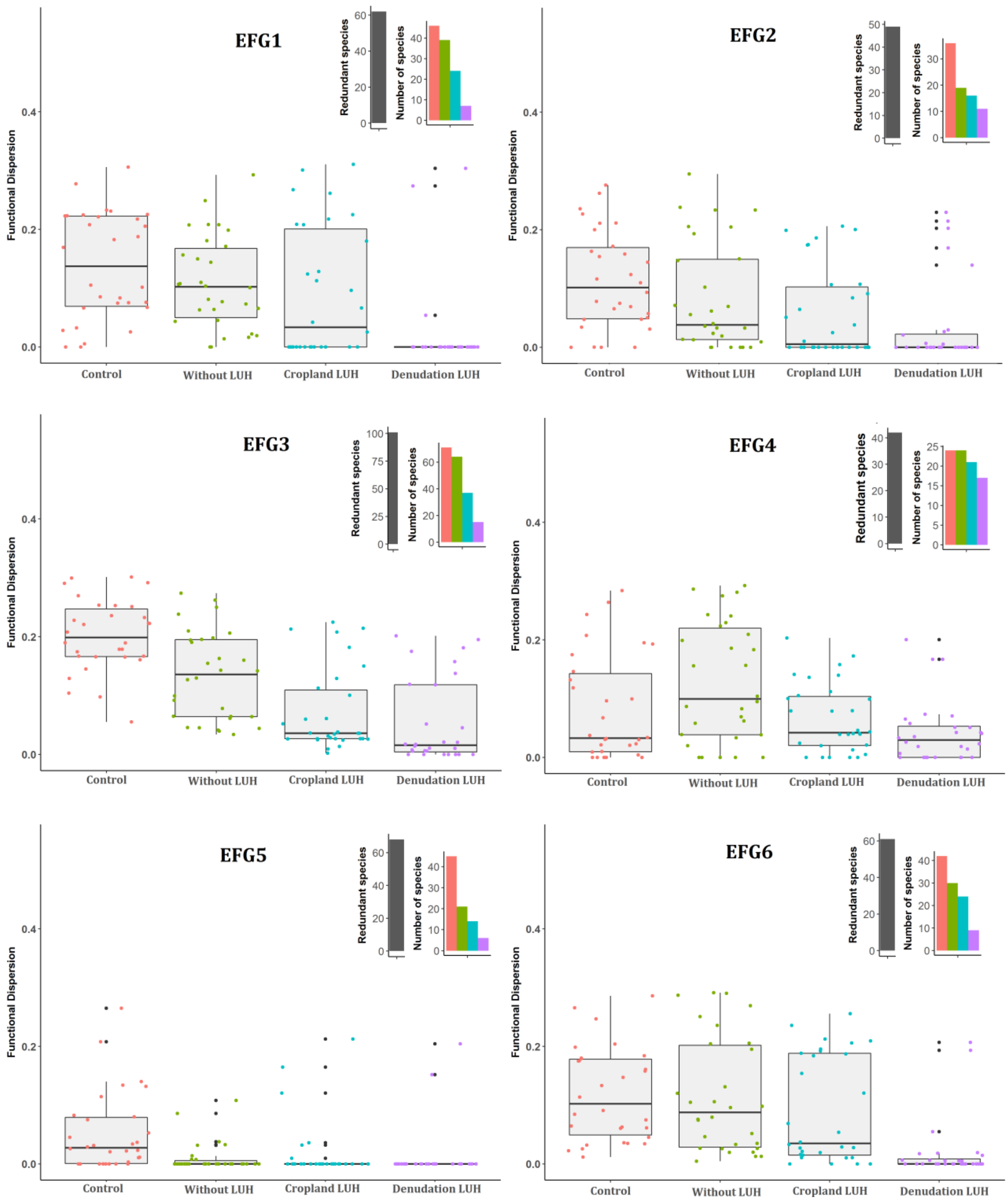

Fig S3: Species and functional dispersion of the 6 functional effects groups (FG) based in their response traits.