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Functional composition enhances aboveground carbon stock during tropical late-secondary forest succession

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ABSTRACT

The 'mass ratio' hypothesis states that ecosystem functioning is driven by the functional traits of the most dominant species in communities. Thus, we aimed to evaluate (i) How topographical conditions and stand age determine changes in tree community composition, richness, abundance and carbon dominant (CD) species, and (ii) Assess whether community-weighted mean of functional trait values of CD species explain aboveground carbon (AGC) stock. We used community-weighted mean of wood density and maximum stem diameter to evaluate the effect of functional dominance in AGC stock. We found that different topographic conditions and stand age change community composition, richness, abundance and CD species along the late-secondary stage. Our results showed that functional trait values of CD species determine AGC stock. Thus, the proportion of CD species was shaped by topography and stand age, whereas carbon stock by the dominant species' functional traits (wood density and diameter). This study advances our understanding of the mechanisms that drive carbon stock in tropical forests and supports the 'mass ratio' hypothesis. We emphasize the relevance of the trait-based approach to understand forest functioning and trait functional composition and taxonomic identity for carbon storage, recovery and increase in secondary Atlantic Forests.

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Functional composition; carbon dominant species; community-weighted mean; topography heterogeneity; stand age; mass ratio hypothesis

1. Introduction

Dominant tree species in tropical forests have a fundamental role in maintaining ecosystem functions (i.e. carbon stock), and their relative importance can change along environmental gradients and secondary succession after disturbance (Fauset et al. 2015; Ali et al. 2019; Poulsen et al. 2020; Villa, Martins, et al. 2020). Dominance has been a widely observed phenomenon where few dominant species explain variation in ecosystem function (Grime 1998). These dominant tree species can determine carbon stock based on the mean values (i.e. functional composition) and variability (i.e. functional diversity) of their functional traits, such as wood density and maximum stem diameter (Grime 1998; Laliberté and Legendre 2010; Ali et al. 2019; Villa, Martins, et al. 2020). Functional composition and diversity are two complementary components representing the functional property of communities (Grime 1998, Laliberté and Legendre 2010). Aboveground carbon (AGC) stock can be affected by environmental factors, stand age, functional trait composition, and taxonomic identity based on relative abundance and dominance of few species, the carbon dominant (CD) species, that disproportionately store a large amount of carbon (Garnier et al. 2004; Fauset et al. 2015; Ali et al. 2020). Thus, understanding the relationships between functional traits, environmental variability, and AGC stock is important for global climate change mitigation (Lohbeck et al. 2015; Ali et al. 2016; Poorter et al. 2019; Villa, Ali, et al. 2020). However, research results on trait-based approaches to evaluate the role of dominant tree species in AGC stock in the second-growth tropical forest that re-growing after disturbance remain unclear.

Based on the 'mass ratio' hypothesis (Grime 1998), dominance pattern is strongly related to functional community-level trait values of the most dominant species (Violle et al. 2007; Ali et al. 2020). This hypothesis states that dominant species in a plant community (those abundant or present some functional traits that account for most of the biomass) contribute most to ecosystem function due to their hard functional traits (Grime 1998). For example, maximum diameter and wood density are traits that explain ecosystem functions, such as AGC stock in tropical forests (Ali et al. 2019; Phillips et al. 2019; Rodrigues et al. 2019; Villa, Ali, et al. 2020). However, the relative contributions to ecosystem function can change substantially between species beyond their abundance (Morlon et al. 2009; Lohbeck et al. 2016). Thus, an abundant tree species may not be dominant in AGC stock

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because it may not have optimal trait values for this ecosystem functioning (Morlon et al. 2009; Rodrigues et al. 2019).

The functional composition can govern an ecosystem function rather than species richness and abundance due to the relative importance of functional traits of tree communities in tropical forests (Lohbeck et al. 2016; Phillips et al. 2019). One way to access this is evaluating whether an ecosystem function is associated with dominant trait values (i.e. community-weighted mean, CWM) in the tree community (Garnier et al. 2004). The CWM is an index of functional diversity that weighs species trait values by the relative abundance of the species in a community (Garnier et al. 2007). This index has been used in several studies to evaluate the effect of functional composition on aboveground biomass (AGB) stock (Prado-Junior et al. 2016; Ali et al. 2017; van der Sande MT, Arets, et al. 2017). Under the mass ratio hypothesis, the CWM of several functional traits determines AGB due to the dominance of few tree species in natural second-growth tropical forests (Conti and Díaz 2013; Lohbeck et al. 2016; Villa, Ali, et al. 2020).

