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The interaction of land-use history and tree species diversity in driving variation in the aboveground biomass of urban versus non-urban tropical forests

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ABSTRACT

Understanding the drivers of aboveground biomass (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, but how diversity interacts with land-use history is less certain. We assessed variation in AGB across forests with different land-use histories and surrounding landscapes in southeastern Brazil and how AGB relates to tree diversity *per se*, while controlling for important factors such as mean functional trait values, stem density and soil fertility. Our findings indicate that aboveground biomass of forests is dependent on land-use history and the landscape matrix in which they occur (urban or non-urban). 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. Forests in an urban matrix, and those that regenerated from cropland (in an urban or non-urban matrix), showed weak or insignificant relationships between AGB and diversity, and forests that regenerated from completely denuded landscapes, including soil removal, actually showed a negative relationship between diversity and AGB. 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. Overall, our 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.

1. Introduction

Tropical biomes have historically faced extreme habitat loss, in part due to policies for economic development. As a result, recent years have seen larger rates of forest degradation, deforestation and fragmentation than ever before observed in human history (Pellens and Grandcolas, 2016; Maxwell et al., 2019; Mitchard, 2018). One of the main consequences of this scenario is not only the loss of biodiversity, but also adverse impacts on various ecosystem services, e.g. anthropogenic

disturbances are one of the main causes of biomass loss (Gardner et al., 2010). Annual losses from deforestation and forest degradation have been reported to be greater than the growth gains by forest regeneration (Baccini et al., 2017). However, the rate at which these forests can recover and provide equivalent levels of carbon uptake is still not well constrained in models (Brose et al., 2016; Chazdon et al., 2016; Elias et al., 2020; Rozendaal et al., 2019), and further research is needed to understand the factors driving variation in carbon uptake of secondary forests, such as land-use history and habitat context (Chazdon, 2014).

Besides disturbance history, abovegound biomass is affected by a large number of biotic (tree diversity, species functional traits and structural features) and abiotic (edaphic and climatic) drivers. Biotic factors relate mostly to species diversity (e.g., via niche complementarity) and identity (e.g., mass-ratio effects via functional traits). 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 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, which may better capture directly the diversification in species traits in a community (functional diversity) or indirectly, by accounting for evolutionary history, which is the basis for trait diversification (phylogenetic diversity) (Pellens and Grandcolas, 2016). The mass-ratio hypothesis proposes that trait values of the most abundant species determine ecosystem processes in the community (Grime, 1998; Loreau and Hector, 2001). In this sense, biomass accumulation is determined by the presence of highly productive species and not by their variety (Cardinale et al., 2007). Variation in wood density has been considered the most important species-variable in controlling patterns of biomass in tropical forests, being also a key functional trait in reflecting a trade-off between resource acquisition and conservation during forest successional change (Coelho de Souza et al., 2019; Finegan et al., 2015; Prado-junior et al., 2016; Pyles et al., 2018; Fauset et al., 2015; Sullivan et al., 2017; Poorter et al., 2019). Abiotic factors also influence tree biomass, with climate acting as an overriding force, with water availability being the key factor in the tropics (Poorter et al., 2016). Soil nutrients and management history are also important abiotic factors affecting tree biomass (Ali et al., 2017; Poorter et al., 2016; Lohbeck et al., 2015b; Van Der Sande et al., 2017). The soil fertility hypothesis states that soil conditions, and associated resource availability, are a key determinant of plant growth, and therefore a more fertile soil results in higher aboveground biomass (Baker et al., 2009; Quesada et al., 2012). Lastly, the apparent nature of the biomass response to abiotic gradients also depends on the scale analyzed (Chisholm et al., 2013).

Microclimatic changes promoted by contrasting landscapes (e.g. urban vs. rural) and land-use history impact sensitive species and favor disturbance tolerant species, which may also lead to a depletion of carbon stocks (Álvarez-Yépiz et al., 2008; Poorter et al., 2016). In order to determine 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 influence. Despite the increasing number of studies of aboveground biomass in tropical forests, no study to date has focused on drivers of biomass in urban forests with different land-use histories.

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 as cities grow (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 represent a significant threat to natural ecosystems across the world (Seto et al., 2012). Forests regenerating in urban matrices 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 overall carbon storage and sequestration (Davies et al., 2011; Nowak and Crane, 2002; Pansit, 2019), anthropogenic land-use changes can set tropical tree communities back to an earlier successional stage causing a reduction in standing biomass (Álvarez-Yépiz et al., 2008; Chazdon and Guariguata,

2016; Letcher and Chazdon, 2009; Velasco and Chen, 2019; Wandelli and Fearnside, 2015; Zhang et al., 2020).

