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Érica Rievrs Borges

PHYLOGENETIC DIVERSITY AND ECOSYSTEM SERVICES OF URBAN FORESTS

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Tese apresentada ao Programa de Pós-graduação em Ecologia, Instituto de Ciências Biológicas da Universidade Federal de Juiz de Fora, como parte dos requisitos necessários para obtenção do título de Doutora em Ecologia. Área de Biodiversidade, subárea Ecologia.

Orientador: Prof. Dr. Fabrício Alvim Carvalho

Co-orientador: Prof. Dr. Marcelo Leandro Bueno

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BANCA EXAMINADORA

Dr. Fabrício Alvim Carvalho- Orientador
Universidade Federal de Juiz de Fora

Dr. Pedro Manuel Villa
Universidade Federal de Viçosa

Dra. Vanessa Leite Rezende
Universidade Federal de Lavras

Simone Jaqueline Cardoso

Dra. Simone Jaquelie Cardoso
Universidade Federal de Juiz de Fora

Luiz Menini Neto

Dr. Luiz Menini Neto
Universidade Federal de Juiz de Fora

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“We have mastered our surroundings, increased food production, built cities, established empires and created far-flung trade networks. But did we decrease the amount of suffering in the world? Time and again, massive increases in human power did not necessarily improve the well-being of individual Sapiens, and usually caused immense misery to other animals.”

— Yuval Noah Harari, Sapiens: A Brief History of Humankind

RESUMO

A urbanização é uma das maiores causas de conversão do uso da terra, levando a intensas modificações na estrutura da paisagem e funções ecossistêmicas. Florestas dentro de áreas urbanas estão mais vulneráveis a alterações nas condições ambientais, tais como maior temperatura e intensidade luminosa, deficiência hídrica e maior concentração de CO_2, além de poluição do ar e do solo. Esses filtros ambientais podem favorecer certos traços de espécies ou grupos funcionais, levando à remoção de linhagens inteiras e causando impactos nas funções ecossistêmicas. Apesar das florestas urbanas poderem contribuir para a estocagem e sequestro de carbono, mudanças antropogênicas no uso da terra e a idade dos fragmentos florestais são fatores indicados pela literatura como causadores de alterações do estágio sucessional da comunidade arbórea de florestas tropicais, causando redução de biomassa. O objetivo dessa tese foi investigar como a diversidade e a composição filogenética da comunidade arbórea é afetada pela urbanização propriamente dita (fragmentos florestais urbanos sem histórico de distúrbios) e o histórico de uso da terra (fragmentos florestais urbanos secundários, regenerados após atividades de cultivo agrícola e terraplanagem) (capítulo 1). No capítulo 2, objetivamos investigar como a biomassa acima do solo é afetada pela urbanização e pelo histórico de uso da terra e explorar a contribuição de três importantes preditores de biomassa (hipótese da complementaridade de nicho, razão de massa e fertilidade do solo). Nossos resultados sugerem que a riqueza de espécies e diversidade filogenética são afetadas pelo histórico de uso da terra em florestas urbanas e que florestas urbanas sem histórico de uso da terra podem reter alta diversidade evolutiva de angiospermas, o que destaca a importância da preservação dessas florestas durante a expanção urbana. Além disso, o acúmulo de biomassa em florestas urbanas é altamente dependente do seu histórico de uso da terra. Encontramos que a hipótese de razão de massa (densidade da madeira) é de grande importância para o aumento de biomassa em florestas urbanas e não urbanas, mas que a biomassa aumenta com o aumento da presença de grupos filogeneticamente mais distantes apenas em floretas maduras (ou controle). Para as outras categorias de florestas, especialmente as florestas urbanas com histórico de terraplanagem, alta biomassa está relacionada à presença de espécies mais próximas filogeneticamente.

Palavras-chave: Diversidade filogenética. Urbanização. Histórico de uso da terra.

Biomassa acima do solo. Filtro ambiental.

ABSTRACT

Urbanization is one of the most increasing kinds of land-use conversion, leading to strong modifications to the landscape structure and ecosystem functioning. Forests within urban areas are vulnerable to altered environmental conditions such as higher temperature and light intensity, water deficit, and increased CO_2 availability, besides air and soil pollution. These environmental filters may favor certain species traits or functional groups, leading to the removal of entire lineages and causing impacts on their ecosystem functions. Although urban forests can still contribute to the overall carbon storage and sequestration, anthropogenic land-use changes along with stand age have been shown to set tropical tree communities back to an earlier successional stage causing a reduction in standing biomass. The aim of this thesis was to investigate how phylogenetic diversity and composition of tree species are affected by urbanization itself (urban forest fragments derived directly from intact forest) and land-use history (urban forests regenerated from cropland or otherwise denuded landscapes) (chapter 1). Also, in chapter 2 we aimed at investigating how aboveground biomass (AGB) is affected by urbanization and land-use history and to explore the contribution of three important biomass drivers (niche complementarity, mass-ratio and soil fertility hypothesis). Our results suggest that species richness, rarefied species richness and phylogenetic diversity are all affected by the land-use history of urban forests and that urban forests without previous land use can house substantial amounts of angiosperm evolutionary diversity, which highlights the importance of preserving natural forest fragments as cities expand. Besides, high aboveground biomass in urban forests is greatly dependent on their land-use history. We found that the mass-ratio hypothesis (wood density) is of great importance for driving high aboveground biomass in secondary urban forests, but that aboveground biomass is greater for the groups of phylogenetically distant species only for old-growth forests. For the other forest categories, especially urban forests with cropland and denudation land-use history, high aboveground biomass is related to species being phylogenetically close.

Keywords: Phylogenetic diversity. Urbanization. Land-use history. Aboveground biomass. Environmental filtering.

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GENERAL INTRODUCTION

Natural communities are currently facing extensive land use modifications. Understanding how these different historical disturbances affect species and communities is crucial for prioritizing sites for conservation (CAVENDER-BARES et al., 2009). Urbanization is one of the most increasing kinds of land-use conversion (SECRETARIAT OF THE CONVENTION ON BIOLOGICAL DIVERSITY, 2012), leading to strong modifications to the landscape structure and ecosystem functioning (SETO; PARNELL; ELMQVIST, 2013). Forests within urban areas are vulnerable to altered environmental conditions such as temperature, light intensity, water, and CO_2 availability, besides from air and soil pollution (ZIMMERMAN et al., 2005; NOWAK & DWYER, 2007; JUTRAS et al., 2010;WILLIAMS et al., 2015). Environmental constraints faced by species from urban forests may favor certain traits or functional groups, creating blanks in the phylogeny as entire lineages may disappear (ČEPLOVÁ et al., 2015; WILLIAMS et al., 2015; KNAPP et al., 2017; PALMA et al., 2017; SILVA-JUNIOR et al., 2018). These phylogenetically poor plant communities are more susceptible to a variety of anthropogenic impacts such as the invasion of exotic plant species which can potentially lead to further erosion of diversity and altered biotic interactions (WILLIAMS et al., 2009; GERHOLD et al., 2011).

Many studies on temporal changes in biodiversity consider only measures of species taxonomic diversity. However, such measures do not account for the evolutionary history of species or how communities were modulated (CAVENDER-BARES et al. 2004; CIANCIARUSO et al. 2009; GASTAUER & MEIRA-NETO 2015). Phylogenetic diversity recognizes species evolutionary history in generating patterns of species coexistence and community assembly (WEBB et al., 2002), having an important role for conservation studies as a predictor of ecosystem functions (CLARK et al., 2012; CADOTTE, 2013; HINES et al., 2014). The advance of phylogenetic approach, together with trait-based information of niche conservatism improves our understanding of succession studies, filling a gap between ecological and evolutionary questions (LOSOS, 2008; LETCHER, 2010) by helping elucidate which process defined species occurrence (WEBB et al., 2002; CHASE, 2003; CAVENDER-BARES et al., 2009). This is mostly possible owing to analyses of phylogenetic community structure, which demonstrate how species assemble in a community, being more or less phylogenetically related to each other than expected by chance (clustered or overdispersed pattern of phylogenetic structure, respectively) (WEBB et al., 2002).

Community ecology generally states that species composition is mainly the result of environmental filters (abiotic interactions) and competitive exclusion (biotic interactions) (WEIHER et al., 1998; SILVERTOWN, 2004). Phylogenetic clustering is a consequence of species in a community being arranged mostly by abiotic forces (environmental filtering), as organisms have the same tolerances and preferences, sharing traits associated to regeneration strategies that confer a benefit under adverse environmental conditions (WEBB, 2000; WEBB et al., 2002; WEBB; GILBERT; DONOGHUE, 2006). Conversely, competition among plants leads to phylogenetic overdispersed communities as competition excludes mostly similar (and therefore more closely related) taxa from the community (WEBB, 2000; WEBB et al., 2002). Events causing environmental filtering such as disturbance (natural or human-driven) may reduce the impact of interspecific competition through the extinction of species vulnerable to the recently crated local habitat conditions (WINTER et al., 2009), therefore enhancing the relatedness among remaining species. Besides from abiotic and biotic filters, which are deterministic forces, random processes may also drive community assembly in natural ecosystems (KRAFT; VALENCIA; ACKERLY, 2008). Neutral theory assumes that species are functional equivalents, and communities are the result of stochastic processes (e.g., dispersion limitation) while ecological deterministic processes play a minor role (HUBBELL, 2001).

Despite the large number of studies on urban biodiversity, the lack of land-use history and its role on biodiversity of urban forests might be the reason why the conservation contribution of these forests have yet not been fully understood (RAMALHO and HOBBS, 2012; SCWARTZ et al., 2014). Most tropical urban forests were regenerated from agricultural or other man-made landscapes, meaning that successional processes must be considered while evaluating urban ecosystems (KOWARIK; LIPPE, 2018). The sequence and duration of successional stages may vary substantially among tropical forests, depending upon the nature of the disturbance event (CHAZDON, 2008; MESQUITA et al., 2015; NORDEN et al., 2015). Urbanization and other forms of land-use change is known to cause community clustering due to the intense habitat change (ARROYO-RODRÍGUEZ et al., 2012; ANDRADE et al., 2015; ČEPLOVÁ et al., 2015; PRESCOTT et al., 2016). Besides age and previous land use, successional pathways are known to vary widely with climate, soils, and landscape configuration, initial species and functional composition, last crop planted, nutrient treatments, pathogen and herbivore loads, elevation, slope and drainage (VANDERMEER et al., 2004; ARROYO-MORA et al., 2005; CHAZDON, 2008; NORDEN et al., 2015) .

The strong environmental filters present in secondary forests such as abandoned agricultural areas cause the colonization of close lineages due to the conservatism of traits in disturbed patches (BAETEN et al., 2015a). As a result, pioneer species are selected (fast-growing and disturbance-tolerant) (VAN DER SANDE et al., 2016), allowing the coexistence of functionally similar ones (CAVENDER-BARES et al., 2009; PAKEMAN, 2011). Following the abandonment of intensive agriculture, the first seedling shrub and tree recruits emerge from the seed bank or tend to be wind- or bird-dispersed species with small seeds that require direct light or high temperatures to germinate (UHL & JORDAN, 1984; VÁZQUEZ-YANES & OROZCO-SEGOVIA, 1984). These composition shifts can alter vegetation structure (e.g., reduced stem density, greater canopy openness) and microclimatic conditions (e.g., increased habitat desiccation), imposing additional environmental filters (MEHTA et al. 2008). Therefore, biotic homogenization is achieved as pre-disturbance biota leaves place to a set of generalist and disturbance- tolerant species with high dispersal abilities (OLDEN et al., 2004; BENGTSSON, 2010). It is also possible that dispersal limitation has a significant role in controlling the assembly of these forests. Both environmental heterogeneity and dispersal limitations caused by the urban matrix have been reported to result in shifts in species composition in human-disturbed sites (MYERS et al., 2013).

Most studies focus on old-growth forests, due to their role as model forests considering their natural status. However, human-disturbed communities represent an increasing provider of ecosystem services that might not follow the same ecological patterns as “intact” forests, and efforts should be taken to better understand these ecosystems (CHAZDON et al., 2003). Urban forests have a legacy of perception that they have limited ecological value due to high human modification (DAVIES et al., 2011). However, ecosystem services provided by urban areas have received increasing recognition due to their positive impact on the quality of life in cities (GÓMEZ-BAGGETHUN; BARTON, 2013). Urban forests influence air temperature, climate regulation and carbon sequestration, mitigating the urban “heat island” effect (MCDONALD et al., 2007; ARMSON et al., 2012; LAFORTEZZA & CHEN, 2016), regulation of water runoff and erosion (GUO; XIAO; LI, 2000; ROY; BYRNE;

PICKERING, 2012), habitat for flora and fauna (GODDARD; DOUGILL; BENTON, 2009), moderation of air and soil pollution (BARO et al., 2014), besides from improving population well-being (MCKINNEY, 2006). These services have been valued at nearly $1 million per km^2 per year (ENDRENY et al., 2017).

Tropical forests are estimated to store more than half of terrestrial global carbon (in all forms, live biomass, soil, deadwood and litter) (PAN et al., 2011). Surely one very important ecosystem service provided by urban vegetation is the sequestration of carbon from the atmosphere, which has been given little consideration due to their small total area (CHURKINA, 2016). However, terrestrial urban vegetation has been shown to store significant amounts of carbon (HUTYRA; YOON; ALBERTI, 2011). In China, for example (TANG; CHEN; ZHAO, 2016), carbon density and sequestration rate of urban trees was about one third to half compared to non-urban forests. Improving knowledge on urban forests' overall carbon storage and their drivers of biomass accumulation is therefore essential to further assist carbon emission offsets program, as the REDD+ (Reducing Emissions from Deforestation and Degradation) (POUDYAL et al., 2010).

Although urban forests can still contribute to the overall carbon storage and sequestration (NOWAK & CRANE, 2002; DAVIES et al., 2011; NOWAK et al., 2013), anthropogenic land-use changes along with stand age have been shown to set tropical tree communities back to an earlier successional stage causing a reduction in standing biomass (ÁLVAREZ-YÉPIZ et al., 2008; LETCHER & CHAZDON, 2009; WANDELLI & FEARNSIDE, 2015; CHAZDON et al., 2016; POORTER et al., 2016). Forest recovery after land-use may last decades or even centuries, and the intensity of the disturbance events is considered one of the main factors driving species and biomass recovery (CHAZDON, 2008; JAKOVAC et al., 2015; MARTINEZ-RAMOS et al., 2016; FERREIRA et al., 2018). Forest degradation and disturbance are responsible for the lower per-hectare biomass gains in comparison to the loss of biomass across tropical continents (BACCINI et al., 2017).

Secondary tropical forests have been shown to hold significant lower carbon stocks than old-growth forests yet their carbon sequestering potential is high (POORTER et al., 2016). Studies on the biomass recovery of secondary tropical forests have suggested contrasting results. Biomass recovery on tropical forests has been shown to take up to 66 years to achieve 90% of pre-disturbance biomass (POORTER et al., 2016), yet MARTIN et al. (2013) found that they hold only 50% of reference forests’ biomass even after 80 years after regeneration. Hence, efforts should be taken to better predict the rate at which these forests are able to recover.

In tropical forests, aboveground biomass is affected by a large number of drivers, mostly related to biodiversity (niche complementarity hypothesis), mass-ratio hypothesis and soil nutrients. The niche complementarity hypothesis predicts that diversity is the main driver of aboveground biomass because it indicates the presence of coexisting species with different strategies for resource acquisition, and these differences result in more successful exploitation of available resources (TILMAN, 1999). Although the relationship between AGB and biodiversity in forest ecosystems has been widely explored, evidence is still lacking on this functional linkage in urban areas with different land-use histories. The mass-ratio hypothesis proposes that trait values of the most dominant species determine ecosystem processes in the community (GRIME, 1998). In this sense, biomass accumulation is determined by the presence of highly productive species and not by their variety (CARDINALE et al., 2007). The soil fertility hypothesis states that soil conditions are the main determinant of plant growth and stem turnover due to higher resource availability, therefore more fertile soil results in higher aboveground biomass. (BAKER et al., 2009; QUESADA et al., 2012). Besides, microclimatic changes promoted by the contrasting matrix (e.g. urban, rural) and land-use history impact sensitive species and favor disturbance tolerant ones due to dispersal limitations, leading to a depletion of carbon stocks (ÁLVAREZ-YÉPIZ et al., 2008; POORTER et al., 2016).

[1]The evolutionary diversity of urban forests depends on their land-use history

Abstract

Urbanization leads to strong modifications of landscape structure and ecosystem functioning, and urban areas are spreading rapidly. The aim of this study was to investigate how phylogenetic diversity and composition of tree species are affected by urbanization itself and land-use history. We found that species richness, rarefied species richness and phylogenetic diversity are all affected by the land-use history of urban forests. Indeed, forests that regenerated from cropland, and particularly those regenerated from denuded landscapes, showed strong phylogenetic clustering, which was also related to their high perimeter-area ratio. Our analyses of phylogenetic composition show that urban forests without land-use history are compositionally indistinguishable from mature, non-urban forests. These two forest types house a diversity of evolutionary lineages and no specific lineage is a strong indicator of these forest types. In contrast, the two urban forest types with anthropogenic land-use history have a few, distinct lineages that are strongly associated with each of them, respectively. Overall, our results suggest that urban forests without previous land-use can house substantial amounts of angiosperm evolutionary diversity, which highlights the importance of preserving natural forest fragments as cities expand. This study highlights the substantial value of tropical urban forests and the importance of considering information on land-use history, even when studying urban environments.

Keywords: Urbanization. Environmental filtering. Phylogenetic diversity. Phylogenetic composition. Tropical forests. Land-use history

1 Introduction

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Anthropogenic disturbance events such as land-use change and habitat fragmentation have influenced important ecological processes across the world. These events cause the retraction of natural landscapes and shape regional species pools by determining whether lineages adapt to new environmental conditions or become extinct (Hoffmann and Sgró 2011). Land-use change of tropical landscapes is considered one of the main threats to global biodiversity (Lewis et al. 2015), causing high species loss, replacement of forest specialists by generalists and reduction of ecological functions and phylogenetic diversity (Olden et al. 2004; Gibson et al. 2011; Van Meerbeek et al. 2014; Socolar et al. 2016).

Urbanization leads to strong modifications of landscape structure and ecosystem functioning (Seto et al. 2013), and urban areas are spreading at fast rates (Secretariat of the Convention on Biological Diversity 2012). The world's population is projected to increase by 2.3 billion people over the next 30 years, with the majority of this growth concentrated in urban centers (UN Department of Economic and Social Affairs 2013). Cities can thus represent a significant threat to biodiversity and ecosystem function. Forests within urban areas are vulnerable to environmental stresses caused by fragmentation and edge effects, such as higher average temperatures (Beninde et al. 2015; LaPoint et al. 2015), as well as air and soil pollution (Zimmerman, et al. 2005; Nowak and Dwyer 2007). These environmental modifications can filter out species intolerant of novel environmental conditions and benefit the ones with traits that allow persistence in anthropogenic habitats, a phenomenon that can lead to biotic homogenization (McKinney 2006; Williams et al. 2009).

Most ecological studies of forests focus on old-growth forests, due to the idea that they better reflect natural processes. However, human-disturbed forests can provide important ecosystem services, and efforts should be taken to better understand secondary forests (Chazdon et al. 2003). Urban forests provide a variety of societal goods and services such as air filtering, heat moderation, water storage, filtration, drainage and habitat refuges for animal and plant populations (Bolund and Hunhammar 1999; Park et al. 2010). Further, exposing people to nature can improve quality of life and inspire future action for biodiversity conservation (McKinney 2006; Whitburn et al. 2018). Because people tend to occupy cities in regions of high biodiversity (Cincotta et al. 2000), there is a need to understand the ways in which urban centers act as biodiversity filters and how we can maximize the retention of urban biodiversity and the ecosystem services it provides.

Environmental selection pressures faced by species from urban forests may favor certain traits or functional groups, and to the extent that closely related species are functionally similar, entire lineages may disappear from urban forests, which may negatively impact ecosystem function and reduce the breadth of lineages to which people living around urban forests are exposed (McKinney 2006; Williams et al. 2009; Aronson et al. 2016; Nero et al. 2017; Palma et al. 2017; Raymundo et al. 2018; Santana et al. 2018; Silva-Junior et al. 2018). Phylogenetically poor plant communities are more susceptible to a variety of anthropogenic impacts, such as the invasion of exotic plant species, which can potentially lead to further erosion of diversity (Gerhold et al. 2011). Lineage diversity, often quantified using phylogenies, has been shown to be a better predictor of ecosystem function than species richness in some studies (Clark et al. 2012; Cadotte 2013; Hines et al. 2014). Therefore, when studying changes in biodiversity of urban forests, it is important to assess not only taxonomic diversity and composition, but also evolutionary, or lineage, diversity and composition (Cadotte et al. 2008; Faith et al. 2010; Forest et al. 2010; Dexter et al. 2019).

Most tropical urban forests do not represent fragments of intact forest, but were instead regenerated from agricultural or other man-made landscapes (Kowarik and Lippe 2018), which means that successional processes must also be considered when evaluating the taxonomic and evolutionary diversity of urban forests (Chazdon 2008; Williams et al. 2015). Previous research has shown that species richness and lineage diversity increase over the course of succession, and further, that the number of lineages in regenerating plots is even less than that expected given their low species richness, i.e. earlier successional plots show phylogenetic clustering (Letcher 2010; Ding et al. 2012; Norden et al. 2012; Ribeiro et al. 2016). Meanwhile, fragment size and shape impose additional filters, with small forest fragments being exposed to a variety of edge effects that can lead to communities being dominated by few species with a similar and small set of traits unable to sustain ecological processes (Santos et al. 2008).

The aim of this study was to investigate how phylogenetic diversity and composition of tree species are affected by urbanization itself (urban forest fragments derived directly from intact forest) and land-use history (urban forests regenerated from cropland or otherwise denuded landscapes). To our knowledge, this is the first time urban forest fragments are compared with respect to their land-use history. At present, where urban contributions to biodiversity conservation are not entirely clear, this study represents a useful step forward for the field of urban ecology. We used field data from the Atlantic Forest domain in southeastern Brazil, one of the most threatened global biodiversity hotspots (Ribeiro et al. 2009), due largely to human population pressure and concomitant urbanization. We addressed the following main questions: 1) Does urbanization and land-use history impact phylogenetic diversity in urban forests? 2) Do differences in historical land-use intensity affect the phylogenetic composition of communities? 3) Does urbanization and/or land-use history promote loss of certain evolutionary lineages, resulting in phylogenetic clustering? We predict that urbanization and land-use history will drive loss of specific evolutionary lineages resulting in lower phylogenetic diversity. A subset of lineages should be more successful in these stressful environments, and we therefore expect consistent shifts in the phylogenetic composition of tree communities in urban forests.

2 Material and Methods

2.1 Study area

The study was conducted in twelve tropical forests located in the southeast region of Minas Gerais, Brazil (21°24’- 22°1’S and 43°18’ – 43°55’W) (Fig. 1). These forests belong to the Brazilian Atlantic Forest domain and are all classified as Semideciduous Seasonally Dry Forests (IBGE 2012), occurring from 710 to 1070 meters of altitude. Regional climate is classified as Cwb (Mesothermic climate of Köppen), defined by dry winters and mild summers. Mean annual rainfall ranges from 1497 to 1585 mm and mean annual temperature ranges from 17.6°C to 18.9ºC (Alvares et al. 2013). Soils in the region, and underneath all plots, are primarily latosols (Santos and Anjos 2013), and plots were chosen to have similar elevation and aspect, in order to reduce the influence of these factors on our results All sites were classified based on their land-use history and whether or not they are located in the urban matrix (Table 1).