The relationship between CWM of trait values and AGC is affected by stand age and local environmental conditions (van der Sande, Peña-Claros, et al. 2017; Villa, Ali, et al. 2020). Thus, CWM and AGC stock should reflect abiotic and biotic conditions in tropical forests (van der Sande MT, Arets, et al. 2017). Forest stand age is an important driver of biomass accumulation along forest succession, which can drive carbon stock through its effect on tree diversity, dominance and functional traits (Ali et al. 2019). On the other hand, environmental factors such as topography can shape resource availability for plant growth, and consequently affect different stand-age forest attributes in tropical forest, i.e. abundance, species richness, community composition, and carbon stock (Guo et al. 2016; Jucker et al. 2018; Rodrigues et al. 2020). Thus, topographical factors (e.g. elevation, slope and convexity) and stand age can induce variation in the proportion of dominant tree species and biomass (Jucker et al. 2018; Morera-Beita et al. 2019; Villa et al. 2019; Ali et al. 2020). Therefore, the CWM metric can be important for assessing the relationship between the functional traits of CD species and AGC stock along forest succession and topography in tropical forests. This information is critical to understanding forest functioning, restoration, conservation and carbon storage enhancement in threatened ecosystems (Kearsley et al. 2019). In this context, we aim to assess how topographical conditions and stand age determine changes in stand forest attributes (i.e. taxonomical, structural and functional attributes) in a Brazilian Atlantic Forest on late-secondary succession. Specifically, we evaluated whether tree species identity and functional trait composition (i.e. wood density and maximum stem diameter) rather than taxonomic and structural attributes (i.e. species richness and composition and abundance) shape AGC stock along topographical conditions and stand age.

We state the following questions: (1) How do contrasting topographical conditions and stand age determine differences in tree species richness and community composition? (2) What is the carbon dominance and distribution between species and families? (3) What is the relationship between species abundance and CD species along late-secondary succession and contrasting topographical conditions? (4) How do CD species and families change along topographically different stand ages? (5) How do CWM of functional trait values of CD species govern AGC stock in the tree community? We hypothesize that different topographical conditions and late-secondary succession shape change in community composition, species richness, and stem abundance. Thus, we predicted that these changes induce variation in AGC distribution between CD species and families in the tree communities. Second, we assume that the taxonomic identities of the dominant species govern AGC stock, and not the abundance and species richness, due to the relative importance of CWM functional trait values related to carbon stock based on the mass ratio hypothesis. Finally, we predict that the proportion of CD species will be affected by topography and stand age, but the functional composition will govern AGC stock.

2. Methods

2.1. Study area and land-use history

The study was conducted in a Semideciduous Seasonal Atlantic Forest fragment in Minas Gerais, southeast Brazil. Brazilian Atlantic Forests are a hotspot of biodiversity, one of the most species-rich and threatened biomes globally (Scarano and Ceotto 2015). These forests are found mainly as second-growth forests (i.e. forests regenerating, mostly, following anthropogenic disturbance) in small remnant fragments representing less than 12% of the original forest (Scarano and Ceotto 2015).

We studied an Atlantic Forest fragment of approximately 75 ha used for coffee cultivation until 1926; since then, it is in natural regeneration (a passive restoration method). Del Peloso (2012) through the temporal analysis performed through images, observed that, in 1963, the southeastern area of the forest fragment was almost entirely the fragment's border, assigning a regeneration age to this area is ca. 57 years old. On the other hand, the northeastern area of the forest fragment was already part of its nuclear area. Based on the information that this area was abandoned in 1926, it was possible to determine that its natural regeneration is ca. 87 years old.

According to the Köppen-Geiger classification, the study area's climate is tropical altitude (Cw_b), with a dry season between May and September and a wet season between December and March (Alvares et al. 2013). The mean annual temperature is 21 °C, and the mean annual precipitation is 1270 mm, with the highest volumes of rain concentrated in December, January and February (Avila-Diaz et al. 2020; UFV 2020). The study area is between 620 and 820 m a.s.l., and the relief varies from strongly undulating to mountainous. Two dominant soil classes characterize the site: a red-yellow alsicose latosol covers hilltops; while a cambic yellow-red podzolic dominates the upper fluvial terraces (Ferreira-Júnior et al. 2007).

2.2. Vegetation sampling

Two 1-ha permanent plots were established in the forest fragment with contrasting topographical conditions, the southeastern and northeastern patches. The southeastern patch was established in 1984, and five measurements were made in 1984, 1998, 2003, 2011 and 2017, totalizing 33 years of monitoring. On the other hand, the northeastern patch was established in 1993, and four measurements were made in 1993, 2004, 2011 and 2017, totalizing 24 years of monitoring. Each patch was subdivided into 100 subplots of 10 × 10 m to better capture topography's effect on the local-scale. All trees with diameters at breast height (DBH) ≥ 5 cm were inventoried and botanically identified to the species level in both patches and years in each subplot. All individuals were identified using specialized literature, consulting Herbarium, or taxonomists. The Angiosperm Phylogeny Group IV (APG IV 2016) was used for taxon classification.

2.3. Topographical variables survey

We measured vertical and horizontal angles and linear distances at each 200-10 × 10 m patches at the four vertices utilizing a total station (Kahmen and Faig 1988). Thus, we calculate three topographical variables (slope, elevation and convexity) in each patch (see Rodrigues et al. 2019).