While functional diversity provides information about how species respond to their environment (Garnier et al., 2016; Violle and Jiang, 2009), when functional trait data are lacking, phylogenetic diversity can be a useful surrogate for trait diversity, based on the assumption that evolutionary diversification is related to trait diversification. If so, evolutionary relationships among species can produce comparable estimates of niche space (Tucker et al., 2018). Recent studies have found positive relationships between evolutionary diversity metrics and biomass or wood productivity (Ali and Yan, 2018; Coelho de Souza et al., 2019; Yuan et al., 2016), meaning that forest communities with more distantly related taxa have higher levels of ecosystem function (Coelho de Souza et al., 2019). However, it remains unclear whether diversity-biomass relationships become stronger in the course of succession (Cardinale et al., 2007; Lennox et al., 2018; Yuan et al., 2016) or weaker (Lasky et al., 2014; Satdichanh et al., 2018), and how they are affected by disturbance (Osuri et al., 2020).

The main focus of this study was to determine the aboveground biomass (AGB) of forest with different land-use histories and in different landscape matrices, and to investigate how the interaction of AGB and tree species diversity is affected by anthropogenic drivers (by urbanization itself, and land-use history), while controlling for important factors such as mean functional trait values (mass-ratio factors), stem density (structure) and soil fertility (abiotic). We addressed the following main questions: 1) Can urban forests maintain the same AGB as non-urban forests? 2) How does land-use history interact with the landscape matrix (urban vs. non-urban) in determining AGB of forests? 3) Does the effect of tree diversity on AGB vary across forests with different land-use histories and in different landscape matrices? We predict a loss of AGB along a gradient of land-use history intensity, and that the drivers of biomass storage will change across forests that vary in their regeneration history. In a previous study (Borges et al., 2020), we found that diversity was affected by the interactions between land-use history and landscape matrix (urban vs. rural), hence we expect an influence of these factors on AGB as well. We also expect that niche complementarity will play a stronger role in determining AGB in forests without land-use history, where forest stands have had time to achieve an equilibrium among resource competitors. In secondary forests, competition may be less intense as trees are still filling the available niche space, and we expect not to find relationships between measures of niche complementarity and aboveground biomass. In secondary forests, we predict mass-ratio effects related to species composition will be the most important driver of variation in AGB.

2. Materials and methods

2.1. Study area

The study was conducted in 150 plots belonging to fifteen tropical forest fragments located in Minas Gerais, in the southeast 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 m 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 21.8 °C (Alvares et al., 2014; Brasil, 1992; Oliveira-Filho et al., 1994). The soils in the region are primarily latosols (Dos Santos et al., 2013). All forest fragments were classified based on their land-use history and whether or not they are located in the urban versus rural matrix (Table S1). Some plots classified as rural forests were obtained from ForestPlots.net (Lopez-Gonzalez et al., 2009, 2011).
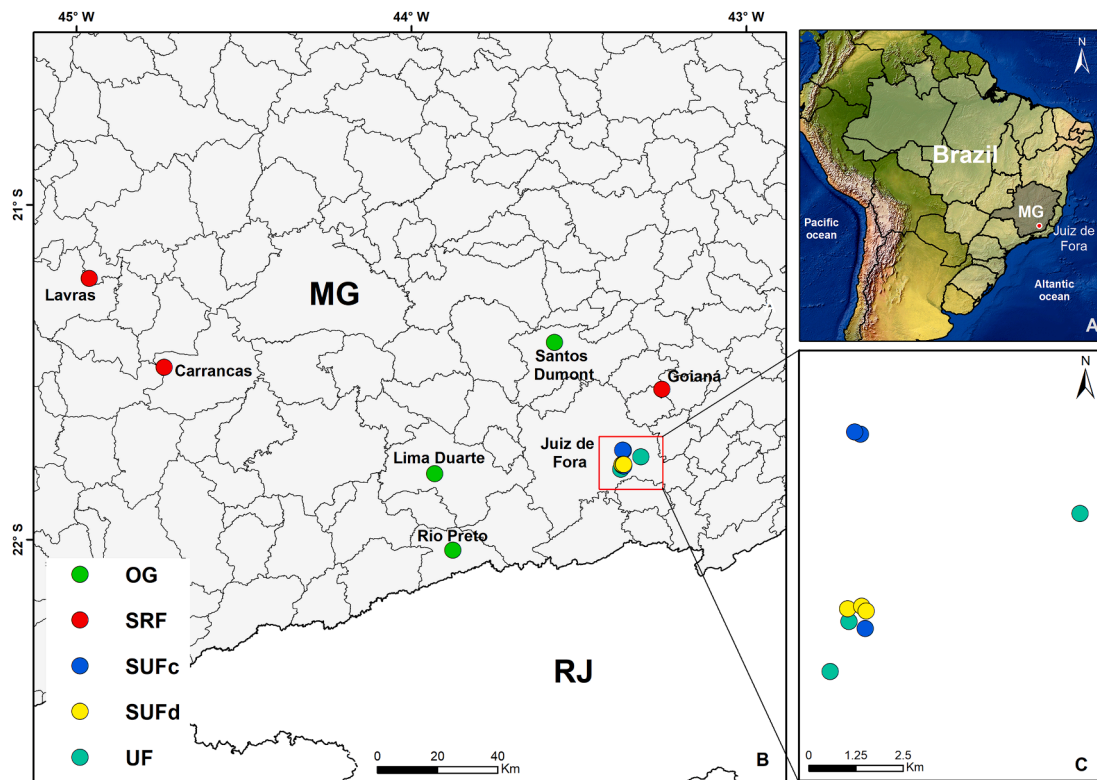
Fig. 1. Geographic location of the study area in the southeast region of Minas Gerais, Brazil. Names and information about forests are given in Table S1. A) Location of Minas Gerais in Brazil; B) Distribution of all sampled forests; C) Closer view of the sampled forests adjacent to each other. The green circles correspond to sampled forests. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2. Forest inventory and land-use history classification