All forest fragments were fully divided into plots of 20 m x 20 m. Afterward, 10 non-contiguous plots were randomly selected, considering a minimum distance to the forest edge of 20 m (except for the smallest fragments where the distance to edge was reduced to ≥ 10 m).We surveyed all trees with a diameter at breast height (DBH; 1.3 m above the ground) of ≥ 5 cm and identified trees to species level. Species identities were checked for nomenclatural synonyms using the online tool Taxonomic Name Resolution Service (TNRS) ver. 3.2 (Boyle et al. 2013). Tree ferns and gymnosperms represent a minor proportion of diversity (0.78% of species) and individuals (7.75%) in these forests, yet their ancient divergences from angiosperms would have a large effect on phylogenetic diversity measures (Kembel and Hubbell 2006; Rezende et al. 2017). Therefore, they were excluded from analyses (sensu Hubbell 2006; Honorio Coronado et al. 2015). The final angiosperm dataset contained a total of 6663 individual trees, belonging to 378 species, 171 genera and 64 families (Table S1).

The city of Juiz de Fora, where the studied urban forests are located, is 166 years old. It experienced the history of forest degradation of the Atlantic Forest, especially related to the expansion of coffee plantations at the end of the 20th century. The city covers an area of 1435 km^2 and hosts approximately half a million inhabitants. When considering fragments with at least 3 ha, 11% of the city is in a forested state and only 4% of these forests are protected by law (SPGE 2008; SOS Mata Atlântica 2015). All urban forest fragments evaluated here are inserted in the urban matrix, including the remnant forests without anthropogenic land-use history (Fig S1).

The twelve forests were categorized into four classes with different historical land use, each one represented by three sites: a) forests outside the urban matrix where there is no documented record of human land use (i.e. forest is presumed to be mature, with the only potential anthropogenic impact being selective logging); b) forest within the urban matrix where there is no documented record of human land use; c) forests within the urban matrix that represent natural regeneration from cropland which was abandoned 70 to 80 years ago; and d) forests within the urban matrix that represent natural regeneration from completely denuded landscapes (land was subjected to earthmoving activities resulting in soil removal), with regrowth beginning 50 to 60 years ago. All mature forests are classified as legally protected reserves according to the Brazilian Forest Code. These categories were assigned according to landowner interviews, government public documents and official records, satellite images and photographs.

2.2 Phylogenetic analysis

An ultrametric calibrated phylogeny was constructed based on the new angiosperm family tree R20160415.new (Gastauer and Meira Neto 2017), which represents phylogenetic relationships among angiosperms as recently proposed by APG IV (2016). Species from the study sites were inserted in the family tree using the phylomatic function of the Phylocom 4.2 package (Webb et al. 2008). The resulting community tree was dated using the bladj (branch length adjustment) algorithm which provides mean age estimates of the nodes for which age information is available (e.g. from molecular age estimation studies).

2.3 Taxonomic and Phylogenetic Diversity metrics

We determined the species richness for sites as the sum of all species found in all plots at a given fragment or site (total area surveyed was the same at all sites). As the sites vary in the total number of trees sampled, we also determined the rarefied species count for each site, with rarefaction down to the number of individuals present at the site with the fewest number of individuals. Phylogenetic diversity (PD, in million years - myrs) was calculated as the sum of all branch lengths of a phylogeny encompassing all species in a given site (Faith 1992).

To assess the phylogenetic structure of communities, we evaluated the standardized effect size of MPD (ses.MPD) and the standardized effect size of MNTD (ses.MNTD). Mean pairwise distance (MPD) is the mean phylogenetic distance between all pairs of individuals (including conspecifics) in a community and the Mean Nearest Taxon Distance (MNTD) evaluates the average phylogenetic distance between each individual and its most closely related (non-conspecific) individual (Webb 2000; Webb et al. 2008). For the standardized effect size calculations, MPD and MNTD values were compared with 10,000 null model randomizations using the null model "phylogeny pool", which also served to test whether each community is more or less phylogenetically related than expected by chance. Negative ses.MPD and ses.MNTD values indicate phylogenetic clustering (species are distributed within clades with relatively recent common ancestors, or are more closely related than expected by chance) while positive values indicate phylogenetic overdispersion (species more evenly distributed across the whole phylogeny than expected by chance) (Webb 2000; Webb et al. 2002; Santos et al. 2010; Arroyo-Rodríguez et al. 2012). In order to investigate if PD was lower or higher than expected by chance given species richness, we also measured the standardized effect size of PD (ses.PD).

2.4 Phylogenetic Composition

To test for differences in phylogenetic composition across sites, we used phylogenetic ordinations that examine the distribution of lineages across a sample of communities. Specifically, we implemented the evolutionary principal component analysis based on Hellinger distance (evoPCAHellinger), developed by Pavoine (2016). This approach balances the influence of deep and shallow nodes in the ordination analysis and represents one of the more powerful methods to study phylogenetic patterns over environmental gradients (Pavoine 2016).

2.5 Landscape Characterization

In order to consider the possible influence of size and shape of the fragments on our results, we measured four landscape metrics for each studied fragment: i) total area (ha) (Area); ii) forest fragment perimeter (km) (Perimeter), i.e. total length of the forest fragment edge; iii) perimeter to area ratio (P:A): perimeter (in meters) divided by area (in meters); and iv) shape index (measures the complexity of the forest fragment shape compared to a standard circle; shape index is close to 1 for circular fragments and increases as fragments become more irregular). Analysis were performed using ArcGis 10.6.1 and its extension V-Late (Lang and Tiede 2003; Lang and Blaschke 2007).

2.5 Statistical analysis

The effects of land use history on species richness (SR), rarefied species richness (RSR) and phylogenetic diversity metrics (PD, ses.PD, ses.MPD and ses.MNTD.) were examined using linear mixed models with fragment as a random factor (to account for the lack of independence of plots within sites). We also tested the effects of fragment area, perimeter, P:A and shape index on the same variables (SR, RSR, PD, ses.PD, ses.MPD and ses.MNTD), together with land-use history, using linear mixed models. Model selection was based on the Akaike Information Criterion, corrected for small sample size (AICc). The set of best models (models equally supported) were considered as those with $\Delta\text{AICc} \leq 2$ (Burnham and Anderson 2002) for each variable. Model residuals were checked to confirm normality and homoscedasticity. Tukey post-hoc tests were used to assess the statistical differences between individual forest categories.

All analyses, figures and graphs were performed using the R Statistical Software (R Development Core Team 2017) and the following packages: picante (Kembel 2010) multcomp (Bretz et al. 2015), lme4 (Bates et al. 2014), lmerTest (Kuznetsova et al. 2016), MuMIn (Barton

2016), adiv (Pavoine 2018), factoextra (Kassambara and Mundt 2017) and ggplot2 (Wickham and Chang 2016).

3 Results

3.1 Phylogenetic Diversity and Structure

All raw phylogenetic diversity metrics were highly correlated with species richness, while the standardized metrics generally were not (Fig. S2). Our models indicated that species richness, rarefied species richness, phylogenetic diversity and phylogenetic structure are affected by land-use history (LUH) of urban forests (Fig 2, Table S2). We observed similar patterns for PD as we found for SR, where the highest value was found for non-urban forests (2697 myrs and 31 species) and urban forests without LUH (2375 myrs and 26 species), while the lowest values were found for urban forests regenerated from cropland (1727 myrs and 19 species) and denudation land-use histories (800 myrs and 8 species). Urban forests regenerated from cropland and denudation LUH presented significantly lower PD than non-urban forests and urban forests without land-use history. Rarefied species richness was significantly different only between forests without LUH (non-urban and urban) and denuded forests. The same tendencies were found for the standardized metrics, where there were also negative values for urban forests regenerated from cropland (ses.PD) and especially denudation LUH (ses.PD and ses.MPD). ses.MNTD was not significantly different between forest classes, but showed strong negative values for cropland and denuded forests. These results indicate that urban forests without land-use history maintained species and phylogenetic diversity equivalent to non-urban forests, whereas cropland and denuded forests had a strong reduction in phylogenetic diversity with shifts toward phylogenetic clustering.

For the landscape metrics tested (one-way ANOVA, $p < 0.05$), only Area and P:A were significantly variable across forest types, specifically between the denuded forest (mean ± se., 1.62 ha ± 0.16 and 0.04 ± 0.01, respectively) and the other forest categories (Table S3; Table

S4). Non-urban forests were on average 32.9 ha ± 14.6 in area and had a perimeter to area ratio of 0.01 ± 0.01, while urban forests and cropland forests' mean areas were 121.3 ha ± (103.3) and 15.1 ha ± 4.5, and perimeter to area ratios were 0.01 ± 0.01 and 0.02 ± 0.01, respectively. When accounting for the effects of landscape, perimeter to area ratio was negatively related to ses.PD (AICc=361.3) and ses.MNTD (AICc=368.5) (Table S5).

3.2 Phylogenetic Composition

Two major gradients of phylogenetic compositional variation were revealed by the first two axes of the phylogenetic ordination, which together explained 27.6% of the total variation (Fig. 3 and 4). The subsequent ten axes each individually explained less than 7% of the variation. The first axis (PC1, 15.2%) separated plots in urban forest with denudation LUH and most of the former cropland plots from the plots of the non-urban and urban forests without land use history (positive versus negative values on axis 1) (Fig. 3). This axis is positively correlated with lineages related to the Asterales clade, especially the family Asteraceae and the species *Eremanthus erythropappus*, which are abundant in urban forests with denudation LUH (Fig. 4). The second axis (PC2, 12.4%) separated most of the plots of the urban forests with cropland LUH, part of the denuded forests plots and a minor portion of urban forests without LUH from the remaining plots. In general, plots from the non-urban and urban forests without LUH have similar phylogenetic composition, which in turn differs markedly from urban forests with cropland and denudation LUH. The second axis is strongly and positively correlated with the family Melastomataceae and the genus *Miconia*, along with the Myrtales order followed by the Myrtaceae family with a less important contribution. The plots with negative values for both of these axes are composed of a mix of lineages, each with a relatively minor contribution to the variation in the ordination space, including Magnoliids, Fabids, Malvids and Lauraceae.

4 Discussion

This study has provided insights into the effects of urbanization and land-use history on the evolutionary structure of tropical tree communities. The different urban forests examined had markedly different patterns of phylogenetic diversity and composition, depending on their land-use history. In fact, there was limited impact of urbanization *per se* on these patterns, as evidenced by the similarity in terms of phylogenetic composition of non-urban forests and urban forests without anthropogenic land-use history (LUH). Urban forests without LUH are indistinguishable from intact, non-urban forests in terms of phylogenetic composition. These two forest types house a diversity of evolutionary lineages and no specific lineage is a strong indicator of these forest types. Urbanization *per se* did reduce phylogenetic diversity slightly, but this reduction was no greater than expected given the slight reduction in species richness in urban forests without LUH. The reduction in species richness in turn may be due simply to the reduced numbers of stems in urban forests without LUH, as rarefied species richness was not reduced in these forests compared to non-urban forests.

In contrast, urban forests with anthropogenic land-use history showed much lower phylogenetic diversity, and less phylogenetic diversity than expected given their observed reductions in species richness. Indeed, forests that regenerated from cropland, and particularly from denuded landscapes, showed clear evidence for phylogenetic clustering. Our analyses of phylogenetic composition help explain these results. While we did find evidence that phylogenetic clustering (ses.PD and ses.MNTD) increases with the perimeter to area ratio of the fragments, and that the denuded forests are significantly smaller when compared to the other forest fragments, these landscape metrics do not explain the other measures of phylogenetic diversity (which were all affected by land-use history), nor why forests regenerated from croplands show clustering. Thus, overall our results do point to an effect of land-use history itself on the phylogenetic diversity and structure of tree communities. The two urban forest types with LUH have few, distinct lineages that are strongly associated with each of them, respectively.

4.1 Phylogenetic Diversity and Structure

The process of urbanization has been reported to cause strong negative effects on biodiversity, with cities worldwide showing reduced species richness compared to rural sites (Mckinney 2006; Aronson et al. 2014; Lopez et al. 2018; Silva-junior et al. 2018). Although one study considering different disturbance regimes in urban forests did not find shifts in phylogenetic diversity (Ceplová et al. 2015), our findings indicate that land-use history for secondary forests, along with time since abandonment, are important drivers of phylogenetic diversity loss, while intact urban forests can be important reservoirs of evolutionary richness. The similar phylogenetic diversity and composition between non-urban and urban forests without land-use history suggests that the urban matrix itself does not represent a sufficiently strong environmental filter to cause significant phylogenetic and taxonomic losses, as long as there is no history of drastic land use changes, and on the timescales considered here. Juiz de Fora is a relatively young city (less than 170 years). While non-urban forests have the greatest tree SR, RSR and PD, urban forests without LUH still show markedly greater values than the urban forests with anthropogenic LUH. This result confirms the value of forests without land-use history, even within the urban matrix. Higher ses.PD values found in urban forests without LUH reflect accumulated lineage diversity, with many deep phylogenetic branches for communities relative to their SR (Swenson 2009).

The decrease in phylogenetic diversity shown by urban forests with cropland and denudation land-use history indicates that the effects of past disturbance events are still persisting after 50 to 80 years (depending on the land use history). A recent study (Rozendaal et al. 2019) has shown that biodiversity in abandoned pastures and cultivated fields is expected to reach the same level of species richness as undisturbed forest within 54 years, but that attaining the species composition of undisturbed forest can take centuries. In our case, the environmental filters in these forests have been strong enough that only a subset of lineages have been successful, hence the shifts in the phylogenetic composition of tree communities that we found. Strong environmental filters, such as conditions present in abandoned agricultural sites and in early successional phases, seem to have lead to colonization by close relatives, likely due to the conservatism of traits that are optimal in disturbed forest fragments (Baeten et al. 2015). As a result, pioneer species with fast-growing and disturbance-tolerant strategies are selected (Van Der Sande et al. 2016). These compositional shifts can alter vegetation structure (e.g., reduced stem density, greater canopy openness) and microclimatic conditions (e.g., increased light intensity and habitat desiccation), imposing additional environmental filters (Mehta et al. 2008). In addition, biotic homogenization, at least in early to mid stages of succession, can occur as the pre-disturbance biota is replaced by a set of generalist and disturbance-tolerant species with high dispersal abilities (Olden et al. 2004; Bengtsson 2010).

The failure of certain evolutionary lineages to colonize sites with anthropogenic land-use history was accompanied by shifts in phylogenetic structure across forests with and without land-use history. Land-use change and the existence of large edge areas is known to cause phylogenetic clustering, as a response to the strong environmental filters and intense habitat change (Santos et al. 2008; Santos et al. 2010; Arroyo-Rodríguez et al. 2012; Arroyo-Rodríguez et al. 2013; Munguía-Rosas et al. 2014; Andrade et al. 2015; Prescott et al. 2016). Small forest fragments with higher exposure to edge effects can lead to communities being dominated by a few species with a similar set of functional traits (Santos et al. 2008; Tabarelli et al. 2008). Biotic filters become increasingly important in the later stages of succession, while environmental filtering dominates in the early stages and during secondary regeneration (Connell and Slatyer 1977; Letcher 2010; Ding et al. 2012; Letcher et al. 2012; Norden et al. 2012; Purschke et al. 2013; Stadler et al. 2017). Meanwhile, intensity of disturbance has been shown to alter successional trajectories (Chazdon et al. 2003; Lugo 2004; Letcher 2010; Whitfeld et al. 2012).

Following abandonment of intensive agriculture, the first shrub and tree recruits either emerge from the seed bank or tend to be wind- or bird-dispersed species with small seeds, which in turn require direct light or high temperatures to germinate (Uhl and Jordan 1984; Vázquez-Yanes, C. and Orozco-Segovia 1984; Stadler et al. 2017). These compositional shifts can alter vegetation structure (e.g., reduced stem density, greater canopy openness) and microclimatic conditions (e.g., increased habitat desiccation), imposing additional environmental barriers for forest succession (Mehta et al. 2008).

The denudation (earthmoving) activities affect soil physical properties, causing loss of soil structure and fertility by compaction and surface sealing (Craul 1999). This sort of disturbance is extremely severe, due to the machinery used for substrate compaction, which eliminates nutrient stocks and plant propagules by removing all topsoil (Uhl et al. 1982; Pinard et al. 1996). Therefore, regeneration depends strictly on seed dispersal into the site, and is further limited to species adapted to deeply impoverished soils (Uhl et al. 1982). Soil degradation and loss is a frequent scenario in urban areas, due to rapid development and poor practices like grading and topsoil removal (Craul 1999). In addition, in our study, due to the high perimeter to area ratios of the denuded forest fragments, species may have faced extra environmental barriers from edge effects, such as increased light intensity, wind disturbance and altered microclimate (Turner and Corlett 1996; Laurance et al. 2006; Tabarelli et al. 2008).

4.2 Phylogenetic Composition

Forests with different histories of land-use change are expected to diverge in taxonomic and phylogenetic composition due to differences in the effects of disturbance, and to the interaction of land-use change with particular environmental conditions (Arroyo-Rodríguez et al. 2013). As predicted, land-use history showed strong effects on phylogenetic composition, with specific clades being favored. In addition, the perimeter to area ratios, which are higher in forests with a denudation history and which show a correlation with ses.PD and ses.MNTD, may have influenced phylogenetic composition, considering the role of edge effects on species composition (Santos et al. 2008). Forests with denudation LUH were strongly associated with members of the Asteraceae family and relatives, especially *Eremanthus erythropappus*, well known for their role as pioneer species (Gavilanes and Filho 1991; Scolforo et al. 2014) and for their general preference for habitats with poor soils that are not densely forested (Luna-vega

2010; Ribeiro et al. 2016b; Borges et al. 2019). Forests with cropland LUH also showed taxa usually identified as pioneers and invasive species in tropical forests, including those belonging to genera such as *Miconia* and some Myrtaceae such as *Syzigium* (Dalling et al. 1998; Fonseca and Carvalho 2012). These taxa belong to the Rosid clade, which was related to early succession in tropical forests in Costa Rica (Norden et al. 2012).

Phylogenetically poor plant communities are especially susceptible to invasion by exotic plant species, which can have long-lasting effects on tropical forests during succession (Martin et al. 2004; Chazdon 2008; Clark et al. 2012). These species colonize habitats after disturbance events that affect resource availability, including denudation, agricultural activities, fires or soil eutrophication (Funk and Vitousek 2007; Denslow 2008). Indeed, urban forests with denudation land-use history showed dominance of not only exotic species, but native disturbance-adapted species that can proliferate in degraded conditions (Marvier et al. 2004; Ribeiro et al. 2016a). *Pinus elliottii* is an exotic species which is very abundant in two of the three sites with denudation LUH. This species shows an aggressive competitive behavior, forming dense monospecific stands, similar to pioneers species in post disturbance forests (Chazdon 2008; Menon and Carvalho 2012). The novel habitat characteristics promoted by past disturbances, edge effects and human activity creates conditions for the formation of novel assemblages, with alien species being in a competitive advantage, which in the absence of human intervention, will reproduce and trigger new trajectories of succession and ecosystem function (Lugo 2004; Stadler et al. 2017).

Surprisingly, there were no detectable differences between non-urban and urban forests without LUH in their phylogenetic composition. In general, they house a variety of major clades such as Magnoliids, Malvids and Fabids, which may be expected due to the higher phylogenetic diversity of these sites compared to forests with land use history. The nodes that represent these clades are deep in the phylogeny, which increases phylogenetic diversity in sites where they co-occur.

5 Conclusion

Overall, our results provide the remarkable finding that undisturbed urban forests are irreplaceable in their broader contribution to the biodiversity of urban landscapes, holding substantial amounts of angiosperm evolutionary diversity, but that this depends on the urban forests being intact fragments of natural forest. While secondary forests can be important in supporting tropical biodiversity (Dent and Wright 2009; Letcher and Chazdon 2009), our findings suggest that 'intact' urban forests are irreplaceable in their broader contribution to the biodiversity of urban landscapes. While our study cannot determine whether the low evolutionary diversity of secondary urban forests is due to the land-use history *per se* or the interaction of land-use history with the urban environment, it is clear that these secondary forests house greatly reduced evolutionary diversity. Our study highlights the importance of preserving natural forest fragments as cities expand. We strongly recommend the protection of urban forest areas without land-use history. This study indicates the importance of considering information on land-use history, even when studying urban environments, to fully understand process that drive patterns of diversity and community assembly.

Conflict of Interest: The authors declare that they have no conflicts of interest.

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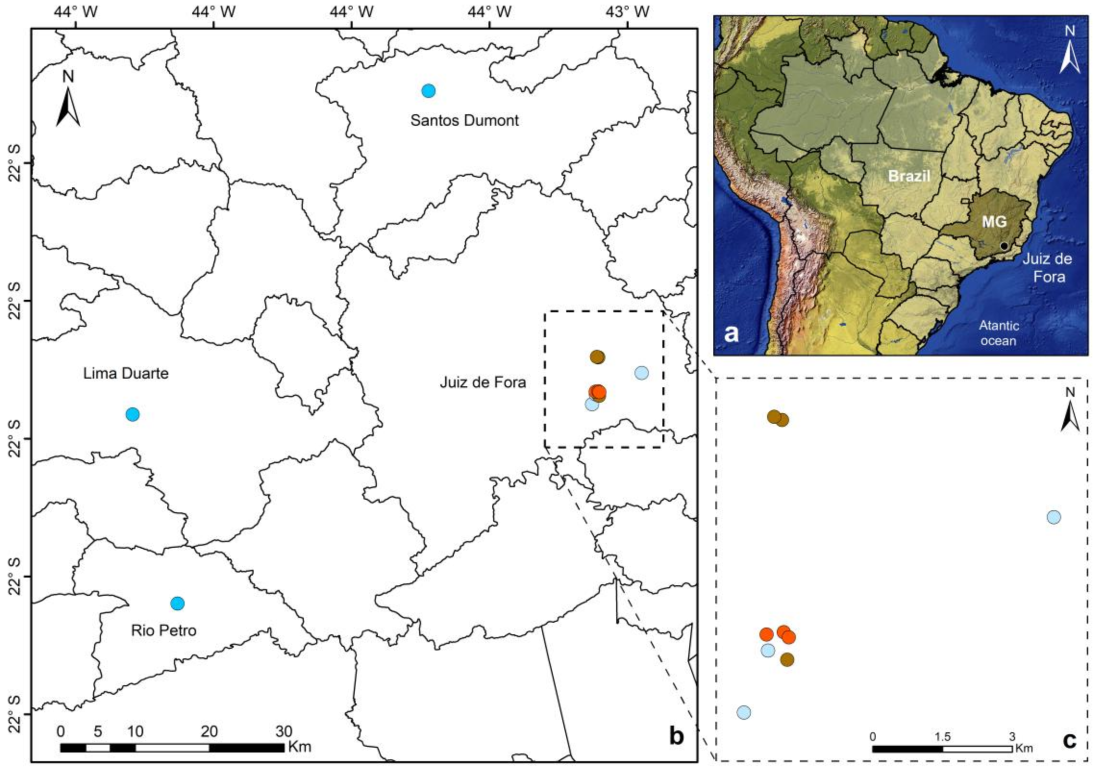


Fig. 1 Geographic location of the study area in the southeast region of Minas Gerais, Brazil. Names and information about forests are given in Table 1. A) Location of Minas Gerais in Brazil; B) Distribution of all sampled forests; C) Distribution of sampled urban forests within the city of Juiz de Fora. The circles correspond to sampled forests, blue: mature, non-urban forests, light blue: urban forests without anthropogenic land-use history, brown: urban forests regenerated from cropland, orange: urban forests regenerated from denuded landscapes.