2.4. Estimation of AGC

The AGC stocks estimation was based on allometric equations for forest biomass. The carbon concentration of a tree's different organs is assumed to be approximately 50% of the biomass (Chave et al. 2009). In this study, AGB of trees for each sampled stem was calculated from a combination of variables using the general allometric equation proposed by Chave et al. (2005) as described below, based on just the measured diameter (*D*) and wood specific density (*ρ*). According to Chave et al. (2005) diameter and wood density are the most critical parameters necessary to predict the tree biomass accurately. We measured the tree diameter in the field, while the wood specific density (*ρ*) was extracted from a global database (Chave et al. 2009).

$$\mathrm{AGB} = \exp\begin{bmatrix} -1.803 - 0.976E + 0.976\ln(p) \\ +2.673\ln(D) - 0.0299\left[\ln(D)\right]^2 \end{bmatrix} \tag{1}$$

The total AGB per patch was the sum of the AGBs of all trees having DBH ≥ 5 cm, which was converted to megagrams per hectare (Mg ha^{-1}) (Ali et al. 2017). Species-level biomass was calculated as the sum of the biomass of all stems from a species. Estimation of AGB was performed using the R package BIOMASS (Réjou-Méchain et al. 2017).

2.5. Quantification of the community-weighted mean of stem traits

The dominant traits in a community can be estimated by the weighted trait mean value in the community (Garnier et al. 2007). Thus, we calculated the functional composition through the CWM metrics based on two key functional traits for AGC stock, the wood density (WD) and maximum stem diameter (D_{max}) (Prado-Junior et al. 2016; Villa, Ali, et al. 2020). Community-weighted mean was calculated as the mean value of the trait in the community, weighting by species' relative abundance (Garnier et al. 2004). After calculated the CWM values of each functional trait (WD and D_{max}) we separated the tree species into two functional categories: (i) CD species and (ii) carbon non-dominant (CND) species. The CD group corresponds to the CWM of functional traits of species that accumulate approximately 50% of the total community AGC stock (i.e. hyperdominant species, see Bastin et al. 2015 and Fauset et al. 2015). On the other hand, the CND group corresponds to the functional traits of different species in the community that contribute little to AGC stock compared to CD species.

We used the relative abundance of species rather than a basal area because it prevents circular redundancy derived from DBH from calculating functional trait and AGB (Conti and Díaz 2013; Ali et al. 2017). Each species' relative abundance was calculated by dividing the number of individual species from the total species found in each patch and stand age (Conti and Díaz 2013). We evaluated differences in the CWM of CD traits among stands and between census years using the following equation:

$$CWM\chi\mathrm{CWM}_{\chi} = \sum\nolimits_{i=1}^{Ss}\left(p_i pi^{*} t_i ti\right) \tag{2}$$

where CWM$_{\chi}$ is the CWM for trait *χ* in each subplot, *s* is the number of species in each southeastern or northeastern patch, p_{i} is the relative abundance of the *i*th species in each plot and stand age, and t_{i} is the trait value for the *i*th species. The CWM was calculated for each subplot from the species abundance and functional traits, and was calculated using the 'FD' package (Laliberté and Legendre, 2010).

2.6. Data analysis

We evaluated whether topographical conditions determine richness, composition, stem abundance, and CD species during late-secondary succession (questions 1 and 4). Thus, we use the three topographic variables to perform a multivariate regression tree (MRT) analysis (De'ath 2002; Larsen and Speckman 2004) to classify habitat types according to topographical variables as a proxy for topographic heterogeneity in each permanent patch studied (Guo et al. 2016; Wang et al. 2016). MRT is a constrained clustering method that identifies clusters (a group of plots) that are most similar to each other based on a set of predefined values (De'ath, 2002). MRT analysis was performed using the 'rpart' package (Therneau et al. 2017). The two study permanent patches have marked differences in the spatial distribution of topographical variables, mainly elevation and convexity (Figure S.3, Appendix/from Electronic Supplement Material, ESM hereafter). We represented the spatial distribution of habitats from each patch using the '*Field*' package (Nychka et al. 2017). According to the MRT, the southeastern area's permanent patch was less topographically heterogeneous, as determined by the two topographical variables (elevation and slope). Conversely, the permanent patch of the northeastern area was more topographically heterogeneous, determined by the three topographical variables elevation, slope and convexity (Figure S.4 from ESM).

We answered our first research question, i.e. whether topography and stand age determine species richness differences, using sampled-based rarefaction and extrapolation curves constructed with the first Hill numbers (Chao et al. 2014). Thus, we assessed species richness differences in each patch and all sampled years (stand ages). Extrapolations were based on presence/absence data (Hill number of order 0 with 100 replicate bootstrapping runs to estimate 95% confidence intervals), up to two the sample size (Colwell et al. 2012), using the '*iNEXT*' package (Hsieh et al. 2016). Whenever the 95% confidence intervals did not overlap, species numbers differed significantly at $P < 0.05$ (Colwell et al. 2012).

Furthermore, non-metric multidimensional scaling (NMDS) analysis was performed based on Bray–Curtis dissimilarities (Clarke 1993) to examine species composition differences between patches and patches between different stand ages. We performed the NMDS using the '*metaMDS*' function (Oksanen et al. 2018) and the permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) to determine differences in species composition by using the '*adonis*' routine available within the '*vegan*' package (Oksanen et al. 2018).