In each study fragment, woody vegetation was surveyed in ten randomly established and non-contiguous plots of 20 m × 20 m, which thus total 0.4 ha per forest fragment. We considered all trees with a diameter at breast height (DBH) ≥ 5 cm, and all trees were 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 fifteen forests fragments were categorized into five categories with different historical land-uses, 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, except for some registers of selective logging over 100 years ago; 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 (see also Borges et al., 2020; Pyles et al., 2020).

To the degree possible, all sampled sites within each region were located in areas with similar climate and topography to avoid the potential confounding effect of these factors.

2.3. Phylogenetic analysis

An ultrametric calibrated phylogeny for tree species occurring in the plots 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). 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 yet their abundance is generally too low to have strong effects on plot-level biomass (Honorio Coronado et al., 2015; Kembel and Hubbell, 2006; Rezende et al., 2017). The resulting community phylogeny 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 mean lineage divergence in a phylogenetic tree: mean pairwise distance (MPD), which is the mean phylogenetic distance between all pairs of individuals (including conspecifics) in a community, and mean nearest taxon distance (MNTD), which is the average distance between an individual and the most closely related (non-conspecific) individual (Webb, 2000; Webb et al., 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, the null expectation was generated by 10,000 null model randomizations. 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. The analyses were calculated using the 'picante' package in R (Kembel, 2010).

2.4. Functional traits

Species maximum height and wood density were considered in the study due to their relevance to species standing biomass (Lohbeck et al., 2015a; Poorter et al., 2015). Species maximum height (Hmax, m) is an indicator of the adult stature of 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 in the entire dataset for a given species. Species wood density (WD, g.cm^{-3}) is positively related with plant carbon storage as it represents biomass per wood volume constructed (Pérez-Harguindeguy et al., 2013). Wood density is also related to trunk resistance to physical damages and hydraulic safety (Sterck et al., 2006; Van Gelder et al., 2006). Information on species WD was obtained from the Global Wood Density database (filtered by Tropical South America, Zanne et al., 2009). For the species without available wood density estimates, we used mean values for the genus or family. We then calculated the mean wood density value across all stems in a plot.

2.5. Soil properties

In each plot, soil samples reaching 20 cm depth were randomly collected using a hoe after the organic layer had been removed, and 500 g of several combined samples were then bagged for transportation. Immediately after arriving in the laboratory, the soil samples were air-dried. After removal of colinear variables to avoid model mis-specification, and selection of the most important environmental variables based on their ecological relevance, we kept the following variables for downstream analyses: 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 × 1.724), interchangeable bases (IB), cation exchange capacity (CEC) and saturation of bases (SB). To simplify characterization of the soil characteristics of the studied forests, a principal component analysis (PCA) was run using basic functions in R. Principal component analysis (PCA) is a widely used multivariate analytical statistical technique that can be applied to reduce the set of dependent variables to a smaller set of underlying variables (principal components, PCs), explaining the greatest variance within the original data (Abdi & Williams, 2010). The first two axes explained together a total of 83.76% of the data set variation (Table S2).