Table 1 Characterization of twelve tropical forest fragments sampled in this study. LUH land use history. NUF non-urban forests, UF urban forests, CRUF cropland regenerated urban forests, DRUF denudation regenerated urban forests, Area (ha), Perimeter (Km), P:A (perimeter to area ratio), Shape Index, BA (Basal Area, m2), Density (Individuals/ha), Mean DBH (Diameter at Breast Height, cm), Native/Non-native (Number of native and non-native species).

Forest	**Category**	**Coordinates**		**Area (ha)**	**Perimeter (km)**	**P:A**	**Shape Index**	**AB (m^2)**	**Density (Ind/ha)**	**Mean DBH (cm)**	**Native/Non-native**
BN	NUF	21°24'45"S	43°34'25"W	32.73	2.95	0.01	1.46	13.31	33.28	13.53	284/0
FS	NUF	21°48'14"S	43°55'52"W	47.19	4.26	0.01	1.75	17.44	43.59	13.98	336/0
ML	NUF	22°1'58"S	43°52'37"W	18.81	1.81	0.01	1.18	15.04	37.61	12.39	314/0
LAJ	UF	21°47'29"S	43°22'33"W	84.38	5.36	0.01	1.65	10.40	26.00	12.82	246/0
PDA	UF	21°45'13"S	43°18'58"W	273.86	8.39	0.00	1.43	10.39	25.99	11.46	305/0
EDF	UF	21°46'46"S	43°22'17"W	5.06	1.47	0.03	1.85	9.87	24.68	13.17	236/0
EM	CRUF	21°46'52"S	43°22'3"W	4.34	1.30	0.03	1.76	6.75	16.87	11.25	209/1
URB	CRUF	21°44'5"S	43°22'7"W	14.85	1.94	0.01	1.42	6.66	16.65	10.57	135/0
SEC	CRUF	21°44'3"S	43°22'12"W	26.04	2.91	0.01	1.61	8.47	21.19	9.78	218/0
ICB	DRUF	21°46'35"S	43°22'18"W	1.44	0.70	0.05	1.64	9.95	24.88	12.52	127/7
PIN	DRUF	21°46'33"S	43°22'6"W	1.97	0.63	0.03	1.26	8.21	20.52	11.93	59/1
CAN	DRUF	21°46'37"S	43°22'2"W	1.45	0.75	0.05	1.75	4.14	10.36	10.23	52/1

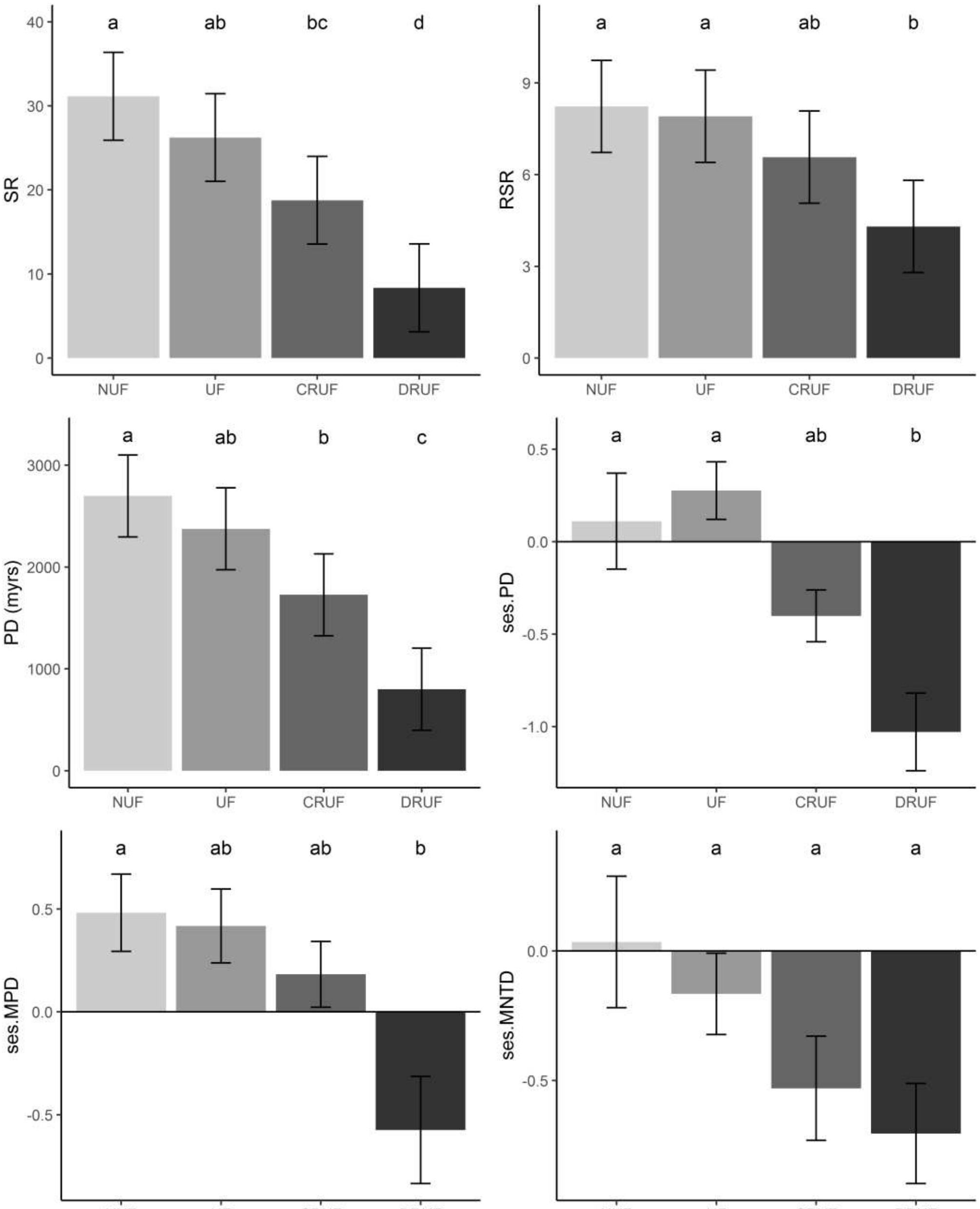


Fig. 2 The effects of land-use history on species and phylogenetic diversity metrics represented by mean values for twelve forests from the Brazilian Atlantic Forest, located in the southeast state of Minas Gerais, Brazil. NUF non-urban forests, UF urban forests, CRUF cropland regenerated urban forests, DRUF denudation regenerated urban forests. Different letters indicate significant differences among mean values ($p < 0.05$) based on pairwise comparisons in mixed linear models (Tukey's HSD). Error bars represent 95% confidence intervals. SR Species

Richness, RSR Rarefied Species Richness, PD Phylogenetic diversity, ses.PD standardized effect size of Phylogenetic Diversity, ses.MPD standardized effect size of Mean Pairwise Distance, ses.MNTD standardized effect size of Mean Nearest Taxon Distance

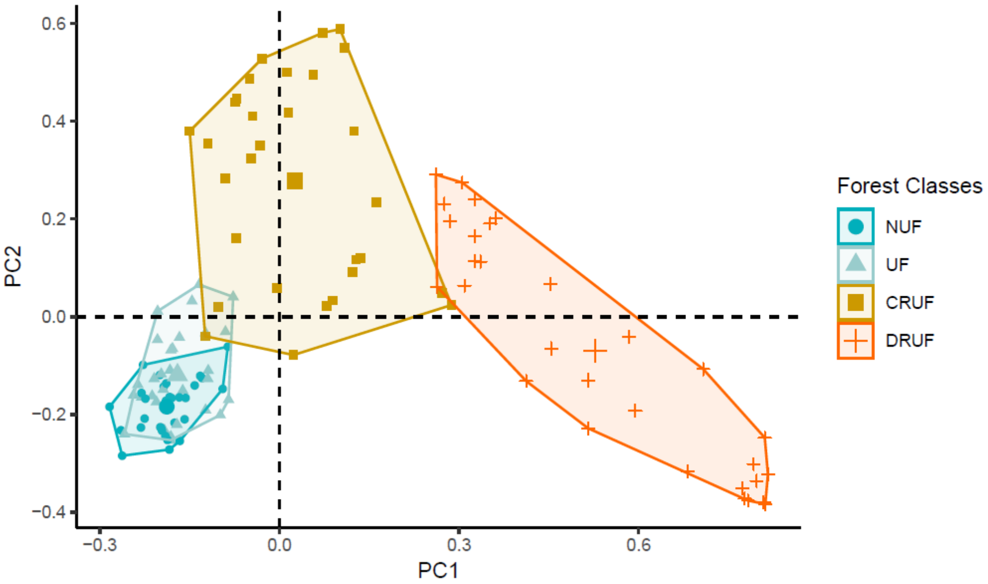


Fig. 3 First two axes (PC1 and PC2) from a principal component analysis with Hellinger distance as the coefficient of dissimilarity (evoPCAHellinger) showing the distribution of plots according to their phylogenetic composition. Point represents individual plots sampled across twelve tropical forests from the Brazilian Atlantic Forest, located in the southeast region of Minas Gerais, Brazil. NUF non-urban forests, UF urban forests, CRUF cropland regenerated urban forests, DRUF denudation regenerated urban forests

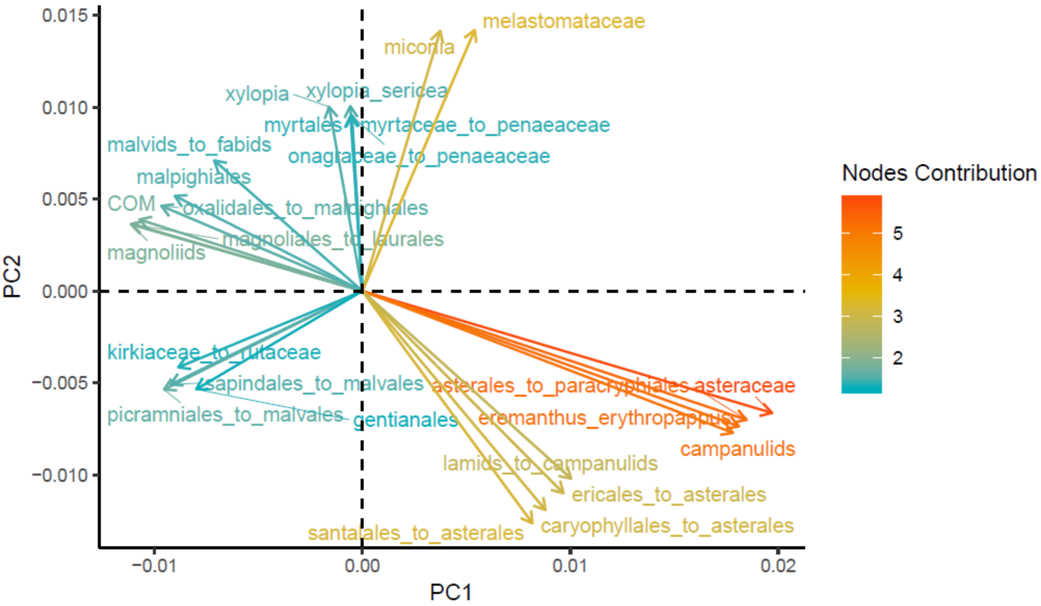


Fig. 4 First two axes (PC1 and PC2) from a principal component analysis with Hellinger distance as the coefficient of dissimilarity (evoPCAHellinger) showing the influence of each lineage in determining the position of the plots in the ordination. Lineages are indicated by an arrow (whose direction and size relate to the correlation with the first two axes and the strength of that correlation).

Supplementary material

Table S1 Overview of the 378 forest tree species sampled in twelve tropical forests from the Brazilian Atlantic Forest located in the southeast region of Minas Gerais, Brazil: scientific name and family.

Species	Family
Abarema langsdorffii (Benth.) Barneby & J.W.Grimes	Fabaceae
Aegiphila integrifolia (Jacq.) Moldenke	Lamiaceae
Alchornea glandulosa Poepp. & Endl.	Euphorbiaceae
Alchornea triplinervia (Spreng.) Muell. Arg.	Euphorbiaceae
Allophylus edulis (A.St.-Hil. et al.) Hieron.	Sapindaceae
Allophylus petiolulatus Radlk.	Sapindaceae
Allophylus racemosus Sw.	Sapindaceae
Amaioua guianensis Aubl.	Rubiaceae
Amaioua intermedia Mart. ex Schult. & Schult.f.	Rubiaceae
Anadenanthera colubrina (Vell). Brenan	Fabaceae
Anadenanthera peregrina (L.) Speg.	Fabaceae
Andira anthelmia (Vell.) Benth.	Fabaceae
Andira fraxinifolia Benth.	Fabaceae
Annona cacans Warm.	Annonaceae
Annona dolabripetala Raddi	Annonaceae
Annona emarginata (Schltdl.) H.Rainer	Annonaceae
Annona glabra L.	Annonaceae
Annona mucosa Jacq.	Annonaceae
Annona sylvatica (A.St.-Hil.)	Annonaceae
Aparisthmium cordatum (A.Juss.) Baill.	Euphorbiaceae

Apuleia leiocarpa (Vogel) J.F.Macbr.	Fabaceae
Aspidosperma olivaceum Müll.Arg	Apocynaceae
Aspidosperma parvifolium A. DC.	Apocynaceae
Aspidosperma polyneuron Müll.Arg.	Apocynaceae
Aspidosperma ramiflorum Müll.Arg.	Apocynaceae
Aspidosperma spruceanum Benth. ex Müll.Arg.	Apocynaceae
Austrocritonia angulicaulis R.M.King & H.Rob.	Asteraceae
Bathysa australis (A.St.-Hil.) K.Schum.	Rubiaceae
Bathysa cuspidata (A.St.-Hil.) Hook.f.	Rubiaceae
Bathysa nicholsonii K.Schum.	Rubiaceae
Bauhinia pulchella Benth.	Fabaceae
Bauhinia ungulata L.	Fabaceae
Beilschmiedia emarginata (Meisn.) Kosterm.	Lauraceae
Beilschmiedia taubertiana (Schwacke & Mez) Kosterm.	Lauraceae
Brosimum guianense (Aubl.) Huber	Moraceae
Buchenavia hoehneana N.F.Mattos	Combretaceae
Buchenavia tomentosa Eichler	Combretaceae
Cabralea canjerana (Vell.) Mart.	Meliaceae
Calyptranthes clusiifolia O.Berg	Myrtaceae
Calyptranthes widgreniana O.Berg	Myrtaceae
Campomanesia guaviroba (DC.) Kiaersk.	Myrtaceae
Campomanesia guazumifolia (Cambess.) O.Berg	Myrtaceae
Campomanesia laurifolia Gardner	Myrtaceae
Campomanesia pubescens (Mart. ex DC.) O.Berg	Myrtaceae
Cariniana estrellensis (raddi) kuntze	Lecythidaceae
Casearia arborea (Rich.) Urb.	Salicaceae
Casearia decandra Jacq.	Salicaceae

Casearia lasiophylla Eichler	Salicaceae
Casearia obliqua Spreng.	Salicaceae
Casearia selloana Eichler	Salicaceae
Casearia sylvestris Sw.	Salicaceae
Casearia ulmifolia Vahl ex Vent.	Salicaceae
Cassia ferruginea (Schrad.) Schrad. ex DC.	Fabaceae
Casuarina equisetifolia L.	Casuarinaceae
Cecropia glaziovii Snethl.	Urticaceae
Cecropia hololeuca Miq.	Urticaceae
Cecropia pachystachya Trécul	Urticaceae
Cedrela fissilis Vell.	Meliaceae
Cedrela odorata L.	Meliaceae
Ceiba speciosa (A.St.-Hil.) Ravenna	Malvaceae
Cheiloclinium cognatum (Miers) A.C.Sm.	Celastraceae
Cheiloclinium serratum (Cambess.) A.C.Sm.	Celastraceae
Chionanthus filiformis (Vell.) P.S.Green	Oleaceae
Chomelia brasiliana A.Rich.	Rubiaceae
Citharexylum myrianthum Cham.	Verbenaceae
Citronella paniculata (Mart.) Howard	Cardiopteridaceae
Clethra scabra Pers.	Clethraceae
Coccoloba declinata (Vell.) Mart.	Polygonaceae
Coccoloba warmingii Meisn	Polygonaceae
Copaifera langsdorffii Desf.	Fabaceae
Copaifera trapezifolia Hayne	Fabaceae
Cordia aberrans I.M.Johnst.	Boraginaceae
Cordia ecalyculata Vell.	Boraginaceae
Cordia magnoliifolia Cham.	Boraginaceae

Cordia sellowiana Cham.	Boraginaceae
Cordia toqueve Aubl.	Boraginaceae
Cordia trichotoma (Vell.) Arráb. ex Steud.	Boraginaceae
Cordiera elliptica (Cham.) Kuntze	Rubiaceae
Coussapoa microcarpa (Schott) Rizzini	Urticaceae
Coussarea nodosa (Benth.) Müll.Arg.	Rubiaceae
Crepidospermum atlanticum Daly	Burseraceae
Croton celtidifolius Baill.	Euphorbiaceae
Croton floribundus Spreng.	Euphorbiaceae
Croton salutaris Casar.	Euphorbiaceae
Croton urucurana Baill.	Euphorbiaceae
Cryptocarya aschersoniana Mez	Lauraceae
Cryptocarya micrantha Meisn.	Lauraceae
Cupania emarginata Cambess.	Sapindaceae
Cupania ludowigii Sommer & Ferrucci	Sapindaceae
Cupania oblongifolia Mart.	Sapindaceae
Cupania racemosa (Vell.) Radlk.	Sapindaceae
Cupania vernalis Cambess.	Sapindaceae
Cybistax antisyphilitica (Mart.) Mart.	Bignoniaceae
Dalbergia foliolosa Benth.	Fabaceae
Dalbergia frutescens (Vell.) Britton	Fabaceae
Dalbergia nigra (Vell.) Alemao ex Benth.	Fabaceae
Dalbergia villosa (Benth.) Benth.	Fabaceae
Daphnopsis brasiliensis Mart.	Thymelaeaceae
Daphnopsis fasciculata (Meisn.) Nevling	Thymelaeaceae
Dictyoloma vandellianum A.Juss	Rutaceae
Duguetia lanceolata A.St-Hil	Annonaceae

Ecclinusa ramiflora Mart.	Sapotaceae
Endlicheria glomerata Mez	Lauraceae
Endlicheria paniculata (Spreng.) J.F. Macbr.	Lauraceae
Enterolobium contortisiliquum (Vell.) Morong	Fabaceae
Eremanthus erythropappus (DC.) MacLeish	Asteracea
Eriobotrya japonica (Thunb.) Lindl.	Rosaceae
Eriotheca candolleana (K. Schum.) A. Robyns	Malvaceae
Erythroxylum citrifolium A.St.-Hil.	Erythroxylaceae
Erythroxylum deciduum A.St.-Hil.	Erythroxylacee
Erythroxylum pelleterianum A.St.-Hil.	Erythroxylaceae
Eugenia brasiliensis Lam.	Myrtaceae
Eugenia candolleana DC.	Myrtaceae
Eugenia capparidifolia DC.	Myrtaceae
Eugenia cerasiflora Miq.	Myrtaceae
Eugenia dodonaeifolia Cambess.	Myrtaceae
Eugenia handroana D.Legrand	Myrtaceae
Eugenia handroi (Mattos) Mattos	Myrtaceae
Eugenia hiemalis Cambess.	Myrtaceae
Eugenia involucrata DC.	Myrtaceae
Eugenia longipedunculata Nied.	Myrtaceae
Eugenia moonioides O.Berg	Myrtaceae
Eugenia pisiformis Cambess.	Myrtaceae
Eugenia subundulata Kiaersk.	Myrtaceae
Eugenia vattimoana Mattos	Myrtaceae
Eugenia widgrenii Sond. ex O.Berg	Myrtaceae
Euphorbia cotinifolia L.	Myrtaceae
Euterpe edulis Mart.	Arecaceae

Faramea hyacinthina Mart.	Rubiaceae
Faramea multiflora A.Rich. ex DC.	Rubiaceae
Faramea nigrescens Mart.	Rubiaceae
Ficus citrifolia Mill.	Moraceae
Ficus elastica Roxb.	Moraceae
Ficus mexiae Standl	Moraceae
Garcinia gardneriana (Planch. & Triana) Zappi	Clusiaceae
Geonoma schottiana Mart.	Arecaceae
Guapira graciliflora (Mart. ex Schmidt) Lundell	Nyctaginaceae
Guapira hirsuta (Choisy) Lundell	Nyctaginaceae
Guapira opposita (Vell.) Reitz	Nyctaginaceae
Guarea kunthiana A. Juss	Meliaceae
Guarea macrophylla Vahl	Meliaceae
Guatteria australis A.St.-Hil.	Annonaceae
Guatteria pohliana Schltdl.	Annonaceae
Guatteria sellowiana Schltdl.	Annonaceae
Guatteria villosissima A.St.Hil.	Annonaceae
Guettarda viburnoides Cham. & Schltdl.	Rubiaceae
Handroanthus chrysotrichus (Mart. ex DC.) Mattos	Bignoniaceae
Handroanthus impetiginosus (Mart. ex DC.) Mattos	Bignoniaceae
Heisteria silvianii Schwacke	Olacaceae
Hirtella hebeclada Moric ex. DC.	Chrysobalanaceae
Holocalyx balansae Micheli	Fabaceae
Hortia brasiliana Vand. ex DC.	Rutaceae
Hyeronima alchorneoides Allemão	Euphorbiaceae
Hyeronima oblonga (Tul.) Müll.Arg.	Euphorbiaceae
Hymenolobium janeirense Kuhlm.	Fabaceae

Hyptidendron asperrimum (Spreng.) Harley	Lamiaceae
Ilex cerasifolia Reissek	Aquifoliaceae
Ilex paraguariensis A.St.-Hil.	Aquifoliaceae
Ilex theezans Mart. ex Reissek	Aquifoliaceae
Inga barbata Benth.	Fabaceae
Inga capitata Desv.	Fabaceae
Inga cylindrica (Vell.) Mart.	Fabaceae
Inga edulis Mart.	Fabaceae
Inga flagelliformis (Vell.) Mart.	Fabaceae
Inga marginata Willd.	Fabaceae
Inga sessilis (Vell.) Mart.	Fabaceae
Inga striata Benth.	Fabaceae
Inga subnuda Salzm.	Fabaceae
Inga virescens Benth.	Fabaceae
Ixora brevifolia Benth.	Rubiaceae
Jacaranda macrantha Cham.	Bignoniaceae
Jacaranda micrantha Cham.	Bignoniaceae
Jacaranda puberula Cham.	Bignoniaceae
Jacaratia spinosa (Aubl.) A. DC.	Caricaceae
Kielmeyera lathrophyton Saddi	Calophyllaceae
Lacistema pubescens Mart.	Lacistemataceae
Lafoensia glyptocarpa Koehne	Lythraceae
Lamanonia cuneata (Cambess.) Kuntze	Cunoniaceae
Lamanonia ternata Vell.	Cunoniaceae
Laplacea fruticosa (Schrad.) Kobuski	Theaceae
Leucaena leucocephala (Lam.) de Wit	Fabaceae
Licania kunthiana Hook. f.	Chrysobalanaceae