We analyzed whether AGC stock was dominant for a small number of species and whether topography and stand age had implications in distributing CD species (questions 2 and 4). We did this by estimating the maximum number of species required to account for approximately 50% of AGC stock in all stand age and patches with different topographical conditions (Rodrigues et al. 2019). Then, we assessed the number of CD species in each patch with different topographical conditions and stand age sampling. We considered 'CD species' those that represented approximately 50% of the total community AGC in each sampled year. To obtain CD species, all species in our database were ranked by decreasing contribution to the total AGC, based on the definitions adopted by Bastin et al. (2015) and Fauset et al. (2015). To understand the relationship between stem abundance, richness and composition with CD species during the late-secondary succession and contrasting topographical conditions (question 3), we calculated the contribution of stem abundance to the total AGC in each patch and stand age. Thus, we regressed each species' percentage contribution to the AGC of the whole dataset against their percentage contribution to the number of stems of the whole dataset, following the methods adopted by Fauset et al. (2015). The same methodology was also used to rank the CD families along late-secondary succession. We constructed species and family rank curves (Magurran 2004) based on species-family abundance and distribution (number of species or family per patch and year of sampling). All species and families were ranked from the most to the least abundant to obtain species or family rank curves.

We answered whether dominant species govern AGC stock due to the relative importance of functional trait values compared to other species of tree community (question 5). Thus, we compared the mean AGC between patches and stand age, and CWM of trait values (WD and $D_{\max}$) between categorical functional groups (CD and CND) performing Wilcoxon-tests (non-normally distributed data). Then, we evaluated, for all stand ages and patches with different topographical conditions, the CWM of functional traits WD and $D_{\max}$ in two functional categories: (i) CD species and (ii) CND species. Data were tested for normal distribution with the Shapiro–Wilks test and a Q-Q plot (Crawley 2012).

Finally, we assessed the spatial autocorrelation of the sampling units (subplots) within each patch (northeastern and southeastern) between the main variables used in our study (AGB and species richness) based on distance classes (0–12), which correspond to the spatial distance in meters (0–100) between subplots according to the Moran test (based on 9999 permutations) using the 'gstat' package (Pebesma 2004). The spatial autocorrelation tests showed no significant spatial correlation in both patches based on spatial correlograms (Figure S.5). All analyses were performed in R version 3.1.2 (R Core Team 2019).

3. Results

3.1. Species richness and composition

Species richness differed significantly between the two study patches with different topographical conditions (Figure 1A). Species richness in the northeastern patch (the more topographically heterogeneous one) was higher than that in the southeastern patch, which is less topographically heterogeneous. Conversely, species richness did not differ significantly between stand ages within each patch (Figure 1B). The NMDS revealed that tree species composition varied considerably between patches; and separated the two study patches along the first axis (Figure 2A). On the other hand, the NMDS during the late-secondary succession revealed no significant differences between stand age in both in both patches (Figure 2B and C, respectively).

3.2. CD species and abundance

We found that both patches have CD species, i.e. accounting for approximately 50% of the carbon storage. Only one species (*Anadenanthera peregrina* Speg.) was classified as CD in all stand age in the southeastern patch (Figure 3). This species presented approximately 3.5% of the total abundance (Table 1). On the other hand, three to five species accumulated 50% of the AGC in the northeastern patch (Figure 3). These species presented together on average, approximately 23.9% of the total abundance (Table 1). The top five most dominant species in AGG and abundance are distributed according to their relative contribution (Table 1; data on all species is found in Appendix Table S.1 from ESM).

3.3. Shifts of CD species and families on topographically different stand age

We did not find in the permanent patch of southeastern area shifts in CD species; the only CD species was *A. peregrina*