2.6. Aboveground biomass

For every tree with DBH ≥ 5 cm, the aboveground biomass (AGB) of each individual tree was calculated using the allometric formula of Chave et al., 2014: AGB $= 0.0673 \times$ (WD DBH^2 H)$^{0.976}$ with measures of DBH (cm), height (H, m), and species wood density (WD, g cm^{-3}). We summed this across all trees in a plot to obtain measures of AGB per unit area for each plot.

2.7. Data and statistical analysis

To determine the AGB of forests with different land-use histories we ran analyses of variance (One way - ANOVA followed by the Tukey's post hoc test) between all five forest categories (old-growth, urban forests, secondary non-urban forests regenerated from cropland land-use, secondary urban forests regenerated from cropland land-use, secondary urban forests regenerated from denuded landscapes). We also used ANOVA to test for differences among forest types in stem density and the

first two main axes of the PCA (soil properties).

For each plot we quantified the following taxonomic and phylogenetic diversity metrics (to test the niche complementarity hypothesis): Species richness (SR), 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).

To investigate how the interaction of AGB and tree species diversity (SR, PD, MPD, MNTD, ses.PD, ses.MPD and ses.MNTD) is affected by anthropogenic drivers (by urbanization itself, and land-use history), we ran linear mixed models including fragment identity as a random effect (to account for the lack of independence of plots within a given fragment, or site). In addition, the following covariates were included in the models to account for their influence on AGB: Stem density (stems/ha; representing forest structure), the community-weighted mean trait values (CWM; representing functional composition weighted by species abundance) of species maximum height (m) and wood density (g.cm^{-3}) (representing mass-ratio effects), calculated per plot and the first two axes of a principal component analysis (PC1 and PC2).

The functional analyses were calculated using the 'FD' package in R (Laliberté et al., 2015).

For a second analysis, forests were categorized according to their landscape matrix (urban versus rural) and their land-use history (secondary versus primary), in order to better separate the drivers affecting AGB (being urban or being secondary). For this analysis, we excluded the secondary urban forests regenerated from denuded landscapes due to their unique and more intense disturbance history, and the fact that we don't have samples with that same land-use history in a rural matrix. We ran linear mixed models to predict AGB, with two categorical factors and their interaction, to check for the interaction of land-use history (categorical variable: secondary versus primary forests) and landscape matrix (urban versus non-urban forests), while also including interactions with tree species diversity (SR, PD, MPD, MNTD, ses.PD, ses.MPD and ses.MNTD), and the CWM of WD as fixed effects. Subsequently, we ran all possible subsets of the full model after analyzing the variation inflation factor (VIF) and tested for correlations between individual predictor variables using Pearson correlation coefficients (Fig. 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). 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 et al., 2016), MuMIn (Barton, 2016), and ggplot2 (Wickham and Chang, 2016).

3. 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. On average, old-growth forest plots (mean ± se., 299 Mg/ha ± 48) showed over 50% greater 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), which in turn were not significantly different from any other forest category. No difference was found in soil properties among forest categories while stem density was significantly lower between forest plots with denuded land-use history and all the other forest categories (Table S5).

The AGB was best predicted by land-use history (categorical variable), ses.MNTD (in interaction with land-use history), and wood density. This model explained 58% of the variation in AGB (Table S6). Wood density had a positive effect on AGB regardless of forest land-use history
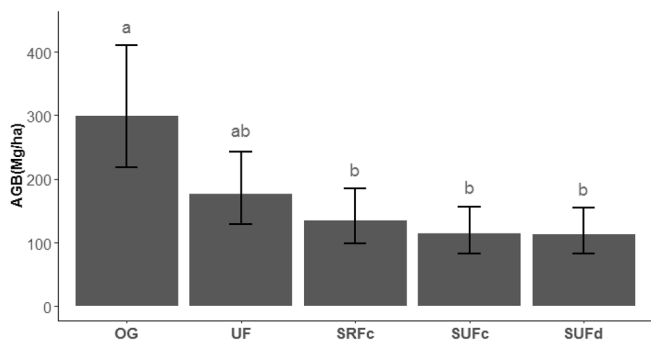
Fig. 2. The effects of land-use history on aboveground biomass (AGB) for 15 forests from the Brazilian Atlantic Forest in the southeast region of Brazil. *OG* old-growth forests, *UF* urban forests, *SRFc* secondary rural cropland forests, *SUFc* secondary urban cropland forests, *SUFd* secondary urban 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). 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 relationship between land-use history and ses.MNTD (Fig. 4) was negative for urban forests with denudation land-use history, while it was flat for forests with cropland land-use history (rural or urban) and for urban forests without land-use history. The relationship between ses. MNTD and AGB was only strongly 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. On the contrary, in urban forests with a history of denudation activities, AGB increases with the presence of phylogenetically close species in the community (Fig. 4).