Licaria bahiana Kurz	Lauraceae
Lonchocarpus cultratus (Vell.) A.M.G.Azevedo & H.C.Lima	Fabaceae
Luehea divaricata Mart.	Malvaceae
Mabea fistulifera Mart.	Euphorbiaceae
Machaerium acutifolium Vogel	Fabaceae
Machaerium brasiliensis Vogel	Fabaceae
Machaerium hirtum (Vell.) Stellfeld	Fabaceae
Machaerium nyctitans (Vell. Conc.) Benth.)	Fabaceae
Machaerium ruddianum C.V.Mendonça & A.M.G.Azevedo	Fabaceae
Machaerium stipitatum Vogel	Fabaceae
Macropeplus schwackeanus (Perkins) I.Santos & Peixoto	Monimiaceae
Mangifera indica L.	Anacardiaceae
Maprounea guianensis Aubl.	Euphorbiaceae
Margaritopsis chaenotricha (DC.) C.M.Taylor	Rubiaceae
Marlierea eugenioides (Cambess.) D.Legrand	Myrtaceae
Marlierea excoriata Mart.	Myrtaceae
Marlierea laevigata (DC.) Kiaersk.	Myrtaceae
Marlierea obscura O.Berg	Myrtaceae
Matayba elaeagnoides Radlk.	Sapindaceae
Matayba guianensis Aubl.	Sapindaceae
Matayba marginata Radlk	Sapindaceae
Maytenus brasiliensis Mart.	Celastraceae
Maytenus communis Reissek	Celastraceae
Maytenus evonymoides Reissek	Celastraceae
Maytenus floribunda Reissek	Celastraceae
Maytenus gonoclada Mart.	Celastraceae
Maytenus salicifolia Reissek	Celastraceae

Melanoxylon brauna Schott	Fabaceae
Meliosma itatiaiae Urb.	Sabiaceae
Miconia budlejoides Triana	Melastomataceae
Miconia chartacea Triana	Melastomataceae
Miconia cinnamomifolia (DC.) Naudin	Melastomataceae
Miconia inconspicua Miq.	Melastomataceae
Miconia latecrenata (DC.) Naudin	Melastomataceae
Miconia mellina DC.	Melastomataceae
Miconia pusilliflora (DC.) Naudin	Melastomataceae
Miconia pyrifolia Naudin	Melastomataceae
Miconia sellowiana Naudin	Melastomataceae
Miconia trianae Cogn.	Melastomataceae
Miconia tristis Spring	Melastomataceae
Miconia urophylla DC.	Melastomataceae
Miconia valtheri Naudin	Melastomataceae
Mimosa artemisiana Heringer & Paula	Fabaceae
Mimosa bimucronata (DC.) Kuntze	Fabaceae
Mollinedia argyrogyna Perkins	Monimiaceae
Mollinedia blumenaviana Perkins	Monimiaceae
Mollinedia schottiana (Spreng.) Perkins	Monimiaceae
Mollinedia triflora (Spreng.) Tul.	Monimiaceae
Mollinedia widgrenii A.DC.	Monimiaceae
Mouriri guianensis Aubl.	Memecylaceae
Myrceugenia miersiana D.Legrand & Kausel	Myrtaceae
Myrcia amazonica DC.	Myrtaceae
Myrcia anceps (Spreng.) O.Berg	Myrtaceae
Myrcia crocea Kiaersk.	Myrtaceae

Myrcia hebepetala DC.	Myrtaceae
Myrcia multiflora (O. Berg) D. Legrand	Myrtaceae
Myrcia pubipetala Miq.	Myrtaceae
Myrcia splendens (Sw.) DC.	Myrtaceae
Myrciaria floribunda (H. West. Ex. Wild.) O. Berg.	Myrtaceae
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	Primulaceae
Myrsine gardneriana A.DC.	Primulaceae
Myrsine lancifolia Mart.	Primulaceae
Myrsine umbellata Mart.	Primulaceae
Myrsine venosa A.DC.	Primulaceae
Nectandra lanceolata Ness	Lauraceae
Nectandra megapotamica (Spreng.) Mez	Lauraceae
Nectandra membranacea (Sw.) Griseb.	Lauraceae
Nectandra nitidula Nees	Lauraceae
Nectandra oppositifolia Nees	Lauraceae
Ocotea aciphylla (Nees & Mart.) Mez	Lauraceae
Ocotea bicolor Vattimo-Gil	Lauraceae
Ocotea brachybotrya (Meisn.) Mez	Lauraceae
Ocotea catharinensis Mez	Lauraceae
Ocotea corymbosa (Meisn.) Mez	Lauraceae
Ocotea cujumary Mart.	Lauraceae
Ocotea diospyrifolia (Meisn.) Mez	Lauraceae
Ocotea glaziovii Mez	Lauraceae
Ocotea indecora (Schott) Mez	Lauraceae
Ocotea lanata (Nees) Mez	Lauraceae
Ocotea lancifolia (Schott) Mez	Lauraceae
Ocotea laxa (Nees) Mez	Lauraceae

Ocotea longifolia Kunth	Lauraceae
Ocotea odorifera (Vell.) Rohwer	Lauraceae
Ocotea puberula (Rich.) Nees	Lauraceae
Ocotea vaccinioides (Meisn.) Mez	Lauraceae
Ocotea velloziana (Meisn.) Mez	Lauraceae
Ocotea villosa Kosterm.	Lauraceae
Ormosia altimontana Meireles & H.C.Lima	Fabaceae
Ouratea parviflora (A.DC.) Baill.	Ochnaceae
Ouratea semiserrata (Mart. & Nees) Engl.	Ochnaceae
Ouratea spectabilis (Mart. & Engl.) Engl.	Ochnaceae
Oxandra martiana (Schltdl.) R.E.Fr.	Annonaceae
Pachira endecaphylla (Vell.) Carv.-Sobr.	Malvaceae
Pachira glabra Pasq.	Malvaceae
Peltophorum dubium (Spreng.) Taub.	Fabaceae
Pera glabrata (Schott) Poepp. ex Baill.	Euphorbiaceae
Persea americana Miller	Lauraceae
Persea willdenovii Kosterm.	Lauraceae
Picramnia glazioviana Engl.	Simaroubaceae
Picramnia ramiflora Planch.	Simaroubaceae
Pimenta pseudocaryophyllus (Gomes) Landrum	Myrtaceae
Piper cernuum Vell.	Piperaceae
Piptadenia gonoacantha (Mart.) J.F.Macbr.	Fabaceae
Piptadenia paniculata Benth.	Fabaceae
Piptocarpha macropoda (DC.) Baker	Asteraceae
Platypodium elegans Vogel	Fabaceae
Pogonophora schomburgkiana Miers ex Benth.	Peraceae
Poincianella pluviosa (DC.) L.P.Queiroz	Fabaceae

Posoqueria latifolia (Rudge) Schult.	Rubiaceae
Pourouma guianensis Aubl	Urticaceae
Pouteria caimito (Ruiz & Pav.) Radlk	Sapotaceae
Pouteria guianensis Aubl.	Sapotaceae
Protium heptaphyllum (Aubl.) Marchand	Burseracea
Protium spruceanum (Benth.) Engl.	Burseracea
Prunus myrtifolia (L.) Urb.	Rosaceae
Pseudobombax longiflorum (Mart. & Zucc.) A.Robyns	Malvaceae
Pseudopiptadenia contorta (DC.) G.P.Lewis & M.P.Lima	Fabaceae
Pseudopiptadenia leptostachya (Benth.) Rauschert	Fabaceae
Psychotria carthagenensis Jacq.	Rubiaceae
Psychotria cephalantha (Müll.Arg.) Standl.	Rubiaceae
Psychotria nuda (Cham. & Schltdl.) Wawra	Rubiaceae
Psychotria suterella Müll.Arg.	Rubiaceae
Psychotria vellosiana Benth.	Rubiaceae
Pterocarpus rohrii Vahl	Fabaceae
Qualea gestasiana A.St.-Hil.	Vochysiaceae
Qualea lundii (Warm.) Warm.	Vochysiaceae
Roupala montana Aubl.	Proteaceae
Sapium glandulatum (Vell.) Pax.	Euphorbiaceae
Schefflera angustissima (Marchal) Frodin	Araliaceae
Schefflera calva (Cham.) Frodin & Fiaschi	Araliaceae
Schefflera longipetiolata (Pohl ex DC.) Frodin & Fiaschi	Araliaceae
Schefflera morototoni (Aubl.) Maguire et al.	Araliaceae
Schefflera vinosa (Cham. & Schltdl.) Frodin & Fiaschi	Araliaceae
Schinus terebinthifolius Raddi	Anacardiaceae
Schizolobium parahyba (Vell.) S.F. Blake	Fabaceae

Seguieria langsdorffii Moq.	Phytolaccaceae
Senegalia polyphylla (DC.) Britton & Rose	Fabaceae
Senna macranthera H.S.Irwin & Barneby	Fabaceae
Senna multijuga (Rich.) H.S.Irwin & Barneby	Fabaceae
Siparuna guianensis Aubl.	Siparunaceae
Sloanea guianensis (Aubl.) Benth.	Elaeocarpaceae
Sloanea hirsuta (Schott) Planch. ex Benth.	Elaeocarpaceae
Sloanea retusa Uittien	Elaeocarpaceae
Solanum argenteum Blanchet ex Dunal	Solanaceae
Solanum cernuum Vell.	Solanaceae
Solanum leucodendron Sendtn.	Solanaceae
Solanum pseudoquina A.St.-Hil.	Solanaceae
Solanum sellowianum Sendtn.	Solanaceae
Sorocea bonplandii (Baill.) W.C. Burger	Moraceae
Sorocea guilleminiana Gaudich.	Moraceae
Stryphnodendron polyphyllum Mart.	Fabaceae
Swartzia flaemingii Raddi	Fabaceae
Swartzia macrostachya Benth.	Fabaceae
Swartzia myrtifolia Sm.	Fabaceae
Syagrus romanzoffiana (Cham.) Glassman	Arecaceae
Symplocos pubescens Klotzsch ex Benth.	Symplocaceae
Syzygium jambos (L.) Alston	Myrtaceae
Syzygium cumin Bark	Myrtaceae
Tabernaemontana laeta Mart.	Bignoniaceae
Tachigali paratyensis (Vell.) H.C.Lima	Fabaceae
Tachigali rugosa (Mart. ex Benth.) Zarucchi & Pipoly	Fabaceae
Tachigali vulgaris L.G.Silva & H.C.Lima	Fabaceae

Tapirira guianensis Aubl.	Anacardiaceae
Tapirira obtusa (Benth.) J.D.Mitch.	Anacardiaceae
Terminalia argentea Mart.	Combretaceae
Tibouchina estrellensis (Raddi) Cogn.	Melastomataceae
Tibouchina fissinervia (Schrank & Mart. ex DC.) Cogn.	Melastomataceae
Tibouchina fothergillae (DC.) Cogn.	Melastomataceae
Tibouchina mutabilis (Vell.) Cogn.	Melastomataceae
Tovomita glazioviana Engl.	Clusiaceae
Tovomitopsis saldanhae Engl.	Clusiaceae
Trema micrantha (L.) Blume	Cannabaceae
Trichilia casarettoi C.DC.	Meliaceae
Trichilia catigua A.Juss.	Meliaceae
Trichilia elegans A.Juss.	Meliaceae
Trichilia emarginata (Turcz.) C.DC.	Meliaceae
Trichilia hirta L.	Meliaceae
Trichilia lepidota Mart.	Meliaceae
Urera baccifera (L.) Gaudich. ex Wedd.	Urticaceae
Vernonanthura discolor (Spreng.) H.Rob.	Asteraceae
Vernonanthura divaricata (Spreng.) H.Rob.	Meliaceae
Vernonanthura phosphorica (Vell.) H.Rob.	Meliaceae
Virola bicuhyba (Schott ex Spreng.) Warb.	Myristicaceae
Vismia guianensis (Aubl.) Choisy	Hypericaceae
Vismia magnoliifolia Schltdl. & Cham.	Hypericaceae
Vitex polygama Cham.	Lamiaceae
Vitex sellowiana Cham.	Lamiaceae
Vochysia bifalcata Warm.	Vochysiaceae
Vochysia magnifica Warm.	Vochysiaceae

Vochysia rectiflora Warm.	Vochysiaceae
Vochysia tucanorum Mart.	Vochysiaceae
Xylopia brasiliensis Spreng.	Annonaceae
Xylopia sericea A.St.-Hil.	Annonaceae
Xylosma ciliatifolia (Clos) Eichler	Salicaceae
Zanthoxylum rhoifolium Lam.	Rutaceae
Zollernia ilicifolia (Brongn.) Vogel	Fabaceae

Table S 1 Tukey test from linear mixed models testing effects of land-use history on taxonomic richness and phylogenetic metrics sampled in twelve tropical forests from the Brazilian Atlantic Forest located in the southeast region of Minas Gerais, Brazil. NUF non-urban forests, UF urban forests, CRUF cropland regenerated urban forests, DRUF denudation regenerated urban forests, SR Species Richness, RSR Rarefied Species Richness, PD Phylogenetic diversity, ses.PD standardized effect size of Phylogenetic Diversity, ses.MPD standardized effect size of Mean Pairwise Distance, ses.MNTD standardized effect size of Mean Nearest Taxon Distance. *significantly different at p < 0 05.

	NUF-UF		NUF-CRUF		NUF-DRUF	
	z-value	*p-value*	*z value*	*p-value*	*z value*	*p-value*
SR	-1.53	0.42	-3.87	<0.01*	-7.10	<0.01*
SRR	-0.35	0.99	-1.80	0.28	-4.24	<0.01*
PD	-1.60	0.38	4.81	<0.01*	-9.45	<0.01*
ses.PD	0.37	0.98	-1.14	0.66	-2.62	0.04*
ses.MPD	-0.20	0.99	-0.46	0.97	-2.54	0.05*
ses.MNTD	-0.43	0.97	-1.22	0.61	-2.05	0.17

	UF-CRUF		UF-DRUF		CRUF-DRUF	
	z value	*p-value*	*z value*	*p-value*	*z value*	*p-value*
SR	-2.36	0.09	-5.57	<0.01*	-3.25	<0.01*
SRR	-1.44	0.47	-3.89	<0.01*	-2.45	0.07
PD	3.21	<0.01*	-7.85	<0.01*	-4.64	<0.01*
ses.PD	-1.51	0.43	-2.97	0.01*	-1.49	0.44
ses.MPD	-0.26	0.99	-2.34	0.09	-2.08	0.16
ses.MNTD	-0.78	0.86	-1.62	0.37	-0.85	0.83

Table S 2 Effects of land use history on landscape metrics represented by fitted mean values sampled in twelve tropical forests from the Brazilian Atlantic ForestFitted means and Standard Error (SE) values from linear models. Area (ha), Perimeter (km), P:A (perimeter to area ratio), Shape Index. NUF non-urban forests, UF urban forests, CRUF cropland regenerated urban forests, DRUF denudation regenerated urban forests.

Metrics	NUF	UF	CRUF	DRUF
Area	32.9 (14.6)	121.3 (103.3)	15.1 (4.5)	1.62 (0.16)
Perimeter	3.01 (1.09)	5.07 (1.09)	2.05 (1.09)	0.69 (1.09)
P:A	0.01 (0.01)	0.01 (0.01)	0.02 (0.01)	0.04 (0.01)
Shape Index	1.46 (0.14)	1.64 (0.14)	1.60 (0.14)	1.55 (0.14)

Table S 3 Tukey test from generalized linear models testing effects of land-use history on landscape metrics sampled in twelve tropical forests from the Brazilian Atlantic Forest located in the southeast region of Minas Gerais, Brazil. NUF non-urban forests, UF urban forests, CRUF cropland regenerated urban forests, DRUF denudation regenerated urban forests, Area (ha), Perimeter (km), P:A (perimeter to area ratio), Shape Index *significantly different at p > 0 05.

	NUF-UF		NUF-CRUF		NUF-DRUF	
	z-value	*p-value*	*z value*	*p-value*	*z value*	*p-value*
Area	1.35	0.49	1.45	0.44	6.61	<0.01*
Perimeter	1.34	0.56	0.62	0.92	1.51	0.48
P:A	0.40	0.38	-1.04	0.73	-4.12	0.01*
Shape Index	0.94	0.76	-0.70	0.97	-0.47	0.96

	UF-CRUF		UF-DRUF		CRUF-DRUF	
	z value	*p-value*	*z value*	*p-value*	*z value*	*p-value*
Area	2.30	0.09	5.02	<0.01*	-7.04	<0.01*
Perimeter	1.97	0.28	2.85	0.08	-0.88	0.81
P:A	-0.64	0.92	-3.72	0.02*	3.01	0.06
Shape Index	0.24	1.00	0.48	0.96	-0.24	1.00

Table S 4 The standardized effect of variables included in each model (M1-M3) and the standard error (SE) values; Intercept Intercept value estimated for each model; df degrees of freedon, AICc Akaike's information criterion of the second order; ΔAICc difference between the AICc of a given model and that of the best model; Wt Akaike weights. LUH Land use history (categorical variable), UF urban forests, CRUF cropland regenerated urban forests, DRUF denudation regenerated urban forests, Area (ha), Perimeter (km), P:A (perimeter to area ratio) *p-value < 0.05

		SR			**RSR**			**PD**
		M1 (SE)	**M2 (SE)**	**M3 (SE)**	**M1 (SE)**	**M2 (SE)**	**M3 (SE)**	**M1 (SE)**
Intercept		32.70 (3.16)	8.44 (1.01)	8.24 (0.69)	8.23 (0.65)	8.26 (0.84)	8.24 (0.69)	2838.99 (30.40)
LUH	UF	-9.39 (4.23)	-0.64 (1.34)	-0.47 (1.12)	-0.32 (0.92)	-0.33 (0.99)	-0.47 (1.12)	-609.56 (306.07)
	CRUF	-12.83 (3.46)*	-1.73 (1.13)	-1.62 (0.98)	-1.65 (0.92)	-1.68 (1.05)	-1.62 (0.98)	-1003.6 (257.06)*
	DRUF	-23.97 (7.35)*	-4.36 (2.06)	-3.87 (1.00)*	-3.92 (0.92)*	-4.03 (1.75)	-3.87 (1.00)*	-2144.32 (470.97)*
Area (ha)		2.86 (1.84)	0.22 (0.60)	0.12 (0.45)			0.12 (0.45)	214.04 (137.13)
Perimeter (km)								
P:A		0.88 (3.43)	0.24 (0.88)			0.05 (0.67)		156.31 (202.35)
Shape Index		1.01 (1.64)						
df		9	8	8	6	7	7	8
AICc		739.09	739.92	741.04	370.38	371.66	372.36	1707.9
ΔAICc		0	0.83	1.94	0	1.28	1.98	0
Wt		0.36	0.23	0.13	0.33	0.17	0.12	0.99

(Continued on next page)

		ses.PD		ses.MPD			ses.MNTD	
		M2 (SE)	**M2 (SE)**	**M1 (SE)**	**M2 (SE)**	**M3 (SE)**	**M1 (SE)**	**M2 (SE)**
Intercept		-0.26 (0.16)	0.11 (0.31)	-0.03 (0.21)	0.48 (0.46)	0.33 (0.58)	-0.39 (0.15)	0.03 (0.32)
LUH	UF		0.16 (0.44)		-0.13 (0.65)	-0.08 (0.69)		-0.20 (0.46)
	CRUF		-0.51 (0.44)		-0.29 (0.65)	-0.18 (0.73)		-0.56 (0.46)
	DRUF		-1.18 (0.45)*		-1.65 (0.65)	-1.21 (1.22)		-0.95 (0.46)*
Area (ha)								
Perimeter (km)								
P:A		-0.47 (0.16)*		-0.62 (0.22)		-0.20 (0.46)	-0.34 (0.15)*	
Shape Index								
df		4	6	4	6	5	4	6
AICc		361.3	361.6	344.9	344.97	345.9	368.5	370.35
ΔAICc		0	0.32	0	0.06	0.99	0	1.85
Wt		0.35	0.29	0.21	0.21	0.13	0.28	0.11

Fig. S 1 Illustration of the three urban forests without land use history studied in the city of Juiz de Fora, showing their complete insertion in the urban matrix. A) EDF, B) LAJ, C) PDA.

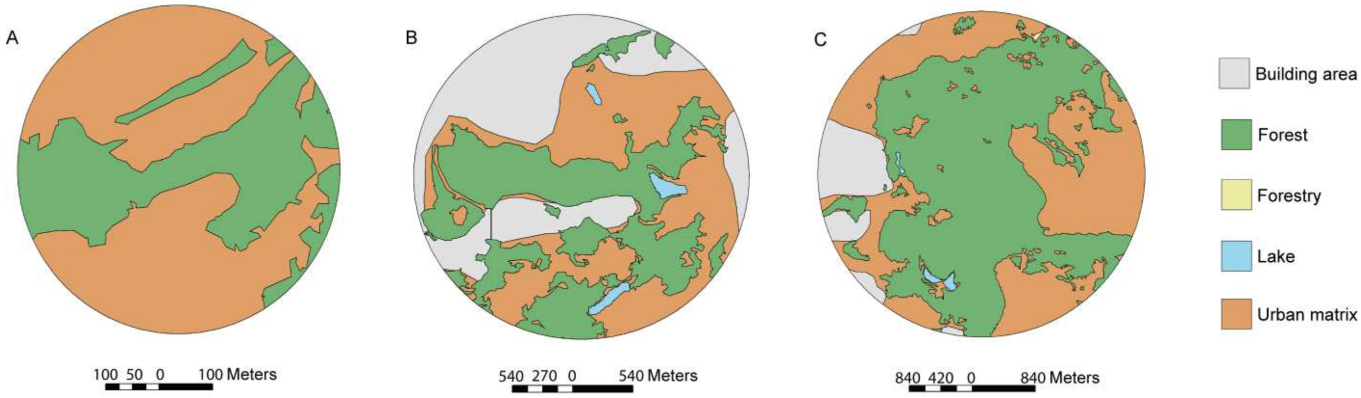
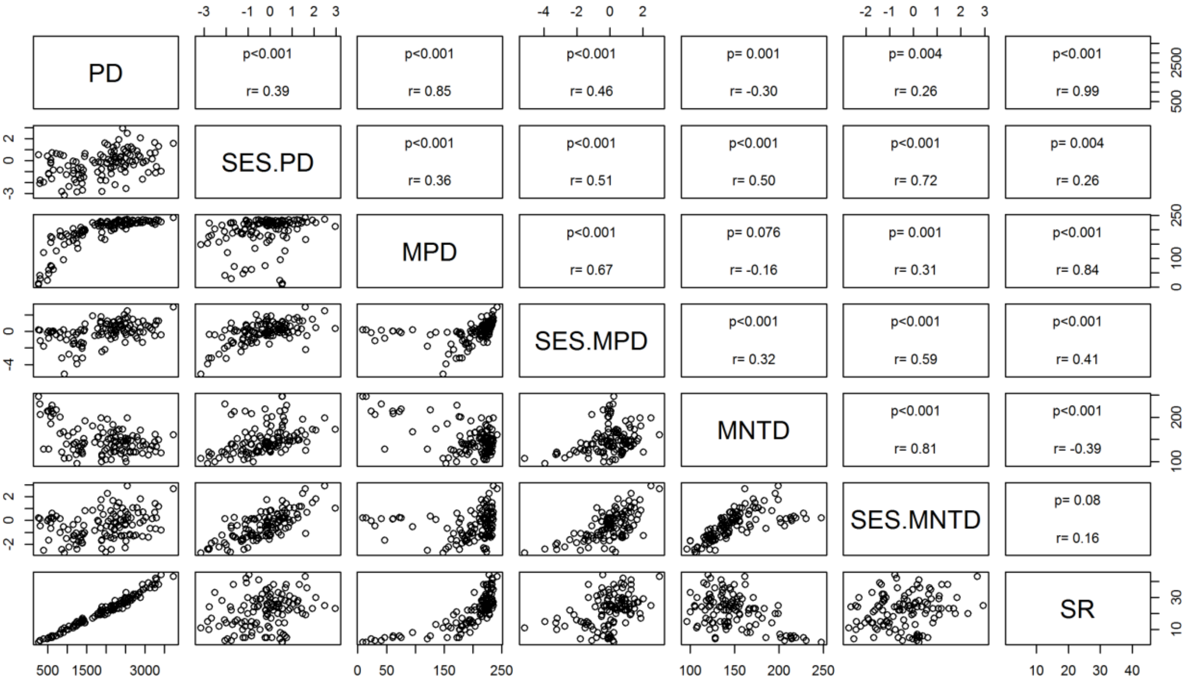


Fig. S 2 Pearson's correlation coefficients between the species richness (SR) and phylogenetic metrics sampled in twelve tropical forests from the Brazilian Atlantic Forest located in the southeast region of Minas Gerais, Brazil. PD Phylogenetic diversity, ses.PD standardized effect size of Phylogenetic Diversity, MPD Mean Pairwise Distance, ses.MPD standardized effect size of Mean Pairwise Distance, MNTD Mean Nearest Taxon Distance, ses.MNTD standardized effect size of Mean Nearest Taxon Distance.