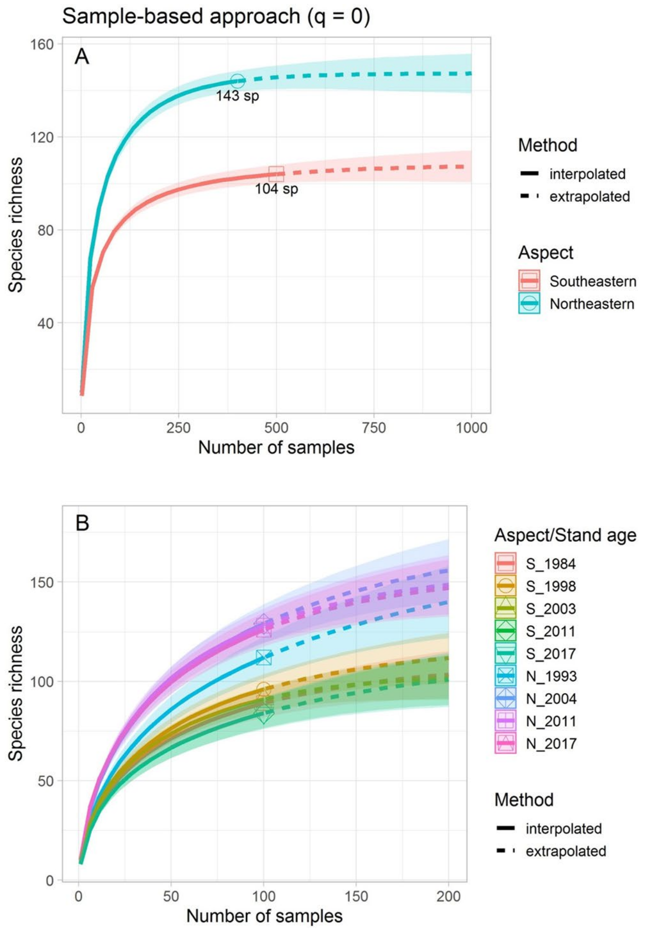

Figure 1. Sample-based rarefaction (solid line) and extrapolation curves (dashed lines) of tree richness for southeastern and northeastern patches (A) and tree richness in all stand age analyzed in the two 1-ha permanent patches (B). Rarefaction and extrapolation curves present the lines that represent the mean values and the bands the standard deviation with 95% confidence intervals.

regardless of stand age (storing 70.2; 74; 78.9; 83 and 84 Mg ha^{-1} of carbon, respectively in the years 1984, 1998, 2003, 2011 and 2017) (Table 1 and Figure S.1 from ESM). The main CD species distribution in the northeastern patch did not change along late-secondary succession. *A. peregrina*, *Piptadenia gonoacantha* (Mart.) J.F.Macbr. and *Machaerium stipitatum* Vogel, were the CD species in 1993 (stocking 15.5, 11.3 and 7 Mg ha^{-1} of carbon, respectively); they shared dominance with *Allophylus edulis edulis* (A.St-Hil., A.Juss. & Cambess) Radlk. in 2004 and *Allophylus edulis* and *Trichilia lepidota* Mart. in 2011 and 2017 (Table 1 and Figure S.1 from ESM). Thus, we observed that different topographical conditions and stand age shape changes in CD species when we evaluate the two patches separately. Still, when assessing each patch, there are no changes in the species identity during the late-secondary succession.

On the other hand, when we analyzed the dominant families, the only CD family in the southeastern patch was Fabaceae, which accounts for 66.4–70.3% of carbon in this late-secondary succession. In the northeastern patch, Fabaceae account for an average of 53% of the carbon stored in 1993 and 2004. In 2011 and 2017, Fabaceae accumulated 48.6% and 45.9% of the total carbon for those years, respectively (Figure S.2 from ESM). There is a decrease in the proportion of carbon accumulated by the family in late-secondary succession and the different topographical conditions (Data on all families is found in Appendix Table S.2. from ESM).

3.4. AGC stock with respect to functional traits and groups

CWM of functional traits WD and D_{max} of the CD species differed significantly from the CND species in most stand age in the patches with different topographical conditions. Nevertheless, CWM of functional trait values WD did not differ in the southeastern patch in the two last sampling periods and CWM of D_{max} in 2017. The highest CWM functional trait values were found for the species that accumulate approximately 50% of the total AGC stock (CD), mainly in the southeastern patch (Figure 4).

4. Discussion

We found that topographical conditions and stand age shape changes in community composition, species richness, abundance and CD species throughout the late-secondary stage. Furthermore, our results showed that the taxonomic identities of the dominant species, and not the species abundance and richness, determine the AGC stock due to the importance of trait values related to carbon stock (WD and D_{max}). In this study, the main novelty was assessing CD and CND species based on CWM functional traits values of WD and D_{max}. Thus, we found that topography and stand age shaped the proportion of CD species. In contrast, AGC stock was driven by the functional composition, expressed in the higher CWM values of conservative functional traits. Moreover, CD species and families do not change along late-secondary succession and topographical conditions when we evaluate each patch separately.

These findings are important for understanding the role of individual species and their traits for ecosystem functioning, which can allow formulating more detailed conservation and restoration plans in highly diverse and threatened ecosystems, such as Atlantic Forest (Scarano and Ceotto 2015; Kearsley et al. 2019). Furthermore, this study highlights the fundamental role of CWM of functional trait values of CD species to estimate AGC stock and the relative importance of functional groups and taxonomic identity in AGC storage in second-growth tropical forests.