We did not find a significant interaction of land-use history (forests being secondary or primary) and landscape matrix (forests being urban or non-urban) on AGB (Fig. 5, Table S7). Land-use history and matrix both had a significant effect on AGB, indicating a reduction of AGB in secondary forests compared to primary forests and a reduction of AGB in urban forests compared to non-urban forests (Fig. 6, Table S9). There was no significant interaction between diversity (ses.MNTD) and land-use history and landscape matrix (urban vs. rural, Fig. 5). However it is noticeable that the correlation of ses.MNTD and AGB is strongly positive in primary non-urban forests (as found for old-growth forests in

Fig. 3. Relationships between aboveground biomass (AGB) and the CWM of wood density over all 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.

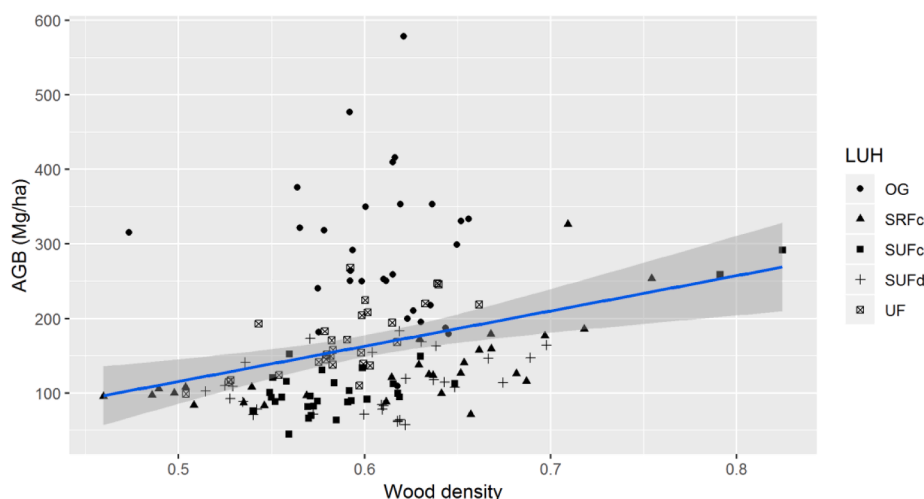**Fig. 4.** Relationships between aboveground biomass (AGB) and ses.MNTD among forest categories of land-use history. *OG* old-growth forests, *UF* urban forests, *SRFc* secondary rural cropland forests, *SUFc* secondary urban cropland forests, *SUFd* secondary urban denuded forests.