The main drivers of aboveground biomass recovery change with the land-use history in urban forests

Abstract

Although urban forests can still contribute to the overall carbon sequestration and storage, anthropogenic land-use changes along with stand age can set tropical tree communities back to an earlier successional stage causing a reduction in standing biomass. This study aimed to investigate how aboveground biomass (AGB) is affected by land-use history within and outside the urban matrix and to identify which are the drivers of AGB in these forests. Our findings indicate that the AGB is dependent on the land-use history and on the matrix where forests are inserted (urban or rural). Besides, the wood density of the dominant trees showed a positive relation with aboveground biomass in all forest categories, indicating the important role of the mass ratio hypothesis. We found that only the AGB of old-growth forests responded positively to ses.MNTD, meaning that the niche complementarity hypothesis is present solely in "intact" fragments of natural forests. The relation between AGB and ses.MNTD is flat (for non-urban forests regenerating from cropland activities) or even negative for the urban forest with land-use history. In urban forests with a history of cropland and denudation activities, AGB increases with the presence of phylogenetically close species in the community. The environmental changes that preceded forest regeneration have filtered many species, and only the ones pre-adapted to persist in these altered habitats remained. Therefore, in secondary urban forests, biomass storage is determined by few species that are adapted to effectively capture resources (species with high wood density), and not by diversity. From a practical point of view, this study suggests that strategies for conservation and restoration should account for past land-use and the matrix where forests are inserted, as the distribution of carbon stocks and biodiversity may need to be considered separately.

Keywords: Urbanization, Environmental filtering, Phylogenetic diversity, Functional diversity, Aboveground biomass, Tropical forests, Land-use history

Introduction

Tropical biomes have historically faced extreme habitat loss, mostly due to their policies for development. As a result, we find in recent years the larger rates of forest degradation, deforestation and fragmentation in a way never observed in human history before (PELLENS & GRANDCOLAS, 2016; MITCHARD, 2018; MAXWELL et al., 2019). One of the main consequences of this scenario is not only the loss of biodiversity but also the impact on various ecosystem services (CARDINALE et al., 2012).

Although Tropical Forest can be considered the major carbon sink from terrestrial ecosystems (PAN et al., 2011), most of these forests are secondary (FAO, 2010; KEENAN et al., 2015). Natural regeneration has been considered an effective low-cost solution in the Neotropics, with potentially important value for the global carbon cycles since secondary tropical forests generally have rapid rates of carbon sequestration (CHAZDON et al., 2016; POORTER et al., 2016). However, annual losses from deforestation and forest degradation have been reported to be greater than the growth gains by forest regeneration (BACCINI et al., 2017). The rate at which these forests can recover and provide equivalent levels of carbon uptake still lacks better predictions (BROSE; HILLEBRAND; BROSE, 2016; CHAZDON et al., 2016) and deeper studies should be taken to account for the effects of forest regeneration status, land-use history and habitat context on biomass recovery (CHAZDON, 2014).

Land-use change is related to a variety of anthropogenic disturbances from urbanization to cropland plantation and soil removal activities. While agricultural activities are responsible for removing primary forests, urbanization leads to the abandonment of agricultural areas as a consequence of the spreading of urban landscapes across the world to absorb the growing population (SECRETARIAT OF THE CONVENTION ON BIOLOGICAL DIVERSITY, 2012). As more than fifty percent of the world's population can now be found in urban centers (UNITED NATIONS, 2018), urbanization can thus represent a significant threat to natural ecosystems across the world (SETO; GÜNERALP; HUTYRA, 2012). Forests regenerating in urban matrix face even stronger filters related to higher local temperature, air pollution and lower humidity, leading to a loss of species diversity (ARONSON et al., 2016; WILLIAMS et al., 2009). Although urban forests can still contribute to the overall carbon storage and sequestration (DAVIES et al., 2011; NOWAK & CRANE, 2002; PANSIT, 2019), anthropogenic land-use changes along with stand age can set tropical tree communities back to an earlier successional stage causing a reduction in standing biomass (ÁLVAREZ-YÉPIZ et al., 2008; LETCHER & CHAZDON, 2009b; CHAZDON & GUARIGUATA, 2016; WANDELLI & FEARNSIDE, 2015; VELASCO & WEE, 2019; ZHANG et al., 2020).

In tropical forests, aboveground biomass is affected by a large number of drivers. Biotic factors rely mostly on diversity (niche complementarity hypothesis) and mass-ratio hypothesis (SOUZA et al., 2019; YUAN et al., 2018). Although species richness and other taxonomic diversity indices have long been considered in ecological studies, they may not be as meaningful as functional and phylogenetic metrics, that can capture the diversification in species traits in a community (functional diversity), and account for the evolutionary history, which is the basis for trait diversification (phylogenetic diversity) (PELLENS & GRANDCOLAS 2016). The niche complementarity hypothesis predicts that diversity is the main driver of aboveground biomass because it indicates the presence of coexisting species with different strategies for resource acquisition, and these differences result in more successful exploitation of available resources (TILMAN, 1999). While functional diversity provides information about how species respond to its environment (VIOLLE & JIANG, 2009; GARNIER & NAVAS, 2016), phylogenetic diversity can be a useful surrogate for trait diversity, based on the assumption that evolutionary diversification generated trait diversification, therefore evolutionary relationships among species should produce comparable estimates of niche space (TUCKER et al., 2018). The mass-ratio hypothesis proposes that trait values of the most dominant species determine ecosystem processes in the community (GRIME, 1998). In this sense, biomass accumulation is determined by the presence of highly productive species and not by their variety (CARDINALE et al., 2007).

Several other factors also influence tree biomass, specially related to soil nutrient and management history (LOHBECK et al., 2015b; POORTER et al., 2016; ALI et al., 2017; VAN DER SANDE et al., 2017). The soil fertility hypothesis states that soil conditions are the main determinants of plant growth and stem turnover due to higher resource availability, therefore a more fertile soil results in higher aboveground biomass. (BAKER et al., 2009; QUESADA et al., 2012). Besides, microclimatic changes promoted by the contrasting matrix (e.g. urban, rural) and land-use history impact sensitive species and favor disturbance tolerant ones due to dispersal limitations, leading to a depletion of carbon stocks (ÁLVAREZ-YÉPIZ et al., 2008; POORTER et al., 2016).

In order to settle climate change mitigation strategies and enhance carbon storage in tropical forests regenerating under anthropogenic activities, it is important to identify, understand and address the most important drivers of biomass storage (e.g. Reduced Emissions from Deforestation and Forest Degradation; REDD+) and their relative strengths. Despite the increasing number of aboveground biomass studies, this is the first one with a focus on drivers of biomass in urban forests with different land-use histories. This study aimed to investigate how aboveground biomass is affected by land-use history when forests are inserted in an urban matrix and when forests are inserted in a rural matrix. We addressed the following main questions: 1) How does aboveground biomass (AGB) respond to land-use history in urban and rural forests? 2) What are the main biotic (niche complementarity and mass-ratio hypotheses) and abiotic (soil fertility hypothesis) drivers of AGB in urban forests? 3) Do drivers of AGB change with urbanization, or with the land-use history? 4) Do evolutionary and functional trait metrics capture variation in aboveground biomass in a similar way? We predict a loss of AGB among a gradient of land-use history intensity and that the drivers of biomass storage will change across the different regeneration histories of secondary forests. We also expect that forests without land-use history will have niche complementary as the stronger predictor. The opposite is expected for secondary urban forests due to the strong environmental filters caused by past disturbance events.

Materials and Methods

Study area

The study was conducted in 150 plots belonging to fifteen tropical forest fragments located in Minas Gerais, in the southest region of Brazil (21°13’- 22°1’S and 43°18’ – 44°57’W) (Fig. 1). These forests belong to the Brazilian Atlantic Forest domain and are classified as Semideciduous Seasonal Forests (IBGE, 2012), occurring from 710 to 1070 meters of altitude. The regional climate is classified as Cwb (Mesothermic climate of Köppen), defined by dry winters and mild summers. Mean annual rainfall ranges from 1343 to 1585 mm and mean temperature ranges from 16°C to 21.8ºC (ALVARES et al., 2013; BRASIL, 1992; OLIVEIRA-FILHO et al., 1994).

The soil type in the region is primarily latosols (SANTOS & ANJOS 2013). All forest fragments were classified based on their land-use history and whether or not they are located in the urban matrix (Table S1). Some plots classified as rural forests were obtained from ForestPlots.net (LOPEZ-GONZALEZ et al., 2009; LOPEZ-GONZALEZ et al., 2011).

At each study fragment, woody vegetation was surveyed in ten randomly established and non-contiguous plots of 20m x 20m, which thus total 0.4 ha per forest fragment. We considered all trees with a diameter at breast height (DBH) ≥5 cm and identified to species level. Species identities were checked for nomenclatural synonyms using the online tool Taxonomic Name Resolution Service (TNRS) ver. 3.2 (BOYLE et al., 2013). The TNRS database is a repository for numerous sources, including TROPICOS, GCC, USDA and NCBI.

All fifteen forests fragments were categorized into five classes with different historical land-use, each one represented by 3 fragments (N=3): a) old-growth forests outside the urban matrix where there is no documented record of human land-use (i.e. forest is presumed to be mature, with the only potential anthropogenic impact being selective logging); b) urban forest where there is no documented record of human land-use; c) secondary forests outside the urban matrix (rural forests) that represent natural regeneration from cropland which was abandoned 70 to 80 years ago; d) secondary urban forests that represent natural regeneration from cropland which was abandoned 70 to 80 years ago; and e) secondary urban forests that represent natural regeneration from completely denuded landscapes (land was subjected to earthmoving activities resulting in soil removal), with regrowth beginning 50 to 60 years ago. All mature forests are classified as legally protected reserves, according to the Brazilian Forest Code. These categories were assigned according to landowner interviews, government public documents and official records, satellite images and photographs. All sampled sites within each region were located in areas with similar soil characteristics, climate and topography to avoid the potential confounding effect of these factors.

Phylogenetic analysis

An ultrametric calibrated phylogeny was constructed based on the new angiosperm family tree R20160415.new (GASTAUER; MEIRA NETO, 2017), which represents phylogenetic relationships among angiosperms as recently proposed by APG IV (2016). Species from the study sites were inserted in the family tree using the phylomatic function of the Phylocom 4.2 package (WEBB; ACKERLY; KEMBEL, 2008). Tree ferns and gymnosperms (0.65% of species) were excluded from this analysis since their ancient divergences from angiosperms would have a large effect on phylogenetic diversity measures (HONORIO CORONADO et al., 2015; KEMBEL & HUBBELL, 2006; REZENDE et al., 2017). The resulting community tree was dated using the bladj (branch length adjustment) algorithm which provides mean age estimates of the nodes for which information is available (e.g. from molecular age estimation studies). Phylogenetic diversity (PD, in myrs) was calculated as the sum of all branch lengths of a phylogeny encompassing all species in a given site (FAITH, 1992). We also evaluated metrics of lineages mean distance in a phylogenetic tree: mean pairwise distance (MPD) which is the mean phylogenetic distance between all combinations of pairs of individuals (including conspecifics) in a community and mean nearest taxon distance (MNTD) as the average distance between an individual and the most closely related (non-conspecific) individual (WEBB, 2000; WEBB; ACKERLY; KEMBEL, 2008). While the phylogenetic diversity (PD) measures the sum of all evolutionary history, MPD and MNTD are related to species overall distribution on the phylogenetic tree, being more dispersed or clustered (communities dominated by closely related species). To assess the phylogenetic structure of communities, we evaluated the standardized effect size of PD (ses.PD), MPD (ses.MPD) and MNTD (ses.MNTD). For the standardized effect size calculations, our tree was compared with 10 000 null model randomizations, which is used to test whether each community is more or less phylogenetically related than expected by chance, or in the case of ses.PD, used to investigate if PD was lower or higher than expected for the given species richness. We used the null model “phylogeny pool”, which randomizes the community data matrix by drawing species from the pool of species occurring in the distance matrix with equal probability.

Functional analysis

The following functional traits were considered in the study due to their relevance to species standing biomass (LOHBECK et al., 2015b; POORTER et al., 2015): maximum height, wood density and seed size. Species maximum height (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. Species wood density (g.cm-^{3}) is positively related with plant carbon storage (PÉREZ-HARGUINDEGUY et al., 2013) as it represents biomass per wood volume constructed and was obtained from the Global Wood Density database (filtered by Tropical South America, Zanne et al., 2009). For the species with wood density not available, we used mean values for the genus or family. Species seed size (SS, categorical data), although usually related to the competitive vigor 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) (OSURI & SANKARAN, 2016; POORTER; ROSE, 2005). 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 (seed length > 1.6 cm), following TABARELLI & PERES (2002) and SANTOS et al. (2008).

To analyze 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; MASON; MOUILLOT, 2008). Functional dispersion is an indicator of species distribution in the niche space and was calculated with the species abundance as a weighting factor (LALIBERTE et al., 2010). These indices are complementary: While FRic measures the extent to which the trait space is filled, FDis measures the average distance of each species to the centroid in the multidimensional trait space (LIEBERGESELL et al., 2016). Both were calculated using Gower's distance (that allows mixed traits types: continuous, ordinal and categorical). The functional analysis were calculated using the 'FD' package in R (LALIBERTE et al. 2015).

Soil properties

In each plot, soil samples reaching 20 cm were randomly collected using a hoe after the organic layers had been removed, and 500 g of the samples were then bagged for transportation. Immediately after arriving in the laboratory, the soil samples were air-dried. After removal of colinearities to avoid model over-fitting and selection of the most important environmental variables based on their ecological relevance, we kept the following variables: soil acidity (pH, extraction with water), the concentrations of phosphorus (P), potassium (K, both Mehlich 1 extraction), aluminum (Al, all three extracted with 1 mol/L KCl), organic matter (OM, organic carbon determined by Walkley-Black method x 1.724), interchangeable bases (IB), cation exchange capacity (CEC) and saturation of bases (SB).

Statistical analysis

For every tree with DBH $\geq$ 5 cm, the aboveground biomass (AGB) was calculated using the allometric formula of CHAVE et al. 2014: $AGB = 0.0673 \times (WD\ DBH^2\ H)^{0.976}$ and the parameters, DBH (cm), height (H, m), and species wood density (WD, $g\ cm^{-3}$).

For each plot we measured the following taxonomic, functional and phylogenetic diversity metrics (representing the niche complementarity hypothesis): Species richness (SR), functional richness (FRic), functional dispersion (FDis), phylogenetic diversity (PD), mean pairwise distance (MPD), mean nearest taxon distance (MNTD), and the standardized effect size metrics of the phylogenetic indices (ses.PD, ses.MPD and ses.MNTD, respectively).

For the mass-ratio hypothesis, three community-weighted mean trait values (CWM; representing functional composition weighted by species abundance) were calculated per plot: maximum height (m), wood density ($g.cm^{-3}$) and seed size (categorical).

To define the soil characteristics of the studied forests, a principal component analysis (PCA) was run using R. To consider the effects of soil properties (soil fertility hypothesis) on the aboveground biomass, we used the first two multivariate axes of a principal component analysis (PC1 and PC2), which explained together a total of 83.76% of the data set variation (Table S2).

To evaluate the effects of soil variables (soil fertility hypothesis), CWM trait values (mass-ratio hypothesis), species richness, functional and phylogenetic diversity indices (niche complementarity hypothesis) on the aboveground biomass among forests with different land-use histories and surrounding matrices, linear mixed models were fitted including fragment as a random factor (to account for the lack of independence of plots within the sites). Subsequently, we ran all possible subsets of the full model after analyzing the variation inflation factor (VIF<4) and tested for correlations between individual predictor variables using Pearson correlation coefficients (Figure S1).

We evaluated model performance based on AICc and considered as equally supported the set of models with ΔAICc ≤ 2 via multimodel inference (BURNHAM et al. 2011; BURNHAM and ANDERSON, 2002). Tukey's post hoc test was used to assess the differences in AGB between forest categories. The analyses were performed using the platform R (R CORE TEAM, 2018) and the following packages: multcomp (BRETZ et al., 2015), lme4 (BATES et al., 2014), lmerTest (KUZNETSOVA; BROCKHOFF; CHRISTENSEN, 2016), MuMIn (BARTON, 2016), and ggplot2 (WICKHAM & CHANG, 2016).

Results

We recorded 8615 individuals from 458 trees species across all 150 plots (Table S3). The AGB decreased gradually with increasing intensity of land-use (Fig. 2, Table S4), showing a large variation among forest categories, especially among forests with and without land-use history. Old-growth forest plots (mean ± se., 299 Mg/ha ± 48) had more than 50% as much biomass than forest plots with cropland land-use history (135 Mg/ha ± 21 and 113 Mg/ha ± 18 for rural and urban forests, respectively) and forests with denudation land-use history (112 Mg/ha ± 18). The AGB of old-growth forests was significantly different from all forest categories, except urban forests without land-use history (177 Mg/ha ± 28), that also was not significantly different than any other forest category.

The AGB was best predicted by land-use history (categorical variable used as interaction with all variables), ses.MNTD (interaction with land-use history), and wood density, explaining a total of 43% of the variation in AGB (Fig. 3, Table S5). The wood density (Mass-ratio hypothesis) had a positive effect on AGB regardless of forest land-use history (Fig. 4). Land-use history had a negative effect on AGB indicating a reduction of AGB in all urban and rural forests compared to old-growth forests. The interaction between land-use and ses.MNTD (Fig. 5) was significantly negative for urban forests with land-use history (cropland and denuded), flat (non-significant) for urban forests and rural forests with cropland land-use history and positive for old-growth forests, indicating that AGB increases with the presence of phylogenetic distant species only in forests outside the urban matrix and without a history of land-use change (niche complementarity hipothesis). On the contrary, in urban forests with a history of cropland and denudation activities, AGB increases with the presence of phylogenetic close species in the community (Fig. 5).

Other factors such as soil variables (PC2), phylogenetic diversity, functional diversity, maximum height and seed size had a negligible effect on AGB, being considered insignificant to explain AGB variation (i.e. confidence intervals did include zero; Fig. 3).

Discussion

Our findings agree with our prediction that AGB would show a reduction among the forest categories according to their intensity of land-use history, suggesting that the AGB of urban forests are highly dependent on their past land-use. There is some impact of urbanization on AGB (although not statistically significant). The old-growth forests have significantly higher biomass than forests with cropland land-use history in the rural matrix but similar biomass with urban forests without land-use history. This pattern shows that the filters promoted by the disturbance events before forest regeneration such as cropland plantations and soil removal may be stronger than the urban matrix itself (ÁLVAREZ-YÉPIZ et al., 2008; CHAZDON & GUARIGATA, 2016; LETCHER & CHAZDON, 2009; WANDELLI & FEARNSIDE, 2015.). Furthermore, we found that the AGB storage results mainly from the mass ratio hypothesis (higher wood density), following several previous studies (FINEGAN, 2015; PRADO-JUNIOR et al., 2016; PYLES et al., 2018; YUAN et al., 2018). As we predicted, only the AGB of old-growth forests responded positively to ses.MNTD, meaning that the niche complementarity hypothesis is present solely in “intact” fragments of natural forests (SOUZA et al., 2019). The relation between AGB and ses.MNTD is flat or even negative for the other forest categories with land-use history. In these communities, the effects of land use change before forest regeneration are still persistent and resulted in a small subset of successful lineages composed by close relatives that tolerate the stressful environmental conditions (KNAPP et al., 2008; SANTOS et al., 2010; ARROYO-RODRÍGUEZ et al., 2012; BRUNBJERG et al., 2012; MUNGUÍA-ROSAS et al., 2014; ANDRADE et al., 2015; ČEPLOVÁ et al., 2015; PRESCOTT et al., 2016). Therefore, the increase in diversity doesn’t imply an increase in AGB in regenerating forests (FAUSET et al., 2015; FINEGAN, 2015; LOHBECK et al., 2016; FOTIS et al., 2018), not as much as the presence of some dominant hardwooded species (FAUSET et al., 2015).

Land-use history and biomass recovery

Forest recovery after land-use may last decades or even centuries, and although the mechanisms underlying forest regeneration remain poorly understood, the intensity of the disturbance events is considered one of the main factors driving species and biomass recovery (CHAZDON, 2008; JAKOVAC et al., 2015; MARTINEZ-RAMOS et al., 2016; FERREIRA et al., 2018). Biomass recovery has been shown to take up to 66 years to achieve 90% of pre-disturbance biomass in Neotropic secondary forests (POORTER et al., 2016). The studied regenerated cropland forests (70 to 80 years of regeneration) holds less than 50% (for forests in the rural matrix) and less than 40% (for forests in the urban matrix) of old-growth forests' AGB. Forest regenerated from denudation (60 years of regeneration) reached similar biomass as the regenerated urban cropland forests. However, our studied sites are mostly located in a non-forested matrix (urban forests) or surrounded by croplands and pastures (rural forests), whilst the forests studied by POORTER et al. (2016) are situated in a higher forested landscape. Besides, other studies showed fewer optimist simulations. MARTIN et al. (2013) computed data from more than 600 secondary tropical forests and found that they hold only 50% of reference forests' biomass even after 80 years after regeneration, a perspective closer to our results.

Niche complmentarity hipothesis

We found that only the AGB of old-growth forests responds positively to ses.MNTD, with the relation between AGB and ses.MNTD being flat (non-significant) or even negative for the urban forest categories with land-use history (cropland and denudation). In the late stages of succession, resources become limited and competition is increased, which shapes the community towards a wider niche space filled with ecologically different species, a strategy to allow coexistence and resource uptake (YUAN et al., 2016). Communities regenerating from agricultural activities and other land-use changes are susceptible to strong environmental filters, besides the additional dispersal limitations when they are situated in areas with less remaining forest cover (MARTINEZ-RAMOS et al., 2016) and especially urban areas. Urban forests face a variety of environmental filters derived from the urban matrix (i.e. increased temperature and decreased humidity, air pollution), which are exacerbated when these forests are secondary (BENINDE; VEITH; HOCHKIRCH, 2015). The consequence is the lost of pre-disturbance lineages, with replacement of forest specialists by a set of disturbance-tolerant generalists species causing a reduction in ecological functions (OLDEN et al., 2004; CARREÑO-ROCABADO et al., 2012; VAN MEERBEEK et al., 2014; VAN DER SANDE et al., 2017; PYLES et al., 2018). A previous study with the same secondary urban forests analyzed here have demonstrated that these forests show phylogenetic clustering, which suggests that abiotic filters are driving community assembly processes towards the colonization of more closely related species (BORGES et al., 2020). The environmental changes that preceded forest regeneration have filtered many species, and only the ones pre-adapted to persist in these altered habitats remained (MCKINNEY, 2006; BAETEN et al., 2015b). Therefore, biomass productivity is determined by few species that are adapted to effectively capture resources (species with high wood density), in spite of all the habitat limitations imposed by the stressful environmental change (CARDINALE et al., 2007).