4.1. Patterns of species richness, abundance and dominance

We found CD species in both patches, but this dominance pattern is not linked to the species abundance in most stand ages. In the southeastern patch, only *A. peregrina* was classified as CD. Besides, this species presented a low stem abundance (on average 58 stems in each stand age) compared to other species, i.e. CND (e.g. *Sorocea bonplandii* (Baill.) W.C.Burger, Lanj. & Wess.Boer, presented an average of 544

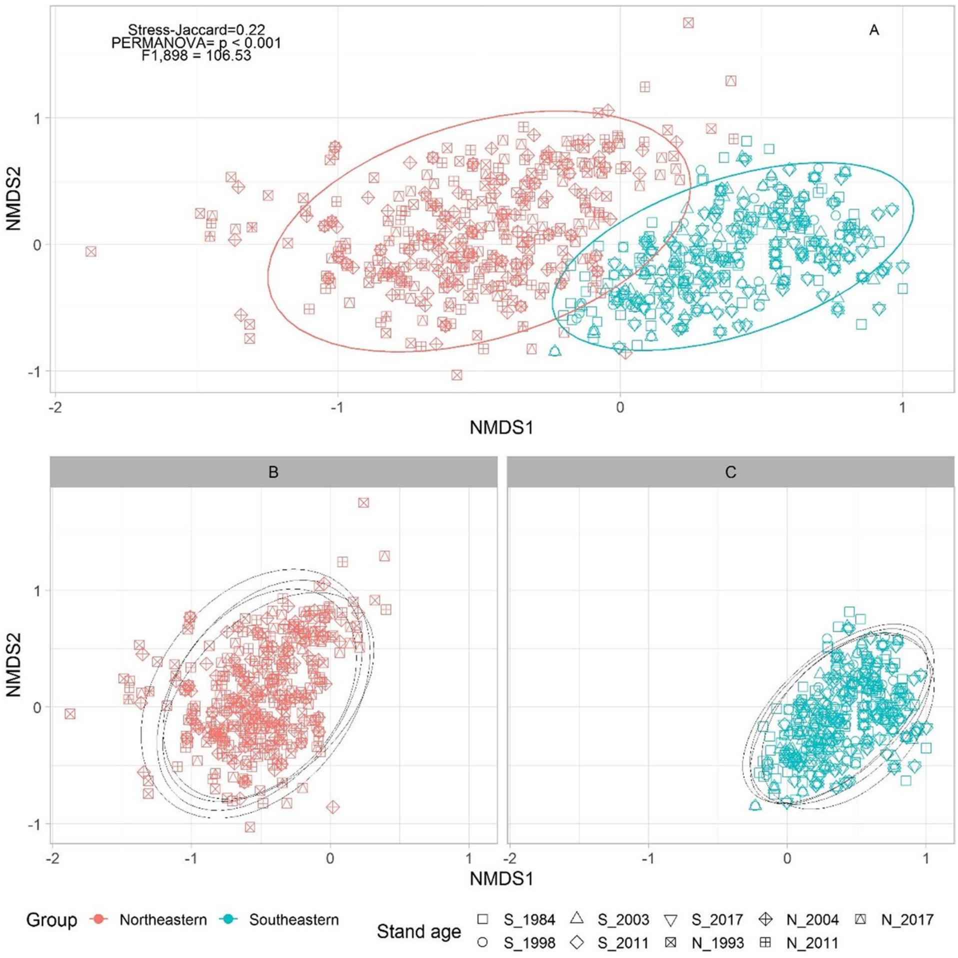

Figure 2. Non-metric multidimensional scaling based (NMDS) on species composition (geometric shapes) and study areas (shapes colors) within two 1-ha permanent plots in Atlantic Forest, Minas Gerais, Brazil (A). NMDS on species composition according to stands ages (shapes colors) in the permanents patches of northeastern (B) and southeastern (C).

stems in each stand age evaluated). The same pattern was observed in the northeastern patch, where three to four species accumulated 50% of the AGC. This different proportion pattern in the number of CD can be explained by the different topographic heterogeneity and the stand age differences between patches. Thus, previous studies report that a higher environmental heterogeneity among patches results in a higher probability that some species dominate the plant communities (Hillebrand et al. 2008; Mattsson et al. 2016), explaining the higher number of CD in the northeastern patch, the most topographically heterogeneous.

According to Hillebrand et al. (2008), dominance responds more rapidly to environmental conditions than species richness and might to lead to rapid responses in terms of ecosystem functions. We found that the number of CD is related to the richness of patches. The most species-rich patch has a higher number of CD compared to the less species-rich patch. Thus, the dominance patterns may affect the species richness in different ways, either through evenness that alters the number of species per unit area or because more species are found in patches with higher evenness, i.e. less species dominance (Hillebrand et al. 2008), such as the northeastern patch.

In this sense, the functional composition (i.e. CWM of functional traits of CD) may be more important for tropical forest functioning than species richness and composition (Prado-Junior et al. 2016; Villa, Ali, et al. 2020). For example, Fotis et al. (2018) found that traits that drove AGB were strongly associated with two dominant species present at the study site. These authors conclude that higher species richness may dilute the effects of traits that drive AGB accumulation in more dominant species. These results agree with our results, which showed that in the less species-rich patch (southeastern $n = 104$), there is a smaller CD than the most species-rich patch (northeastern $n = 143$), which has a high number of CD.

The highest CWM of D_{max} values was found in the southeastern patch, which presents a lower species richness, and showed that the CD are large-sized trees. Furthermore, rather than the topographical condition and stand age, dominant tree species themselves could be limiting the establishment of more species (biotic filter). These large trees limit light, water and soil nutrients available to other trees, hence driving species richness and diversity (Ali et al. 2019). In addition, environmental factors, such as topography, can be considered a filter constraining which individuals bearing specific traits can persist in a community (Violle et al. 2007). Different topographical conditions could influence the breadth of functional traits distribution between them, which can affect the ACG stock distribution through the functional composition and categorical functional groups (CD and CND).