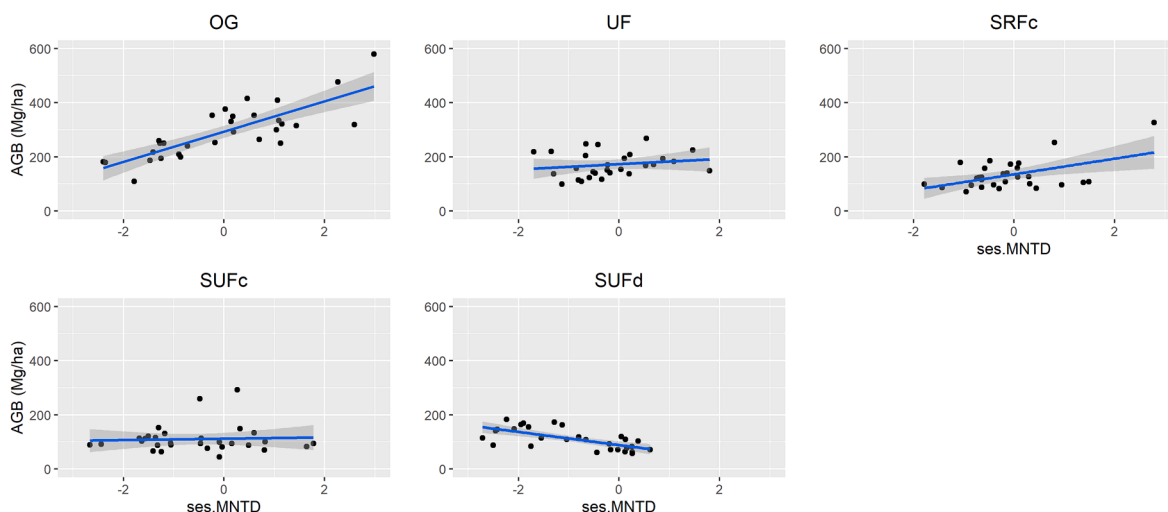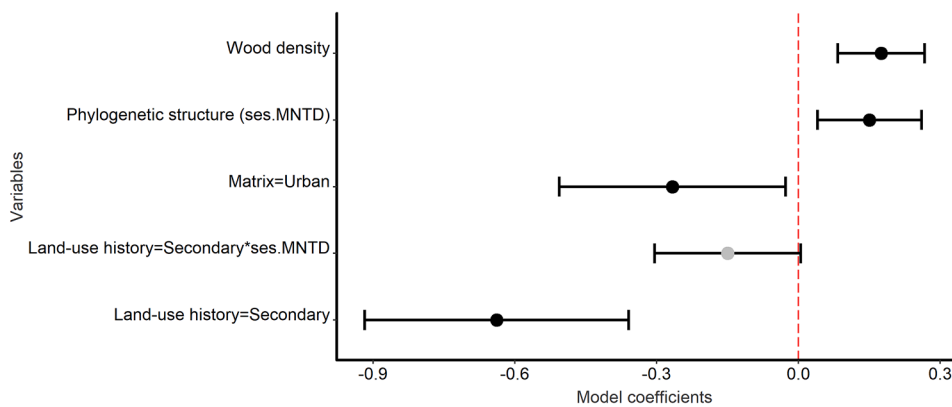
Fig. 5. Variable coefficients (±standard errors) from model averaging of candidate models within $\Delta AICc \leq 2$ for aboveground biomass (AGB). The best models for AGB include wood density, land-use history, matrix, and the interaction between land-use and ses.MNTD. For the categorical variables (Land-use history and matrix), the base model is rural (for matrix) and primary (for land-use history), thus the graph represents the difference between urban vs. rural (base model for matrix) and secondary vs. primary (base model for land-use history). Black circles indicate significant effects on AGB ($p < 0.05$). Interactions are indicated with *. Error bars represent 95% confidence intervals.
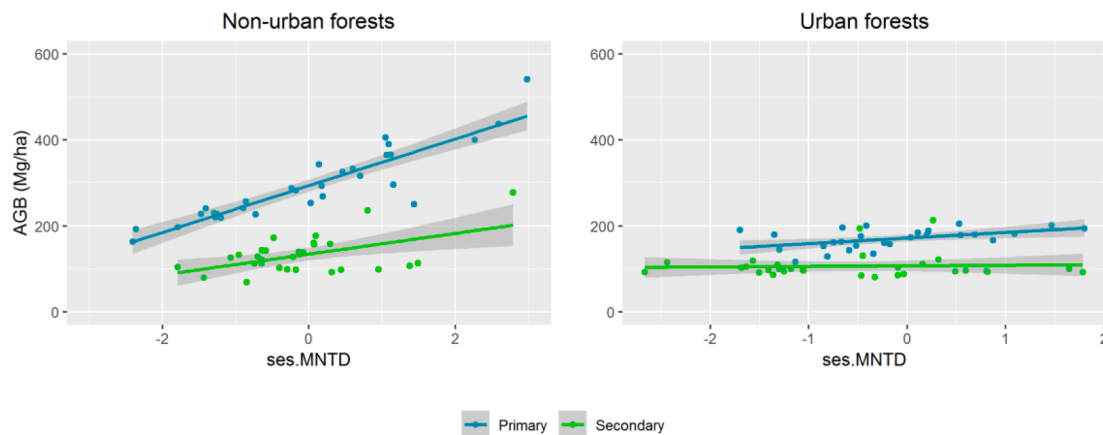

Fig. 6. Relationships between aboveground biomass (AGB) and ses.MNTD among primary and secondary forests in an urban and non-urban matrix.

comparison with the other forest categories), and then it continually reduces in more impacted forests until reaching a flat slope for the secondary urban forests (Fig. 6, Table S8).