Mass-ratio hypothesis

Higher wood density contributed significantly to biomass accumulation for all forest categories as predicted by the mass-ratio hypothesis, in line with previous studies in tropical forests (FINEGAN, 2015; PRADO-JUNIOR et al., 2016; PYLES et al., 2018; YUAN et al., 2018). Not all species are of equal importance for ecosystem processes, with dominant species being responsible for most of the community fluxes of energy and resources (GRIME, 1998; BAKER et al., 2009;). Regarding the secondary forests, the effects of species dominance are stronger, with only a subset of dominant traits contributing to different functions (LOHBECK et al., 2016; PYLES et al., 2020). The presence of phylogenetically close species with ecological similarity may be an efficient resource use strategy to biomass accumulation under resource-limited environments. As these forests face strong habitat filtering, the selection of species based on their higher wood density is perhaps a more important requirement than having a wider niche (VAN DER SANDE et al., 2016).

The role of phylogenetic metrics

We found that the phylogenetic structure (ses.MNTD) was the only variable that showed a different effect on AGB across forest categories of land-use history, suggesting that the diversity-productivity relationship changes throughout a gradient of past land-use intensity. The phylogenetic and functional diversity approach offer different but complementary information about species assembly mechanisms and ecosystem functions. Phylogenetic diversity assumes that shared ancestry accounts for all kinds of variation among taxa as more evolutionary time means a greater accumulation of trait change and therefore all important aspects of ecological features are present within its metrics (TUCKER et al., 2018). This assumption is based on the consensus that functional differences between species show an evolutionary signal and that close relatives are more similar to one another than more distantly related species (BARALOTO et al., 2012; DEXTER & CHAVE, 2016). However, trait information for a large number of species is still lacking, and traits that are most often measured are generally the easiest to collect, rather than the most ecologically important ones (HORTAL et al., 2015; SCHWEIGER et al., 2018). All these issues have driven recent studies to consider phylogenetic diversity as a valuable tool when analyzing ecosystem functions. Indeed, our findings support a number of them which has found a significant prediction power of evolutionary diversity on plant biomass accumulation (CADOTTE; CARDINALE; OAKLEY, 2008; CADOTTE, 2013; POTTER & WOODALL, 2014; PAQUETTE; JOLY; MESSIER, 2015; YUAN et al., 2016; ALI & YAN, 2018; SATDICHANH et al., 2018; SOUZA et al., 2019).

As we expected, AGB depends strongly on land-use history and has a negligible influence of other factors like soil properties, suggesting that abiotic factors related to disturbance events might be stronger filters limiting biomass accumulation (SATDICHANH et al., 2018). It is possible that the strong effect of land-use history on productivity covered our models' ability to detect more subtle effects.

Conclusions

The main findings of this study are determining that the drivers of aboveground biomass in urban forests are greatly dependent on their land-use history. Our results suggest that the mass-ratio hypotheses (CWM of wood density) is of great importance for driving aboveground biomass storage in secondary urban forests, and that aboveground biomass is greater for the groups of phylogenetically distant species only for old-growth forests. For the secondary urban forests (with cropland and denudation land-use history), high aboveground biomass is related to species being phylogenetically close.

Urban forests differ in their biomass recovery driven by variation in land-use history. From a practical point of view, this study suggests that strategies for conservation and restoration should account for past land-use and the matrix where forests are inserted, as tropical forests can have many combinations of biodiversity-biomass relationships. The success of initiatives under REDD+ relies on the recognition of situations when biodiversity and biomass accumulation can be conserved simultaneously and when not only species diversity, but also other metrics of phylogenetic diversity should be considered to promote the selection of more phylogenetically close species as a solution to enhance biomass accumulation in other specific situations.

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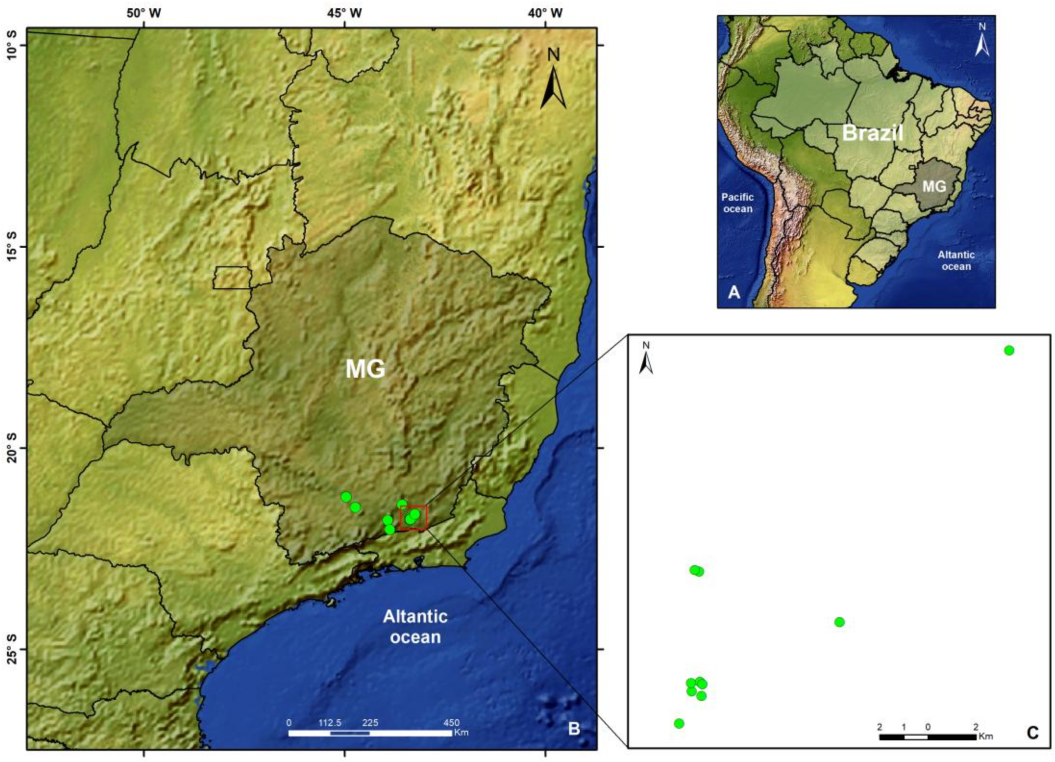


Fig 1 Geographic location of the study area in the southeast region of Minas Gerais, Brazil.Geographic location of the study area in the southeast region of Minas Gerais, Brazil. Names and information about forests are given in Table S1. A) Location of Minas Gerais in Brazil; B) Distribution of all sampled forests; C) Closer view of the sampled forests adjacent to each other. The green circles correspond to sampled forests.

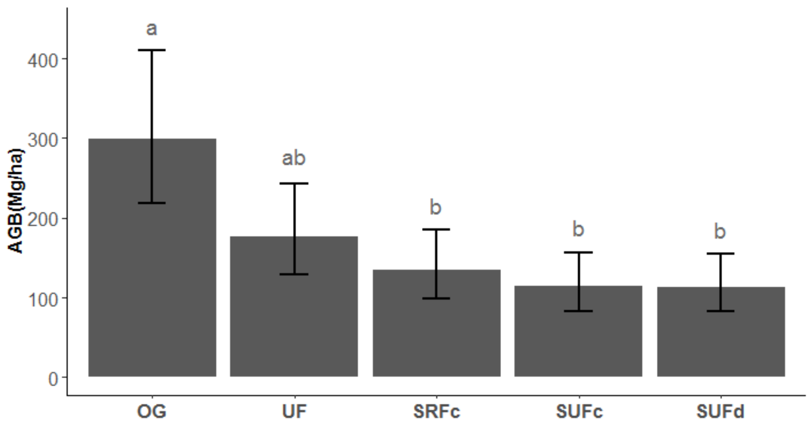


Fig 2 The effects of land-use history on aboveground biomass (AGB) for 15 forests from the Brazilian Atlantic Forest in the southeast region of Brazil. *OG* old-growth forests, *UF* urban forests, *SRFc* secondary rural cropland forests, *SUFc* secondary urban cropland forests, *SUFd* secondary urban denuded forests. Different letters indicate significant differences among mean values ($p < 0.05$) based on pairwise comparisons in mixed linear models (Tukey's HSD). Error bars represent 95% confidence intervals.

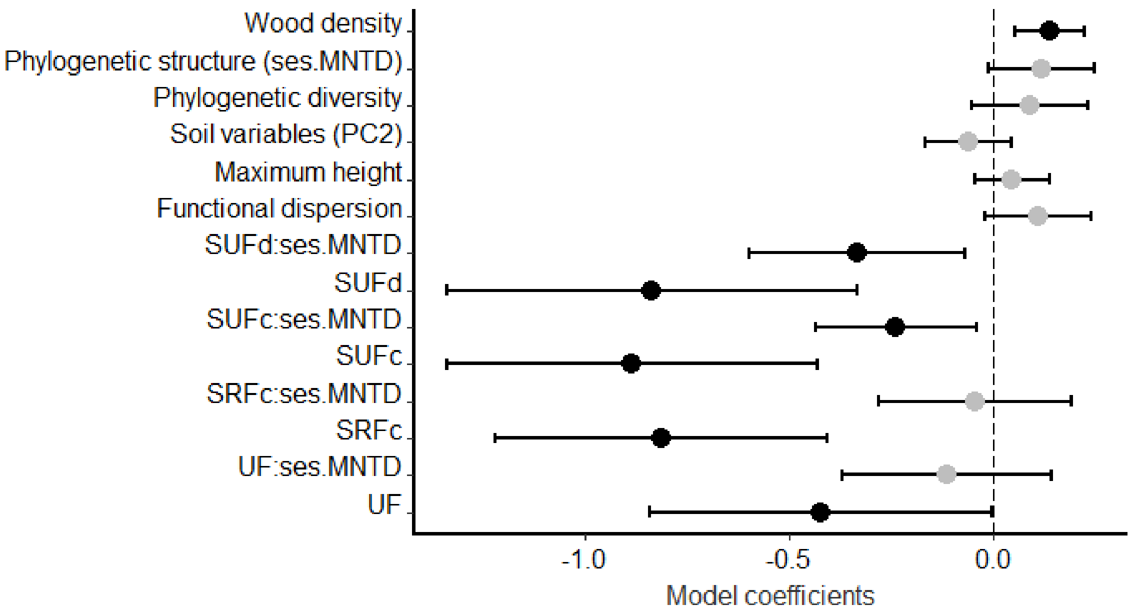


Fig 3 Variable coefficients (±standard errors) from model averaging of candidate models within ΔAICc ≤ 2 for aboveground biomass (AGB). The best models for AGB includes wood density, land-use history and the interaction between land-use and ses.MNTD. For the categorical variables (forests with different land-use history),tThe coefficients are measured in relation to the old-growth forests. *SUFd* secondary urban forests with denudation history, *SUFc* secondary urban forests with cropland history, *SRFc* secondary rural forests with cropland history, *UF* urban forests. Black circles indicate significant effects on AGB ($p < .05$). Error bars represent 95% confidence intervals.

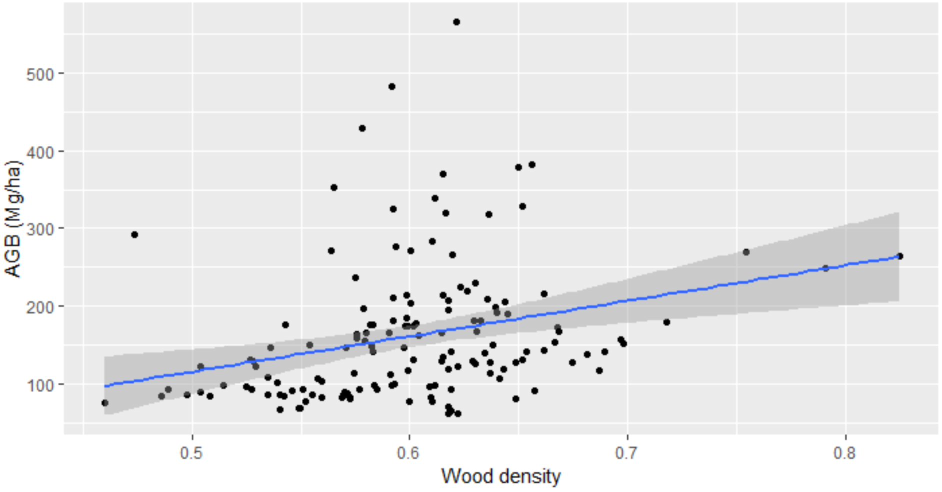


Fig 4 Relationships between aboveground biomass (AGB) and wood density within all forest categories (β =0.14; p<0.05).

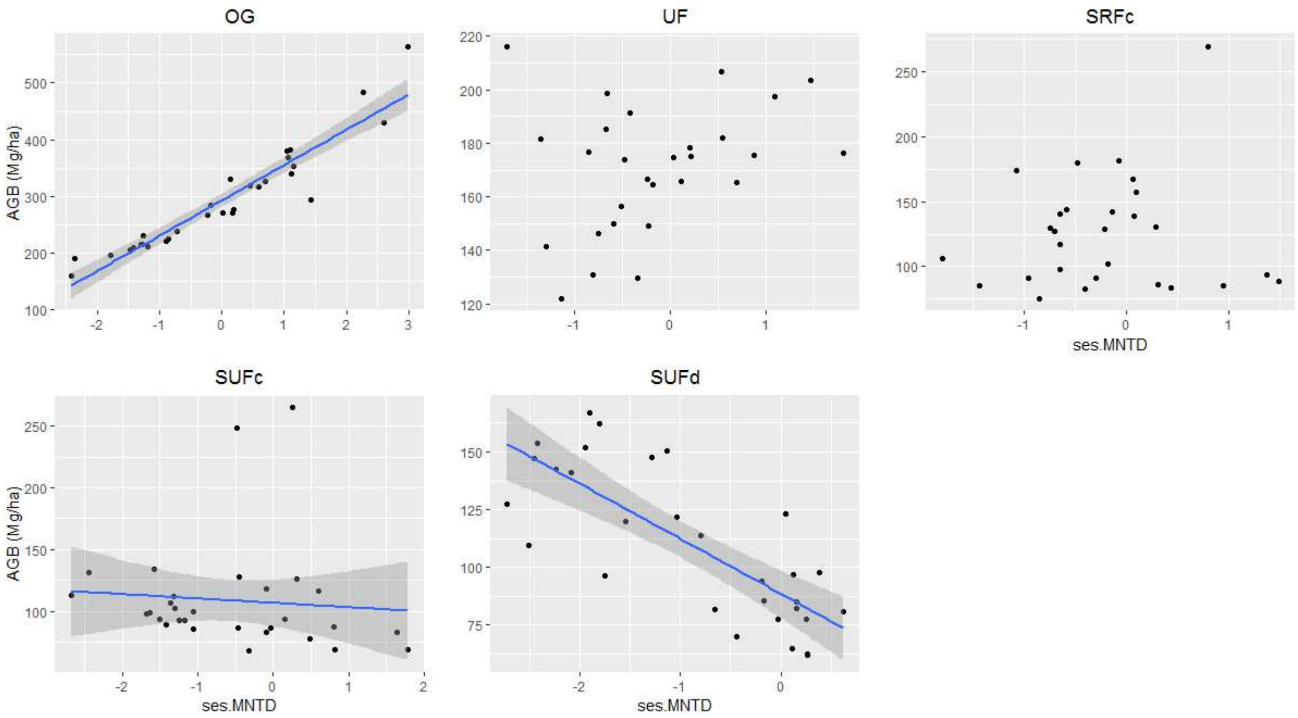


Fig 5 Relationships between aboveground biomass (AGB) and ses.MNTD among forest categories of land-use history. *OG* old-growth forests, *UF* urban forests, *SRFc* secondary rural cropland forests, *SUFc* secondary urban cropland forests, *SUFd* secondary urban denuded forests.

Supplementary material

Table S1: Characterization of the fifteen forest fragments sampled in this study. *LUH* land-use history. *OG* old-growth forests, *UF* urban forests, *SRFc* secondary rural cropland forests, *SUFc* secondary urban cropland forests, *SUFd* secondary urban denuded forests.

Forest	Category	Coordinates		Altitude (m)	Climate	Area (ha)
BN	OG	21°24'45"S	43°34'25"W	964	Cwb	32.73
FS	OG	21°48'14"S	43°55'52"W	1070	Cwb	47.19
ML	OG	22°1'58"S	43°52'37"W	1030	Cwb	18.81
LAJ	UF	21°47'29"S	43°22'33"W	840	Cwa	84.38
PDA	UF	21°45'13"S	43°18'58"W	820	Cwa	273.86
EDF	UF	21°46'46"S	43°22'17"W	870	Cwb	5.06
LUM	SRF	21°29'11"S	44°44'20"W	485	Cwb	77.00
SUB	SRF	21°13'17"S	44°57'47"W	920	Cwa	8.75
COR	SRF	21°33'9"S	43°15'10"W	940	Cwb	80.00
EM	SUFc	21°46'52"S	43°22'3"W	868	Cwa	4.34
URB	SUFc	21°44'5"S	43°22'7"W	710	Cwa	14.85
SEC	SUFc	21°44'3"S	43°22'12"W	780	Cwa	26.04
ICB	SUFd	21°46'35"S	43°22'18"W	915	Cwb	1.44
PIN	SUFd	21°46'33"S	43°22'6"W	850	Cwb	1.97
CAN	SUFd	21°46'37"S	43°22'2"W	870	Cwb	1.45

Table S2:

Principal Component Analysis (PCA) of 150 forest plots for soil variables. Values in parentheses indicate the variance (%) accounted for by each axis. Values in the table indicate the eigenvector scores of each of the variables on the two main PCA axes.

Variables	PC1 (48.79%)	PC2 (34.97%)
pH	0.882	-0.216
Soil total phosphorus (P)	-0.353	0.754
Soil total Potassium (K)	0.662	0.606
Soil total aluminum (Al)	-0.669	0.647
Interchangeable bases (IB)	0.950	0.256

Cation exchange capacity (CEC)	0.486	0.796
Saturation of bases (SB)	0.961	0.054
Soil total organic matter (OM)	-0.232	0.833

Table S3:

Overview of the 458 forest tree species sampled in fifteen tropical forests from the Brazilian Atlantic Forest located in the southeast region of Minas Gerais, Brazil: scientific name and family, wood density (WD, g.cm^{-3}), maximum height (Hmax, m) and seed size category (small seeds species < 1.5 cm) and large seeds species > 1.6 cm).

Species	**Family**	**WD**	**Hmax**	**Seed size**
Lithraea molleoides (Vell.) Engl.	Anacardiaceae	0.505	15	Large
Mangifera indica L.	Anacardiaceae	0.553	7.85	Large
Schinus terebinthifolia Raddi	Anacardiaceae	0.820	8	Small
Tapirira guianensis Aubl.	Anacardiaceae	0.437	22.4	Small
Tapirira obtusa (Benth.) J.D.Mitch.	Anacardiaceae	0.293	20.75	Small
Annona glabra L.	Annonaceae	0.590	12.4	Large
Duguetia lanceolata A.St.-Hil.	Annonaceae	0.920	15.05	Large
Annona cacans Warm.	Annonaceae	0.424	20	Small
Annona dolabripetala (Raddi) G.Don	Annonaceae	0.424	14	Small
Annona emarginata (Schltdl.) H.Rainer	Annonaceae	0.413	8	Small
Annona mucosa (Jacq.) Baill.	Annonaceae	0.387	14.6	Small
Annona sylvatica (A. St.-Hil.) Martius	Annonaceae	0.373	11.6	Small
Guatteria australis A.St.-Hil.	Annonaceae	0.543	9.85	Small
Guatteria pohliana Schltdl.	Annonaceae	1.090	12	Small
Guatteria sellowiana Schltdl.	Annonaceae	0.550	18	Small
Guatteria villosissima A.St.-Hil.	Annonaceae	0.540	13.4	Small
Oxandra martiana (Schltdl.) R.E. Fr.	Annonaceae	0.748	25.8	Small
Xylopia brasiliensis Spreng.	Annonaceae	0.528	23	Small
Xylopia sericea A.St.-Hil.	Annonaceae	0.421	17.05	Small
Aspidosperma olivaceum Müll.Arg.	Apocynaceae	0.793	9	Large

Aspidosperma parvifolium A.DC.	Apocynaceae	0.790	16.65	Large
Aspidosperma polyneuron Müll.Arg.	Apocynaceae	0.790	22.3	Large
Aspidosperma ramiflorum Müll.Arg.	Apocynaceae	0.790	10	Large
Aspidosperma spruceanum Benth. ex Müll.Arg.	Apocynaceae	0.753	15.4	Large
Himatanthus bracteatus (A.DC.) Woodson	Apocynaceae	0.367	20.35	Large
Tabernaemontana laeta Mart.	Apocynaceae	0.462	17.6	Small
Ilex cerasifolia Reissek	Aquifoliaceae	0.528	7	Small
Ilex paraguariensis A.St.-Hil.	Aquifoliaceae	0.528	21.6	Small
Ilex theezans Mart.	Aquifoliaceae	0.528	10.45	Small
Dendropanax cuneatus (DC.) Decne. & Planch.	Araliaceae	0.467	15	Small
Schefflera angustissima (Marchal) Frodin	Araliaceae	0.450	14	Small
Schefflera calva (Cham.) Frodin & Fiaschi	Araliaceae	0.450	17.5	Small
Schefflera longipetiolata (Pohl ex DC.) Frodin & Fiaschi	Araliaceae	0.450	7.95	Small
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	Araliaceae	0.620	22	Small
Schefflera vinosa (Cham. & Schltdl.) Frodin & Fiaschi	Araliaceae	0.450	8.9	Small
Araucaria angustifolia (Bertol.) Kuntze	Araucariaceae	0.550	14.9	Large
Syagrus romanzoffiana (Cham.) Glassman	Arecaceae	0.557	9.4	Large
Euterpe edulis Mart.	Arecaceae	0.407	19	Small
Geonoma schottiana Mart.	Arecaceae	0.557	3.5	Small
Austrocritonia angulicaulis (Sch.Bip. ex Baker) R.M.King & H.Rob.	Asteraceae	0.505	11.9	Small
Eremanthus erythropappus (DC.) MacLeish	Asteraceae	0.590	10	Small
Piptocarpha macropoda (DC.) Baker	Asteraceae	0.615	14	Small
Vernonanthura discolor H.Rob.	Asteraceae	0.540	6	Small
Vernonanthura divaricata (Spreng.) H.Rob.	Asteraceae	0.540	15	Small
Vernonanthura phosphorica (Vell.) H.Rob.	Asteraceae	0.540	11.75	Small
Cybistax antisyphilitica (Mart.) Mart.	Bignoniaceae	0.590	13.4	Large
Handroanthus chrysotrichus (Mart. ex DC.) Mattos	Bignoniaceae	0.615	13.5	Large
Handroanthus heptaphyllus (Vell.) Mattos	Bignoniaceae	0.898	30	Large
Handroanthus impetiginosus (Mart. ex DC.) Mattos	Bignoniaceae	0.960	8.5	Large