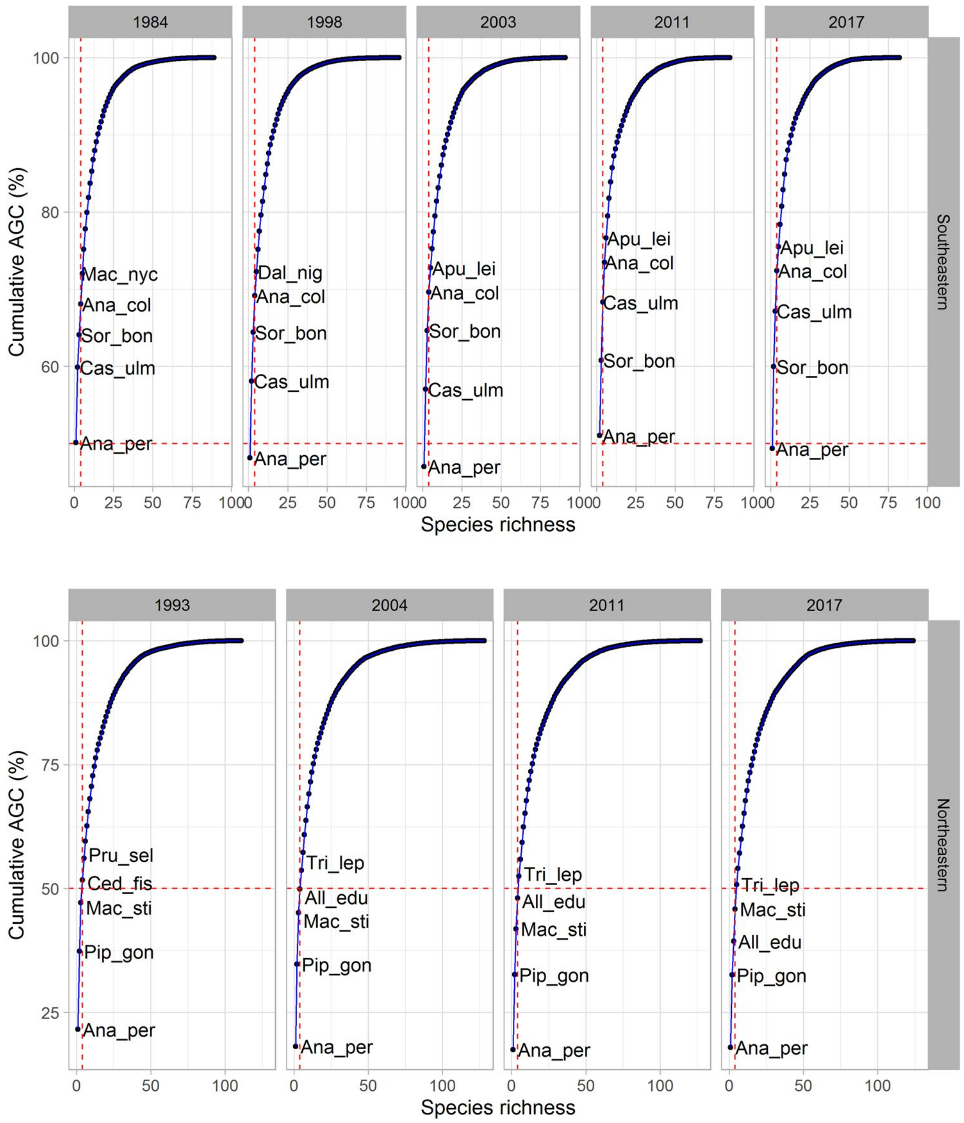

Figure 3. Cumulative aboveground carbon (AGC) distribution for the permanent plot of southeastern (A) and northeastern (B) patches for carbon dominants species in the Atlantic Forest, Minas Gerais, Brazil. The dashed horizontal red line indicates the limit of species that accumulate approximately 50% of the total carbon in all stands ages.

4.2. CD species and Fabaceae family are stable along the late-secondary succession

We did not find changes of CD species and families and CWM of functional traits values during late-secondary succession in both patches. The Fabaceae was the unique CD family, represented mainly by *A. peregrina* (Fabaceae) in all stand ages. These results are consistent with those of Terra et al. (2017), who found that 220 species (5.38%) of all species studied in Minas Gerais state belong to the Fabaceae family. Our results indicated that there was a prolonged late-secondary succession decrease in Fabaceae abundance in the northeastern patch, the oldest one. Consistent with these results, van der Sande et al. (2016) reported that the Fabaceae family has become less abundant in the old-growth forest due to decreased nitrogen limitation and an increase in drought stress, which should be better explored in future research. In this context, ecological theories predict that community stability is due, among other factors, to the persistence of dominant species, as found in our analyses (e.g. Yuan et al. 2019). Meanwhile, other studies suggest that the stabilizing of species richness along succession can only be observed at low dominance (e.g. Hillebrand et al. 2008; Lohbeck et al. 2013). Under high plant dominance, one or few species (as shown in our results) make significant contributions to the biomass or carbon that reduces the stabilizing effect of species richness (Hillebrand et al. 2008).