4. Discussion

The main focus of this study was to determine the drivers of aboveground biomass (AGB) of forest with different land-use histories. Our findings support our prediction that AGB would show a reduction across forest categories according to their intensity of land-use history, suggesting that the AGB of tropical forests are highly dependent on their past land-use and whether they are set in an urban or rural matrix. Furthermore, by addressing how the interaction of AGB and tree species diversity is affected by anthropogenic drivers (by urbanization itself, and land-use history), we found that only the AGB of old-growth forests showed a positive relationship with tree species diversity, as quantified by the average divergence of close relatives (i.e., ses.MNTD), suggesting that niche complementarity operates to increase AGB solely in "intact" fragments of natural forest. This result of our study, from the Atlantic Forest of eastern South America, has also recently been reported from the Amazon Basin (Coelho de Souza et al., 2019), suggesting at least some level of generality for Neotropical moist forests. In incorporating other important factors that have been shown to affect biomass, we also found that AGB storage is mainly affected by wood density, in agreement with several previous studies (Finegan et al., 2015; Prado-Junior et al., 2016; Pyles et al., 2018; Yuan et al., 2018).

Forest recovery after land-use may take decades or even centuries, and although the mechanisms underlying forest regeneration remain poorly understood, the intensity of the initial disturbance event is considered one of the main factors driving the trajectory of species and

biomass recovery (Chazdon, 2008; Ferreira et al., 2018; Jakovac et al., 2015; Martínez-Ramos et al., 2016). Interestingly, we found that not only land-use history, but also the matrix in which a forest is found had a significant effect on AGB. A reduction of AGB was found in urban forests compared to non-urban forests, in accordance with findings in China e. g., where the carbon density and sequestration rate of urban trees was about one third to half of that of non-urban forests (Tang et al., 2016). However, the urban forests studied here do have some registers of selective logging over 100 years ago, hence there is also the possibility that these forests are still going through a slow process of biomass recovery.

Biomass has been shown to take up to 66 years to achieve 90% of pre-disturbance levels in Neotropical secondary forests (Poorter et al., 2016). The forests that are regenerating on former croplands in this study (70 to 80 years of regeneration) hold<50% of the AGB of old-growth forests. Forests regenerated on denuded landscapes where soil was removed (60 years of regeneration) reached similar biomass as the regenerated urban cropland forests. However, our study 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 more continuously forested landscape. Besides, other studies showed a less optimistic scenario than Poorter et al. (2016). 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 result more similar to our own. A more recent study found that carbon recovery in the Amazon in secondary forests takes 150 years after abandonment to regain carbon levels similar to adjacent primary forests (Elias et al., 2020).

The interaction of biomass and diversity has been found to increase through time, as in more stable ecosystems complementarity among

species is expected to be higher (Cardinale et al., 2007; Elias et al., 2020; Yuan et al., 2016). 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 that can allow coexistence and increased resource uptake (Yuan et al., 2016).

The relation between AGB and ses.MNTD is flat or even negative for the forest categories with an anthropogenic land-use history. In these communities, the effects of human land-use before forest regeneration are persistent, including lingering dominance by a small subset of successful lineages that tolerate the stressful environmental conditions, resulting in a reduction in ecological functions (Andrade et al., 2015; Arroyo-Rodríguez et al., 2012; Brunbjerg et al., 2012; Čeplová et al., 2015; Knapp et al., 2008; Munguía-Rosas et al., 2014; Prescott et al., 2016; Santos et al., 2010; Pyles et al., 2018). Communities regenerating from agricultural activities and other land-use changes are susceptible to stronger environmental filters compared to primary forests (Norden et al., 2012; Gonzalez-Caro et al., 2014), resulting in a community composed by closely related species. Besides additional dispersal limitations are intensified when forests are situated in areas with less remaining forest cover (Martínez-Ramos et al., 2016), 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 et al., 2015). A previous study in the same secondary urban forests analysed here demonstrated that these forests show phylogenetic clustering, which suggests that abiotic filters are driving community assembly processes that favour the colonization of more closely related species particularly within the Asteraceae and Melastomataceae families (Borges et al., 2020). Therefore, biomass productivity is determined by the few species that are adapted to effectively capture resources, in spite of all the habitat limitations imposed by the stressful environmental change (Cardinale et al., 2007).