Handroanthus ochraceus (Cham.) Mattos	Bignoniaceae	0.892	13.2	Large
Jacaranda macrantha Cham.	Bignoniaceae	0.395	10.25	Large
Jacaranda puberula Cham.	Bignoniaceae	0.580	20.1	Large
Handroanthus serratifolius (Vahl) S.O.Grose	Bignoniaceae	0.922	25.4	Small
Jacaranda micrantha Cham.	Bignoniaceae	0.482	14	Small
Cordia aberrans I.M.Johnst.	Boraginaceae	0.485	13.4	Small
Cordia ecalyculata Vell.	Boraginaceae	0.485	8	Small
Cordia magnoliifolia Cham.	Boraginaceae	0.520	19.2	Small
Cordia sellowiana Cham.	Boraginaceae	0.485	24.8	Small
Cordia toqueve Aubl.	Boraginaceae	0.485	19.55	Small
Cordia trichotoma (Vell.) Arráb. ex Steud.	Boraginaceae	0.780	21	Small
Crepidospermum atlanticum Daly	Burseraceae	0.578	10.6	Small
Protium heptaphyllum (Aubl.) Marchand	Burseraceae	0.770	16.25	Small
Protium spruceanum (Benth.) Engl.	Burseraceae	0.560	8	Small
Kielmeyera lathrophyton Saddi	Calophyllaceae	0.670	4	Large
Trema micrantha (L.) Blume	Cannabaceae	0.267	10.8	Small
Citronella paniculata (Mart.) R.A.Howard	Cardiopteridaceae	0.470	10	Small
Jacaratia spinosa (Aubl.) A.DC.	Caricaceae	0.265	12	Small
Caryocar edule Casar.	Caryocaraceae	0.697	31	Large
Casuarina equisetifolia L.	Casuarinaceae	0.809	13.95	Small
Cheiloclinium cognatum (Miers) A.C.Sm.	Celastraceae	0.732	7	Large
Cheiloclinium serratum (Cambess.) A.C.Sm.	Celastraceae	0.732	15.85	Large
Maytenus aquifolium Mart. ex Reissek	Celastraceae	0.745	12.75	Small
Maytenus brasiliensis Mart.	Celastraceae	0.745	14.65	Small
Maytenus communis Reissek	Celastraceae	0.745	10	Small
Maytenus evonymoides Reissek	Celastraceae	0.745	13.1	Small
Maytenus floribunda Steyerm.	Celastraceae	0.745	14	Small
Maytenus gonoclada Mart.	Celastraceae	0.745	15.05	Small
Hirtella hebeclada Moric. ex DC.	Chrysobalanaceae	0.720	10.6	Large
Parinari brasiliensis (Schott) Hook.f.	Chrysobalanaceae	0.750	25	Large

Licania kunthiana Hook.f.	Chrysobalanaceae	0.689	17.2	Small
Clethra scabra Pers.	Clethraceae	0.530	14.55	Small
Garcinia gardneriana Mart.	Clusiaceae	0.870	20.3	Large
Tovomita glazioviana Engl.	Clusiaceae	0.679	12	Small
Tovomitopsis saldanhae Engl.	Clusiaceae	0.628	20.6	Small
Buchenavia tomentosa Eichler	Combretaceae	0.705	8	Large
Buchenavia hoehneana N.F.Mattos	Combretaceae	0.705	18	Small
Terminalia argentea Mart.	Combretaceae	0.810	20.8	Small
Terminalia fagifolia Mart.	Combretaceae	0.903	12.5	Small
Terminalia glabrescens Mart.	Combretaceae	0.714	20	Small
Connarus regnellii Schellenb.	Connaraceae	0.600	12	Small
Lamanonia cuneata (Cambess.) Kuntze	Cunoniaceae	0.513	8	Small
Lamanonia ternata Vell.	Cunoniaceae	0.513	19.9	Small
Diospyros inconstans Jacq.	Ebenaceae	0.692	15	Large
Sloanea guianensis (Aubl.) Benth.	Elaeocarpaceae	0.484	14.55	Small
Sloanea hirsuta (Schott) Planch. ex Benth.	Elaeocarpaceae	0.809	15.7	Small
Sloanea retusa Uittien	Elaeocarpaceae	0.930	14.6	Small
Erythroxylum citrifolium A.St.-Hil.	Erythroxylaceae	0.710	7	Small
Erythroxylum deciduum A.St.-Hil.	Erythroxylaceae	0.810	14.5	Small
Erythroxylum pelleterianum A.St.-Hil.	Erythroxylaceae	0.808	19.25	Small
Alchornea glandulosa Poepp.	Euphorbiaceae	0.378	17.3	Small
Alchornea triplinervia (Spreng.) Müll.Arg.	Euphorbiaceae	0.467	20	Small
Aparisthmium cordatum (A.Juss.) Baill.	Euphorbiaceae	0.484	12	Small
Croton celtidifolius Baill.	Euphorbiaceae	0.459	10	Small
Croton floribundus Spreng.	Euphorbiaceae	0.600	12.5	Small
Croton salutaris Casar.	Euphorbiaceae	0.408	13	Small
Croton urucurana Baill.	Euphorbiaceae	0.830	14.4	Small
Euphorbia cotinifolia L.	Euphorbiaceae	0.731	7.85	Small
Gymnanthes klotzschiana (Baill.) L.B.Sm. & Downs	Euphorbiaceae	0.552	7.768356616	Small
Hyeronima alchorneoides Allemão	Euphorbiaceae	0.648	13	Small

Hyeronima oblonga (Tul.) Müll.Arg.	Euphorbiaceae	0.603	22	Small
Mabea fistulifera Mart.	Euphorbiaceae	0.360	7	Small
Maprounea guianensis Aubl.	Euphorbiaceae	0.720	18.65	Small
Pera glabrata (Schott) Poepp. ex Baill.	Euphorbiaceae	0.670	11.2	Small
Pogonophora schomburgkiana Miers ex Benth.	Euphorbiaceae	0.833	8	Small
Sapium glandulatum (L.) Morong	Euphorbiaceae	0.421	13.7	Small
Andira anthelmia (Vell.) Benth.	Fabaceae	0.736	8.7	Large
Andira fraxinifolia Benth.	Fabaceae	0.788	18.1	Large
Dalbergia frutescens (Vell.)Britton	Fabaceae	0.690	5.85	Large
Holocalyx balansae Micheli	Fabaceae	0.859	8	Large
Lonchocarpus cultratus (Vell.) A.M.G. Azevedo & H.C. Lima	Fabaceae	0.734	8	Large
Ormosia altimontana Meireles & H.C.Lima	Fabaceae	0.621	15	Large
Platycyamus regnellii Benth.	Fabaceae	0.825	25	Large
Poincianella pluviosa (DC.) L.P.Queiroz	Fabaceae	0.833	15.55	Large
Pseudopiptadenia contorta (DC.)G.P.Lewis & M.P.Lima	Fabaceae	0.523	9.65	Large
Schizolobium parahyba (Vell.) S.F. Blake	Fabaceae	0.320	15.5	Large
Swartzia flaemingii Raddi	Fabaceae	0.834	21.55	Large
Swartzia macrostachya Benth.	Fabaceae	0.920	6	Large
Swartzia myrtifolia Sm.	Fabaceae	0.900	18.2	Large
Tachigali vulgaris L.F. Gomes da Silva & H.C. Lima	Fabaceae	0.560	29	Large
Abarema cochliacarpos (Gomes) Barneby & J.W. Grimes	Fabaceae	0.494	30	Small
Abarema langsdorffii (Benth.) Barneby & J.W. Grimes	Fabaceae	0.585	17.4	Small
Albizia polycephala (Benth.)Killip	Fabaceae	0.589	25	Small
Anadenanthera colubrina (Vell.)Brenan	Fabaceae	0.866	22.8	Small
Anadenanthera peregrina (L.)Speg.	Fabaceae	1.080	15.35	Small
Apuleia leiocarpa (Vogel) J.F.Macbr.	Fabaceae	0.610	18	Small
Bauhinia longifolia (Bong.)Steud.	Fabaceae	0.709	16.1	Small
Bauhinia pulchella Benth.	Fabaceae	0.600	6.9	Small
Bauhinia ungulata L.	Fabaceae	0.940	8.7	Small
Cassia ferruginea (Schrad.)DC.	Fabaceae	0.500	4	Small

Copaifera langsdorffii Desf.	Fabaceae	0.700	11.6	Small
Copaifera trapezifolia Hayne	Fabaceae	0.615	25	Small
Dalbergia foliolosa Benth.	Fabaceae	0.800	16.4	Small
Dalbergia nigra (Vell.)Benth.	Fabaceae	0.870	10.6	Small
Dalbergia villosa (Benth.)Benth.	Fabaceae	0.808	9.7	Small
Enterolobium contortisiliquum (Vell.)Morong	Fabaceae	0.540	21.3	Small
Hymenolobium janeirense Kuhlm.	Fabaceae	0.576	9.35	Small
Inga barbata Benth.	Fabaceae	0.576	4	Small
Inga capitata Desv.	Fabaceae	0.592	9.8	Small
Inga cylindrica (Vell.)Mart.	Fabaceae	0.480	25	Small
Inga edulis Mart.	Fabaceae	0.576	24.1	Small
Inga flagelliformis (Vell.)Mart.	Fabaceae	0.576	13.5	Small
Inga ingoides (Rich.)Willd.	Fabaceae	0.514	23	Small
Inga marginata Willd.	Fabaceae	0.547	8.85	Small
Inga sessilis (Vell.)Mart.	Fabaceae	0.430	8	Small
Inga striata Benth.	Fabaceae	0.576	11	Small
Inga subnuda Salzm.	Fabaceae	0.576	17	Small
Inga virescens Benth.	Fabaceae	0.576	20.35	Small
Leucaena leucocephala (Lam.) de Wit	Fabaceae	0.605	7.9	Small
Leucochloron incuriale (Vell.)Barneby & J.W.Grimes	Fabaceae	0.601	19.2	Small
Machaerium acutifolium Vogel	Fabaceae	1.120	14	Small
Machaerium brasiliense Vogel	Fabaceae	0.660	22.55	Small
Machaerium hirtum (E.Mey.)Standl.	Fabaceae	0.660	13.6	Small
Machaerium nyctitans (Vell. Conc.) Benth.)	Fabaceae	0.591	13	Small
Machaerium ruddianum C.V.Mendonça & A.M.G.Azevedo	Fabaceae	0.591	5	Small
Machaerium stipitatum (DC.)Vogel	Fabaceae	0.840	5	Small
Machaerium villosum Vogel	Fabaceae	0.756	24.7	Small
Melanoxylon brauna Schott	Fabaceae	0.605	17	Small
Mimosa artemisiana Heringer & Paula	Fabaceae	0.910	18	Small
Mimosa bimucronata (DC.) Kuntze	Fabaceae	0.610	8	Small

Myroxylon balsamum (L.)Harms	Fabaceae	0.760	7.32	Small
Myroxylon peruiferum L.f.	Fabaceae	0.802	30	Small
Peltophorum dubium (Spreng.) Taub.	Fabaceae	0.690	12	Small
Piptadenia gonoacantha (Mart.)J.F.Macbr.	Fabaceae	0.750	20	Small
Piptadenia paniculata Benth.	Fabaceae	0.814	11.7	Small
Platypodium elegans Vogel	Fabaceae	0.820	16.8	Small
Pseudopiptadenia leptostachya (Benth.)Rauschert	Fabaceae	0.664	22	Small
Pterocarpus rohrii Vahl	Fabaceae	0.427	13	Small
Senegalia polyphylla (DC.) Britton	Fabaceae	0.790	11	Small
Senna macranthera (Collad.)H.S.Irwin & Barneby	Fabaceae	0.561	12	Small
Senna multijuga (Rich.) H.S.Irwin & Barneby	Fabaceae	0.582	22.2	Small
Stryphnodendron polyphyllum Mart.	Fabaceae	0.619	16	Small
Tachigali paratyensis (Vell.) H.C. Lima	Fabaceae	0.559	14.85	Small
Tachigali rugosa (Mart. ex Benth.) Zarucchi & Pipoly	Fabaceae	0.599	15.75	Small
Zollernia ilicifolia (Brongn.)Vogel	Fabaceae	1.050	7	Small
Vismia brasiliensis Choisy	Hypericaceae	0.640	15.4	Small
Vismia guianensis (Aubl.) Pers.	Hypericaceae	0.475	12	Small
Vismia magnoliifolia Cham. & Schltdl.	Hypericaceae	0.475	10.3	Small
Lacistema hasslerianum Chodat	Lacistemataceae	0.513	10.2	Small
Lacistema pubescens Mart.	Lacistemataceae	0.480	14	Small
Aegiphila integrifolia (Jacq.) B.D.Jacks.	Lamiaceae	0.860	17.3	Small
Hyptidendron asperrimum (Spreng.) Harley	Lamiaceae	0.430	12	Small
Vitex polygama Cham.	Lamiaceae	0.589	16.25	Small
Vitex sellowiana Cham.	Lamiaceae	0.710	10	Small
Beilschmiedia emarginata (Meisn.) Kosterm.	Lauraceae	0.610	34.7	Large
Beilschmiedia taubertiana (Schwacke & Mez) Kosterm.	Lauraceae	0.563	11	Large
Cryptocarya aschersoniana Mez	Lauraceae	0.570	5	Large
Cryptocarya micrantha Meisn.	Lauraceae	0.563	18	Large
Endlicheria glomerata Mez	Lauraceae	0.496	7	Large
Endlicheria paniculata (Spreng.) J.F.Macbr.	Lauraceae	0.580	14	Large

Licaria bahiana Kurz	Lauraceae	0.815	13.75	Large
Persea americana Mill.	Lauraceae	1.100	12.85	Large
Aniba firmula (Nees & Mart.) Mez	Lauraceae	0.388	22.4	Small
Nectandra lanceolata Nees & Mart.	Lauraceae	0.583	11.05	Small
Nectandra megapotamica (Spreng.) Mez	Lauraceae	0.583	14.1	Small
Nectandra membranacea (Sw.) Griseb.	Lauraceae	0.583	9	Small
Nectandra nitidula Nees & Mart.	Lauraceae	0.770	18.7	Small
Nectandra oppositifolia Nees & Mart.	Lauraceae	0.432	17.1	Small
Ocotea aciphylla (Nees & Mart.) Mez	Lauraceae	0.511	20	Small
Ocotea bicolor (Meisn.) Mez	Lauraceae	0.519	10	Small
Ocotea brachybotrya (Meisn.) Mez	Lauraceae	0.525	3.5	Small
Ocotea catharinensis Mez	Lauraceae	0.750	11	Small
Ocotea corymbosa (Meisn.) Mez	Lauraceae	0.501	23.4	Small
Ocotea cujumary Mart.	Lauraceae	0.501	8	Small
Ocotea diospyrifolia (Meisn.) Mez	Lauraceae	0.519	18	Small
Ocotea glaziovii Mez	Lauraceae	0.501	16.55	Small
Ocotea indecora (Schott) Mez	Lauraceae	0.605	23.4	Small
Ocotea lanata (Nees & Mart.) Mez	Lauraceae	0.501	10.8	Small
Ocotea lancifolia (Schott) Mez	Lauraceae	0.501	14.1	Small
Ocotea laxa (Nees) Mez	Lauraceae	0.501	16.95	Small
Ocotea longifolia Kunth	Lauraceae	0.501	12.85	Small
Ocotea odorifera (Vell.) Rohwer	Lauraceae	0.563	20	Small
Ocotea puberula (Rich.) Nees	Lauraceae	0.455	14.8	Small
Ocotea pulchella (Nees & Mart.) Mez	Lauraceae	0.618	29.2	Small
Ocotea vaccinioides (Meisn.) Mez	Lauraceae	0.501	13.9	Small
Ocotea velloziana (Meisn.) Mez	Lauraceae	0.519	16.8	Small
Ocotea villosa Kosterm.	Lauraceae	0.519	8.425	Small
Persea major (Meisn.) L.E.Kopp	Lauraceae	0.466	20.5	Small
Persea willdenovii Kosterm.	Lauraceae	0.612	22.65	Small
Cariniana estrellensis (Raddi) Kuntze	Lecythidaceae	0.780	34.75	Large

Cariniana legalis (Mart.) Kuntze	Lecythidaceae	0.493	40	Large
Lafoensia glyptocarpa Koehne	Lythraceae	0.960	35	Large
Byrsonima laxiflora Griseb.	Malpighiaceae	0.656	22.4	Small
Byrsonima ligustrifolia Mart.	Malpighiaceae	0.467	23.564	Small
Pachira glabra Pasq.	Malvaceae	0.448	7	Large
Ceiba speciosa (A.St.-Hil.) Ravenna	Malvaceae	0.392	15.8	Small
Eriotheca candolleana (K.Schum.) A.Robyns	Malvaceae	0.430	15.75	Small
Guazuma ulmifolia Lam.	Malvaceae	0.509	18.4	Small
Luehea candicans Mart.	Malvaceae	0.507	18	Small
Luehea divaricata Mart.	Malvaceae	0.640	13.4	Small
Luehea grandiflora Mart.	Malvaceae	0.579	22.7	Small
Pachira endecaphylla (Vell.) Carv.-Sobr.	Malvaceae	0.448	20.6	Small
Pseudobombax longiflorum (Mart. & Zucc.) A.Robyns	Malvaceae	0.285	5	Small
Miconia argyrophylla DC.	Melastomataceae	0.637	20.9	Small
Miconia budlejoides Triana	Melastomataceae	0.613	8.6	Small
Miconia chartacea Triana	Melastomataceae	0.618	13	Small
Miconia cinnamomifolia (DC.) Naudin	Melastomataceae	0.730	20	Small
Miconia inconspicua Miq.	Melastomataceae	0.613	9.5	Small
Miconia latecrenata (DC.) Naudin	Melastomataceae	0.623	15.15	Small
Miconia mellina DC.	Melastomataceae	0.624	7.75	Small
Miconia pusilliflora (DC.) Naudin	Melastomataceae	0.613	8	Small
Miconia pyrifolia Naudin	Melastomataceae	0.613	16.55	Small
Miconia sellowiana Naudin	Melastomataceae	0.613	5	Small
Miconia trianae Cogn.	Melastomataceae	0.624	16.65	Small
Miconia tristis Spring	Melastomataceae	0.613	9	Small
Miconia urophylla DC.	Melastomataceae	0.623	14	Small
Miconia valtheri Naudin	Melastomataceae	0.613	6	Small
Mouriri glazioviana Cogn.	Melastomataceae	0.836	24	Small
Mouriri guianensis Aubl.	Melastomataceae	1.100	10.85	Small
Pleroma stenocarpum Schrank et Mart. ex DC	Melastomataceae	0.686	12.9	Small

Tibouchina estrellensis (Raddi) Cogn.	Melastomataceae	0.595	12	Small
Tibouchina fissinervia Cogn.	Melastomataceae	0.627	20	Small
Tibouchina fothergillae (DC.) Cogn.	Melastomataceae	0.627	8	Small
Tibouchina mutabilis (Vell.) Cogn.	Melastomataceae	0.660	12	Small
Cedrela fissilis Vell.	Meliaceae	0.550	19.3	Large
Cedrela odorata L.	Meliaceae	0.660	19.4	Large
Cabralea canjerana (Vell.) Mart.	Meliaceae	0.690	18	Small
Guarea kunthiana A.Juss.	Meliaceae	0.820	8	Small
Guarea macrophylla Vahl	Meliaceae	0.645	8.3	Small
Trichilia casaretti C. DC.	Meliaceae	0.780	24.9	Small
Trichilia catigua A.Juss.	Meliaceae	0.688	13.55	Small
Trichilia elegans A.Juss.	Meliaceae	0.651	12.55	Small
Trichilia emarginata L.	Meliaceae	0.565	12	Small
Trichilia hirta L.	Meliaceae	0.600	15	Small
Trichilia lepidota Mart.	Meliaceae	0.635	23.65	Small
Macropeplus schwackeanus (Perkins) I.Santos & Peixoto	Monimiaceae	0.665	13.65	Small
Mollinedia argyrogyna Perkins	Monimiaceae	0.630	14.9	Small
Mollinedia blumenaviana Perkins	Monimiaceae	0.665	6	Small
Mollinedia schottiana (Spreng.) Perkins	Monimiaceae	0.630	9.85	Small
Mollinedia triflora Ruiz & Pav.	Monimiaceae	0.665	4	Small
Mollinedia widgrenii A. DC.	Monimiaceae	0.630	10.45	Small
Naucleopsis oblongifolia (Kuhlm.) Carauta	Moraceae	0.504	26.5	Large
Brosimum guianense (Aubl.) Huber ex Ducke	Moraceae	0.504	18	Small
Ficus citrifolia Mill.	Moraceae	0.618	13	Small
Ficus elastica Roxb. ex Hornem.	Moraceae	0.618	4	Small
Ficus mexiae (Miq.) Miq.	Moraceae	0.600	7	Small
Helicostylis tomentosa (Poepp. & Endl.) J.F.Macbr.	Moraceae	0.378	26	Small
Maclura tinctoria (L.) D.Don ex Steud.	Moraceae	0.791	27.6	Small
Sorocea bonplandii (Baill.) W.C.Burger, Lanj. & de Boer	Moraceae	0.491	9	Small
Sorocea guilleminiana Gaudich.	Moraceae	0.578	12	Small

Virola bicuhyba (Schott) Warb.	Myristicaceae	0.323	25	Large
Eugenia handroana D.Legrand	Myrtaceae	0.726	11	Large
Eugenia handroi (Mattos) Mattos	Myrtaceae	0.726	15.25	Large
Syzygium cumini (L.) Skeels	Myrtaceae	0.673	4	Large
Syzygium jambos (L.) Alston	Myrtaceae	0.700	14	Large
Blepharocalyx salicifolius (Kunth) O.Berg	Myrtaceae	0.736	22.3	Small
Calyptranthes clusiifolia O.Berg	Myrtaceae	0.720	7.95	Small
Calyptranthes widgreniana O.Berg	Myrtaceae	0.820	12.6	Small
Campomanesia guaviroba (DC.) Kiaersk.	Myrtaceae	0.760	19.75	Small
Campomanesia guazumifolia (Cambess.) O.Berg	Myrtaceae	0.730	9.85	Small
Campomanesia laurifolia Gardner	Myrtaceae	0.760	10.85	Small
Campomanesia pubescens (Mart. ex DC.) O.Berg	Myrtaceae	0.730	12	Small
Eugenia acutata (Miq.) Toledo	Myrtaceae	0.760	18.8	Small
Eugenia brasiliensis Lam.	Myrtaceae	0.761	8.9	Small
Eugenia candolleana DC.	Myrtaceae	0.910	15.5	Small
Eugenia capparidifolia DC.	Myrtaceae	0.726	16.25	Small
Eugenia cerasiflora Miq.	Myrtaceae	0.650	16.6	Small
Eugenia dodonaeifolia Cambess.	Myrtaceae	0.761	8	Small
Eugenia florida DC.	Myrtaceae	0.648	17	Small
Eugenia hiemalis Cambess.	Myrtaceae	0.726	19.85	Small
Eugenia involucrata DC.	Myrtaceae	0.726	15.4	Small
Eugenia longipedunculata (O.Berg) D.Legrand	Myrtaceae	0.726	11	Small
Eugenia moonioides O.Berg	Myrtaceae	0.726	9	Small
Eugenia moraviana O.Berg	Myrtaceae	0.726	8.925	Small
Eugenia pisiformis Cambess.	Myrtaceae	0.726	13.2	Small
Eugenia sonderiana O.Berg	Myrtaceae	0.612	10.4	Small
Eugenia sphenophylla Cambess.	Myrtaceae	0.726	7	Small
Eugenia subundulata Kiaersk.	Myrtaceae	0.722	13.75	Small
Eugenia umbellata DC.	Myrtaceae	0.726	16	Small
Eugenia vattimoana D.Legrand	Myrtaceae	0.726	8.9	Small