Higher wood density contributed significantly to biomass accumulation for all forest categories, as predicted by the mass-ratio hypothesis and in line with previous studies in tropical forests (Finegan et al., 2015; Phillips et al., 2019; 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 (Baker et al., 2009; Grime, 1998). Regarding secondary forests, the effects of species dominance are stronger (Lohbeck et al., 2016; Pyles et al., 2020). The presence of phylogenetically close species with putatively high ecological similarity may be an efficient resource use strategy for biomass accumulation under resource-limited environments Wood density might also be considered as an additional criterion for forest restoration practices when dealing with harsh environmental conditions and desiccation stresses due to their trunk resistance to physical damages and hydraulic safety properties (Poorter et al., 2019; Sterck et al., 2006; Van Gelder et al., 2006). Indeed, Pyles et al. (2020) found higher values of mean wood density for urban forests, including the ones with denudation land-use history.

We found that the phylogenetic structure (ses.MNTD) showed a variable effect on AGB depending on the land-use history of forests, indicating that the diversity-productivity relationship changes throughout a gradient of past land-use intensity, and with the landscape matrix (urban vs. rural). The use of phylogenetic diversity metrics to understand community assembly assumes 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 and 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, and not necessarily 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 studies which have found that evolutionary diversity can predict plant biomass accumulation (Ali and Yan, 2018; Cadotte, 2013; Cadotte et al., 2008; Coelho de Souza et al., 2019; Paquette et al., 2015; Potter and Woodall, 2014; Satdichanh et al., 2018; Yuan et al., 2016). As we hypothesized for landscapes with mixed land-use history (i.e., not just old-growth forest), AGB depends strongly on the nature of land-use history and is less influenced by other factors such as soil properties, suggesting that abiotic factors related to disturbance events might be stronger effectors of biomass accumulation (Satdichanh et al., 2018).

We acknowledge that this study might have methodological limitations with regards to the allometric equation used to calculate the AGB, which was not build specifically for urban forests. Competition in urban forests could be less intense if the trees are more sparse within the plots (lower stem density), influencing the interaction between AGB and diversity. Although we show that there are only significant differences in stem density for forests with denudation land-use history, we are mindful that stem density does not necessarily relate to the competitive environment present when the trees were growing, which could have affected their allometry. Future studies should explore this issue after the development of a specific allometric equation for such open canopy environments, which is beyond the scope of the present article. Nevertheless, our results show clear trends that can be discussed in the light of the interactions between diversity and biomass, and how these interactions can be context dependent.

5. Conclusions

The main finding of this study is that the effect of diversity on aboveground biomass is greatly dependent on forests' land-use history and whether or not a forest sits in an urban or rural landscape matrix. In old-growth forests, aboveground biomass is greater where tree species are more phylogenetically diverged from each other. For forests regenerating on landscapes that were completely denuded, including soils, the opposite holds, and aboveground biomass is greater when species are more closely related to each other. In other forest classes, there does not seem to be a relationship between aboveground biomass and phylogenetic divergence. This study provides further recognition of the role of evolutionary diversity in predicting biomass, indicating further the need for the inclusion of phylogenetic diversity assessments in restoration interventions and forest management practices. Our results also show that the mean wood density of communities is a signification driver of variation in aboveground biomass storage (c.f. Phillips et al., 2019), whether forests are primary or secondary, urban or non-urban.

Urban forests differ from rural forests in their pattern of biomass recovery, while also being affected 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 landscape matrix where forests are inserted, as tropical forests can have many types of biodiversity-biomass relationships. The success of initiatives under REDD + in advancing biodiversity conservation relies on the recognition of situations when biodiversity and biomass accumulation can be conserved simultaneously (Sullivan et al., 2017), which we show to be the case for old-growth forests, but not for increasingly prevalent secondary forests in the Neotropics. Forest conservation policies should account the fact that tropical forests can have different diversity-biomass relationship at a stand-level; therefore, choosing forests to protect based on their carbon storage values may not always lead to maximizing the preservation of tree diversity (Sullivan et al., 2017).

CRediT authorship contribution statement

Erica R. Borges: Conceptualization, Methodology, Software, Data curation, Formal analysis, Writing - original draft, Visualization, Investigation. **Kyle G. Dexter:** Conceptualization, Methodology, Supervision, Writing - review & editing, Validation. **Marcela V. Pyles:**

Conceptualization, Methodology, Software, Visualization, Investigation. **Marcelo L. Bueno:** Supervision, Writing - review & editing, Validation. **Rubens M. Santos:** Funding acquisition, Data curation. **Marco Aurelio L. Fontes:** Funding acquisition, Data curation. **Fabrício A. Carvalho:** Supervision, Validation, Data curation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107915.

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