Eugenia widgrenii Sond. ex O.Berg	Myrtaceae	0.726	7	Small
Marlierea eugenioides (Cambess.) D.Legrand	Myrtaceae	0.936	8	Small
Marlierea excoriata Mart.	Myrtaceae	0.936	10	Small
Marlierea laevigata (DC.) Kiaersk.	Myrtaceae	0.936	25	Small
Marlierea obscura O.Berg	Myrtaceae	0.936	19	Small
Myrceugenia campestris (DC.) D.Legrand & Kausel	Myrtaceae	0.603	12.8	Small
Myrceugenia miersiana (Gardner) D.Legrand & Kausel	Myrtaceae	0.650	11.4	Small
Myrcia amazonica DC.	Myrtaceae	0.801	8	Small
Myrcia anceps (Spreng.) O.Berg	Myrtaceae	0.538	16.65	Small
Myrcia crocea (Vell.) Hook.f.	Myrtaceae	0.801	6	Small
Myrcia hebepetala DC.	Myrtaceae	0.801	5.85	Small
Myrcia multiflora (Lam.) DC.	Myrtaceae	0.801	13	Small
Myrcia pubipetala Miq.	Myrtaceae	0.801	16.7	Small
Myrcia pulchra (O.Berg) Kiaersk.	Myrtaceae	0.757	21	Small
Myrcia splendens (Sw.) DC.	Myrtaceae	0.580	16	Small
Myrcia tomentosa (Aubl.) DC.	Myrtaceae	0.749	13.2	Small
Myrcia vellozoi Mazine	Myrtaceae	0.799	15.7	Small
Myrciaria floribunda (H.West ex Willd.) O.Berg	Myrtaceae	0.890	12	Small
Pimenta pseudocaryophyllus (Gomes) Landrum	Myrtaceae	1.000	11.9	Small
Siphoneugena densiflora O.Berg	Myrtaceae	0.838	16.8	Small
Guapira graciliflora (Mart. ex J.A.Schmidt) Lundell	Nyctaginaceae	0.492	12.4	Small
Guapira hirsuta (Choisy) Lundell	Nyctaginaceae	0.492	11.35	Small
Guapira opposita (Vell.) Reitz	Nyctaginaceae	0.830	12	Small
Ouratea parviflora Engl.	Ochnaceae	0.774	4.875	Small
Ouratea semiserrata (Mart. & Nees) Engl.	Ochnaceae	0.774	9.625	Small
Ouratea spectabilis (Mart. ex Engl.) Engl.	Ochnaceae	0.640	6	Small
Quiina glaziovii Engl.	Ochnaceae	0.841	16.5	Small
Heisteria silvianii Schwacke	Olacaceae	0.700	20.7	Small
Chionanthus filiformis (Vell.) P.S.Green	Oleaceae	0.855	9.85	Large
Ternstroemia brasiliensis Cambess.	Pentaphylacaceae	0.470	13	Small

Seguieria langsdorffii Moq.	Phytolaccaceae	0.590	18	Small
Picramnia glazioviana Engl.	Picramniaceae	0.395	11	Small
Picramnia ramiflora Planch.	Picramniaceae	0.395	14.7	Small
Pinus elliottii Engelm.	Pinaceae	0.482	16	Large
Piper cernuum Vell.	Piperaceae	0.330	4.95	Small
Podocarpus sellowii Klotzsch ex Endl.	Podocarpaceae	0.474	13	Small
Coccoloba alnifolia Casar.	Polygonaceae	0.830	20	Small
Coccoloba declinata (Vell.) Mart.	Polygonaceae	0.568	5	Small
Coccoloba warmingii Meisn.	Polygonaceae	0.568	13.4	Small
Myrsine coriacea (Sw.) R.Br. ex Roem. & Schult.	Primulaceae	0.647	11.1	Small
Myrsine gardneriana A. DC.	Primulaceae	0.563	9	Small
Myrsine lancifolia Mart.	Primulaceae	0.563	10.7	Small
Myrsine umbellata Mart.	Primulaceae	0.860	18.2	Small
Myrsine venosa A. DC.	Primulaceae	0.563	9	Small
Roupala montana Aubl.	Proteaceae	0.730	15	Large
Colubrina glandulosa G.Perkins	Rhamnaceae	0.827	26.4	Small
Eriobotrya japonica (Thunb.) Lindl.	Rosaceae	0.880	5.5	Large
Prunus myrtifolia (L.) Urb.	Rosaceae	0.741	15.2	Small
Amaioua guianensis Aubl.	Rubiaceae	0.625	8.6	Small
Amaioua intermedia Mart. ex Schult. & Schult.f.	Rubiaceae	0.536	13.55	Small
Bathysa australis (A.St.-Hil.) K.Schum.	Rubiaceae	0.414	15	Small
Bathysa cuspidata (A.St.-Hil.) Kainul. & B.Bremer	Rubiaceae	0.640	13.5	Small
Bathysa mendoncae K.Schum.	Rubiaceae	0.637	11.2	Small
Bathysa nicholsonii K.Schum.	Rubiaceae	0.637	17.55	Small
Chomelia brasiliana A.Rich.	Rubiaceae	0.570	3	Small
Chomelia sericea Müll.Arg.	Rubiaceae	0.570	9.5	Small
Cordiera concolor (Cham.) Kuntze	Rubiaceae	0.575	16.4	Small
Cordiera elliptica (Cham.) Kuntze	Rubiaceae	0.637	6.5	Small
Coussarea nodosa (Benth.) Müll.Arg.	Rubiaceae	0.610	8	Small
Coutarea hexandra (Jacq.) K.Schum.	Rubiaceae	0.600	16	Small

Faramea hyacinthina Mart.	Rubiaceae	0.637	17.75	Small
Faramea latifolia (Cham. & Schltdl.) DC.	Rubiaceae	0.523	9.4	Small
Faramea multiflora A.Rich.	Rubiaceae	1.137	5.875	Small
Faramea nigrescens Mart.	Rubiaceae	0.637	5.95	Small
Guettarda uruguensis Cham. & Schltdl.	Rubiaceae	0.796	8.4	Small
Guettarda viburnoides Cham. & Schltdl.	Rubiaceae	0.730	15.7	Small
Ixora brevifolia Benth.	Rubiaceae	0.880	8.7	Small
Margaritopsis chaenotricha (DC.) C.M.Taylor	Rubiaceae	0.520	4	Small
Posoqueria latifolia (Rudge) Schult.	Rubiaceae	0.582	13	Small
Psychotria carthagenensis Jacq.	Rubiaceae	0.700	11.8	Small
Psychotria cephalantha (Müll.Arg.) C.M.Taylor	Rubiaceae	0.520	7.8	Small
Psychotria deflexa DC.	Rubiaceae	0.527	8.2	Small
Psychotria nuda (Cham. & Schltdl.) Wawra	Rubiaceae	0.520	18.35	Small
Psychotria suterella Müll.Arg.	Rubiaceae	0.520	8	Small
Psychotria vellosiana Benth.	Rubiaceae	0.520	12.6	Small
Zanthoxylum monogynum A. St.-Hil.	Rutaceae	0.900	14.4	Large
Dictyoloma vandellianum A.Juss.	Rutaceae	0.639	15.3	Small
Esenbeckia febrifuga (A.St.-Hil.) A.Juss. ex Mart.	Rutaceae	0.850	11.2	Small
Galipea jasminiflora (A.St.-Hil.) Engl.	Rutaceae	0.850	13.6	Small
Hortia brasiliana Vand. ex DC.	Rutaceae	0.483	10.95	Small
Metrodorea stipularis Mart.	Rutaceae	0.769	22.9	Small
Zanthoxylum caribaeum Lam.	Rutaceae	0.707	22	Small
Zanthoxylum rhoifolium Lam.	Rutaceae	0.493	14	Small
Meliosma itatiaiae Urb.	Sabiaceae	1.180	19.3	Large
Casearia arborea (Rich.) Urb.	Salicaceae	0.574	17.4	Small
Casearia decandra Jacq.	Salicaceae	0.664	18.5	Small
Casearia lasiophylla Eichler	Salicaceae	0.664	12	Small
Casearia obliqua Spreng.	Salicaceae	0.678	8	Small
Casearia selloana Eichler	Salicaceae	0.664	12.4	Small
Casearia sylvestris Sw.	Salicaceae	0.505	15.4	Small

Casearia ulmifolia Vahl ex Vent.	Salicaceae	0.574	15.7	Small
Xylosma ciliatifolia (Clos) Eichler	Salicaceae	0.820	8	Small
Xylosma prockia (Turcz.) Turcz.	Salicaceae	0.701	14.5	Small
Cupania ludowigii Somner & Ferrucci	Sapindaceae	0.619	19.3	Large
Allophylus edulis (A.St.-Hil., A.Juss. & Cambess.) Radlk.	Sapindaceae	0.651	16.65	Small
Allophylus petiolulatus (Turcz.) Radlk.	Sapindaceae	0.700	16	Small
Allophylus racemosus Sw.	Sapindaceae	0.435	16.9	Small
Cupania emarginata Cambess.	Sapindaceae	0.650	13.8	Small
Cupania oblongifolia Mart.	Sapindaceae	0.670	12	Small
Cupania racemosa (Vell.) Radlk.	Sapindaceae	0.622	18.4	Small
Cupania vernalis Cambess.	Sapindaceae	0.650	18.4	Small
Cupania zanthoxyloides Cambess.	Sapindaceae	0.628	16	Small
Diatenopteryx sorbifolia Radlk.	Sapindaceae	0.682	30	Small
Matayba elaeagnoides Radlk.	Sapindaceae	0.771	11.95	Small
Matayba guianensis Aubl.	Sapindaceae	0.840	7	Small
Matayba marginata Radlk.	Sapindaceae	0.602	13.6	Small
Pouteria caimito (Ruiz & Pav.) Radlk.	Sapotaceae	0.950	15.75	Large
Pouteria guianensis Aubl.	Sapotaceae	0.930	15	Large
Pouteria torta (Mart.) Radlk.	Sapotaceae	0.701	31.5	Large
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	Sapotaceae	0.702	24.7	Small
Chrysophyllum marginatum (Hook. & Arn.) Radlk.	Sapotaceae	0.692	17.8	Small
Ecclinusa ramiflora Mart.	Sapotaceae	0.455	20	Small
Siparuna guianensis Aubl.	Siparunaceae	0.444	9.3	Small
Solanum argenteum Dunal	Solanaceae	0.280	20.1	Small
Solanum cernuum Vell.	Solanaceae	0.280	8.8	Small
Solanum leucodendron Sendtn.	Solanaceae	0.240	15.85	Small
Solanum pseudoquina A. St.-Hil.	Solanaceae	0.809	16.1	Small
Solanum sellowianum Dunal	Solanaceae	0.280	16	Small
Styrax ferrugineus Nees & Mart.	Styracaceae	0.523	14.5	Small
Styrax latifolius Pohl	Styracaceae	0.517	22.8	Small

Symplocos pubescens Klotzsch ex Benth.	Symplocaceae	0.490	16	Small
Laplacea fruticosa (Schrad.) H.Keng	Theaceae	0.660	22.5	Small
Daphnopsis brasiliensis Mart. & Zucc.	Thymelaeaceae	0.520	5	Small
Daphnopsis fasciculata (Meisn.) Nevling	Thymelaeaceae	0.470	9	Small
Cecropia hololeuca Miq.	Urticaceae	0.430	23.6	Large
Cecropia glaziovii Snethl.	Urticaceae	0.410	17.7	Small
Cecropia pachystachya Trécul	Urticaceae	0.410	16.1	Small
Coussapoa microcarpa (Schott) Rizzini	Urticaceae	0.590	27.6	Small
Pourouma guianensis Aubl.	Urticaceae	0.320	15	Small
Urera baccifera (L.) Gaudich. ex Wedd.	Urticaceae	0.180	3	Small
Citharexylum myrianthum Cham.	Verbenaceae	0.643	11.4	Small
Vochysia bifalcata Warm.	Vochysiaceae	0.750	30	Large
Vochysia laurifolia Warm.	Vochysiaceae	0.510	14.75	Large
Vochysia magnifica Warm.	Vochysiaceae	0.780	24	Large
Vochysia rectiflora Warm.	Vochysiaceae	0.457	31.5	Large
Vochysia tucanorum Mart.	Vochysiaceae	0.457	19.6	Large
Qualea cordata Spreng.	Vochysiaceae	0.579	19	Small
Qualea gestasiana A.St.-Hil.	Vochysiaceae	0.633	25.1	Small
Qualea lundii (Warm.) Warm.	Vochysiaceae	0.633	15.95	Small

Table S4. Tukey test from generalized linear models testing effects of land-use history on above-ground biomass sampled in 15 forests from the Brazilian Atlantic Forest located in the southeast region of Brazil. *OG* old-growth, *UF* urban forests, *SRFc* secondary rural forests with cropland history, *SUFc* secondary urban forests with cropland history, *SUFd* secondary urban forests with denudation history . *significantly different at p > 0 05.

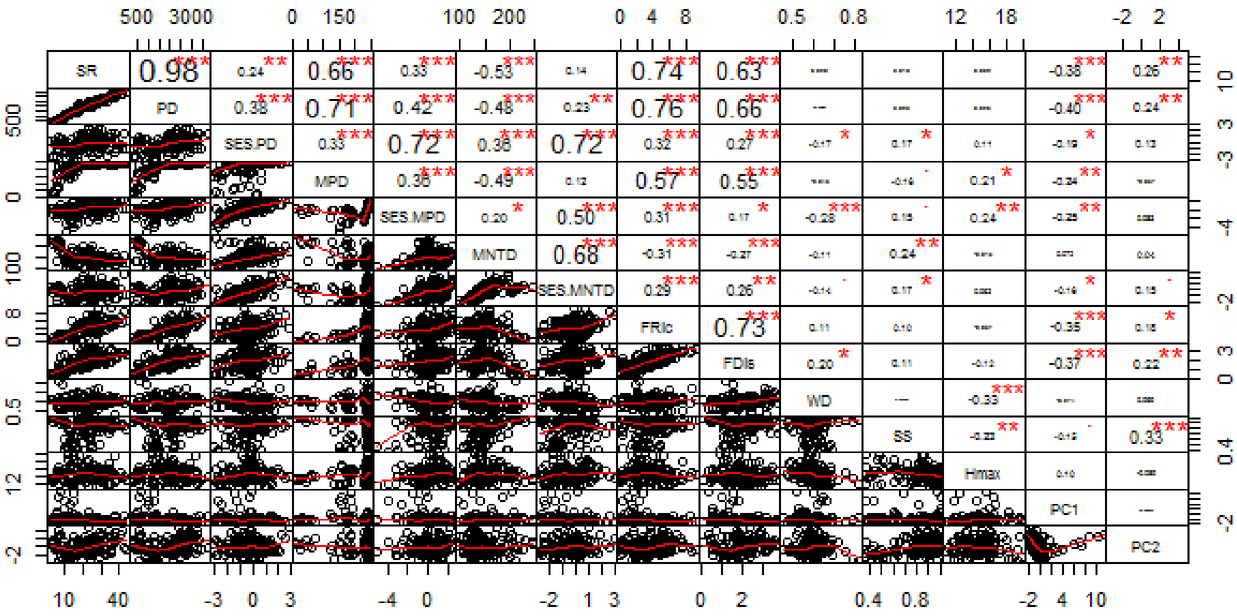
	z-value	*p-value*
UF-OG	-2.07	0.22
SRFc-OG	-3.33	<0.05*

SUFc-OG	-3.99	<0.05*
SUFd-OG	-4.06	<0.05*
SRFc-UF	-1.25	0.72
SUFc-UF	-1.91	0.3
SUFd-UF	-1.98	0.27
SUFc-SRFc	-0.66	0.96
SUFd-SRFc	-0.72	0.95
SUFd-SRFc	-0.06	1

Table S5. Set of models generated by multimodel selection procedure within ΔAICc ≤ 2 for aboveground biomass (AGB), followed by degrees of freedom (df), model log-likelihood (logLik), AICc, ΔAICc and model weight. *LUH* land use history, *FDis* functional dispersion, *Hmax* Community weighted mean of maximum height, *PC1* first axis from a PCA of soil variables, *PC2* second axis from a PCA of soil variables, *PD* phylogenetic diversity, *ses.MNTD* standardized effect size of mean nearest taxon distance, *SS* Community weighted mean of seed size, *WD* Community weighted mean of wood density.

Intercept	LUH	FDis	Hmax	PC1	PC2	PD	ses.MNTD	SS	WD	LUH:ses.MNTD	df	logLik	AICc	ΔAICc	weight
5.51	+	0.11	NA	NA	NA	NA	0.09	NA	0.12	NA	10	-815.16	1651.94	0.00	0.11
5.56	+	NA	NA	NA	NA	NA	0.22	NA	0.15	+	13	-811.92	1652.58	0.64	0.08
5.60	+	NA	NA	NA	NA	NA	0.10	NA	0.14	NA	9	-816.63	1652.58	0.64	0.08
5.52	+	NA	NA	NA	NA	0.09	0.10	NA	0.14	NA	10	-815.85	1653.31	1.37	0.06
5.64	+	NA	NA	NA	-0.06	NA	0.10	NA	0.14	NA	10	-816.02	1653.65	1.71	0.05
5.62	+	NA	0.05	NA	NA	NA	0.10	NA	0.15	NA	10	-816.12	1653.85	1.92	0.04

Figure S1. Pearson's correlation coefficients between the all potential predictor variables



FINAL DISCUSSION AND CONCLUSIONS

While most studies focus on old-growth forests, human-disturbed secondary forests represent an increasing provider of ecosystem services that might not follow the same ecological patterns as “intact” old-growth forests (CHAZDON et al., 2003). Although natural regeneration of the tree community has been considered an effective low-cost solution in the Neotropics, forest recovery after land-use may last decades or even centuries, and several altered successional trajectories have been shown for secondary tropical forests (SANTOS et al., 2008; ROCHA-SANTOS et al., 2016; EWERS et al., 2017).

This thesis has given important contributions to the ecology of urban forests, mostly due to the integration of the land-use history on the analyses. Despite the large number of studies on urban biodiversity, the lack of land-use history and its role on biodiversity of urban forests might be the reason why the conservation contribution of these forests have yet not been fully understood (RAMALHO & HOBBS, 2012; SCWARTZ et al., 2014). Tropical biomes have faced extreme habitat loss, mostly due to anthropogenic disturbance events such as land-use change. In recent years the rates of forest degradation, deforestation and fragmentation area larger than ever observed in human history before (PELLENS and GRANDCOLAS, 2016; MITCHARD, 2018; MAXWELL et al., 2019). As a consequence, more than half of the tropical forests are now secondary (FAO, 2010; KEENAN et al., 2015). Most tropical urban forests were regenerated from agricultural or other man-made landscapes, meaning that successional processes must be considered while evaluating urban ecosystems (KOWARIK & LIPPE, 2018). The sequence and duration of successional stages may vary substantially among tropical forests, depending upon the nature of the disturbance event (CHAZDON, 2008; MESQUITA et al., 2015; NORDEN et al., 2015). Secondary forests face strong environmental filters that cause the colonization of close lineages due to the conservatism of traits, and we showed here that this is also true for urban forests.

We found that species richness, rarefied species richness and phylogenetic diversity are all affected by the land-use history of urban forests and that urban forests without previous land use can house substantial amounts of angiosperm evolutionary diversity, which highlights the importance of preserving natural forest fragments as cities expand. Indeed, forests that regenerated from cropland, and particularly those regenerated from denuded landscapes, showed strong phylogenetic clustering, which was also related to their high perimeter-area ratio. During succession, pioneer species are expected to be replaced by shade-tolerant ones, with the community gradually accumulating species diversity and ecological functions (Richards, 1996; Guariguata and Ostertag, 2001). Strong environmental filters, such as conditions present in abandoned agricultural sites and in early successional phases, seem to have lead to colonization by close relatives, likely due to the conservatism of traits that are optimal in disturbed forest fragments (BAETEN et al. 2015). These new environmental conditions filters cause the selection of species that share the adaptation strategies required to colonize and survive in a changed post disturbance habitat (VAN DER SANDE et al. 2016). which can also alter vegetation structure (e.g., reduced stem density, greater canopy openness) and microclimatic conditions (e.g., increased light intensity and habitat desiccation), imposing additional environmental filters (METHA et al. 2008).

Our study has also given important contributions regarding the effects of urbanization and land-use history on aboveground biomass (AGB), especially about the main drivers of biomass storage in these habitats. Understanding the drivers of AGB variation in present-day tropical forests can contribute to management strategies that help mitigate against CO_2-driven climate change and provide other services related to high AGB. Higher tree diversity can lead to higher woody productivity and carbon storage (TILMAN, 1999), but how diversity interacts with land-use history is less certain.

We found that tree diversity, measured as the average evolutionary divergence among close relatives, shows a strong positive relationship to AGB, but only in old-growth, non-urban forests. This suggests that higher niche complementarity leads to higher AGB in certain ecological contexts. Although urban forests can still contribute to the overall carbon storage and sequestration, anthropogenic land-use changes along with stand age have been shown to set tropical tree communities back to an earlier successional stage causing a reduction in standing biomass (CHAZDON & GUARIGUATA, 2016; WANDELLI & FEARNSIDE, 2015; VELASCO & WEE, 2019; ZHANG et al., 2020). In urban forests with a history of cropland and denudation activities, aboveground biomass increases with the presence of phylogenetically close species in the community, meaning that biomass storage is determined by few species that are adapted to effectively capture resources (species with high wood density), and not by diversity. Meanwhile, across all forest classes, the abundance-weighted mean wood density of tree species present showed a consistent positive correlation with AGB, indicating the ubiquity of mass-ratio effects on AGB. Previous studies have reported that fragmentation have no significant effect on biomass, with the productivity of the shade-intolerant trees having a high role in the accumulation of biomass (MAGNAGO et al., 2014; LIU et al., 2019). Therefore, we believe that the lower AGB found in our study is related to their land-use history.

From a practical point of view, this study suggests that strategies for conservation and restoration should account for past land-use and the matrix where forests are inserted, as the distribution of carbon stocks and biodiversity may need to be considered separately. In these communities with history of disturbance event, the effects of land use change before forest regeneration are still persistent and resulted in a small subset of successful lineages composed by close relatives that tolerate the stressful environmental conditions (KNAPP et al., 2008; SANTOS et al., 2010; ARROYO-RODRÍGUEZ et al., 2012; BRUNBJERG et al., 2012; MUNGUÍA-ROSAS et al., 2014; ANDRADE et al., 2015; ČEPLOVÁ et al., 2015; PRESCOTT et al., 2016). Therefore, the increase in diversity doesn't imply an increase in AGB in regenerating forests (FAUSET et al., 2015; FINEGAN, 2015; LOHBECK et al., 2016; FOTIS et al., 2018), not as much as the presence of some dominant hardwooded species (FAUSET et al., 2015).

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