4.3. Functional traits composition shapes the highest AGC stock by CD species

The results support our hypothesis that species' taxonomic identity is more important than abundance. This is due to the relative importance of CWM of functional trait values that govern ecosystem functioning, i.e. AGC stock. These findings support the approach that ecosystem properties depend more on functional traits than species or abundance

Table 1. Top 5 most important species for AGC stock and abundance in the patches for all year's sampling.

Southeastern	N°Sp.	Species	Ab	%Ab	%Ab.Ac.	AGC	AGC.Ac.	%AGC	% AGC.Ac.
1984	1	***Anadenanthera peregrina*** (Ana_per)	68	4.51	4.51	70.22	70.22	50.11	50.11
1984	2	*Casearia ulmifolia* (Cas_ulm)	158	10.47	14.98	13.69	83.91	9.77	59.88
1984	3	*Sorocea bonplandii* (Sor_bon)	328	21.74	36.71	5.86	89.77	4.18	64.07
1984	4	*Anadenanthera colubrina* (Ana_col)	1	0.07	36.78	5.61	95.38	4	68.07
1984	5	*Machaerium nyctitans* (Mac_nyc)	60	3.98	40.76	5.55	100.93	3.96	72.03
1998	1	***Anadenanthera peregrina*** (Ana_per)	61	3.44	3.44	74.08	74.08	48.15	48.15
1998	2	*Casearia ulmifolia* (Cas_ulm)	154	8.69	12.13	15.31	89.39	9.95	58.09
1998	3	*Sorocea bonplandii* (Sor_bon)	518	29.23	41.37	9.74	99.13	6.33	64.42
1998	4	*Anadenanthera colubrina* (Ana_col)	3	0.17	41.53	7.27	106.4	4.72	69.15
1998	5	*Dalbergia nigra* (Dal_nig)	13	0.73	42.27	4.79	111.19	3.11	72.26
2003	1	***Anadenanthera peregrina*** (Ana_per)	60	3.39	3.39	78.5	78.5	47.03	47.03
2003	2	*Casearia ulmifolia* (Cas_ulm)	144	8.14	11.53	16.7	95.19	10	57.04
2003	3	*Sorocea bonplandii* (Sor_bon)	583	32.94	44.46	12.71	107.9	7.62	64.65
2003	4	*Anadenanthera colubrina* (Ana_col)	5	0.28	44.75	8.26	116.17	4.95	69.6
2003	5	*Apuleia leiocarpa* (Apu_lei)	69	3.9	48.64	5.27	121.43	3.16	72.76
2011	1	***Anadenanthera peregrina*** (Ana_per)	51	3.29	3.29	83.1	83.1	51.02	51.02
2011	2	*Sorocea bonplandii* (Sor_bon)	608	39.23	42.52	15.89	98.99	9.76	60.78
2011	3	*Casearia ulmifolia* (Cas_ulm)	104	6.71	49.23	12.27	111.27	7.54	68.32
2011	4	*Anadenanthera colubrina* (Ana_col)	7	0.45	49.68	8.41	119.68	5.16	73.48
2011	5	*Apuleia leiocarpa* (Apu_lei)	58	3.74	53.42	5.1	124.78	3.13	76.61
2017	1	***Anadenanthera peregrina*** (Ana_per)	50	3.1	3.1	84.01	84.01	49.36	49.36
2017	2	*Sorocea bonplandii* (Sor_bon)	683	42.37	45.47	18.06	102.07	10.61	59.97
2017	3	*Casearia ulmifolia* (Cas_ulm)	94	5.83	51.3	12.22	114.29	7.18	67.15
2017	4	*Anadenanthera colubrina* (Ana_col)	6	0.37	51.67	8.95	123.24	5.26	72.41
2017	5	*Apuleia leiocarpa* (Apu_lei)	55	3.41	55.09	5.25	128.49	3.09	75.49
Northeastern	N°Sp.	Species	Ab	%Ab	%Ab.Ac.	AGC	AGC.Ac.	%AGC	% AGC.Ac.
1993	1	***Anadenanthera peregrina*** (Ana_per)	58	5.48	5.48	15.54	15.54	21.6	21.6
1993	2	***Piptadenia gonoacantha*** (Pip_gon)	68	6.43	11.91	11.32	26.86	15.73	37.33
1993	3	***Machaerium stipitatum*** (Mac_sti)	42	3.97	15.88	7.08	33.95	9.85	47.18
1993	4	*Cedrela fissilis* (Ced_fis)	12	1.13	17.01	3.29	37.23	4.57	51.75
1993	5	*Prunus sellowii* (Pru_sel)	94	8.88	25.9	3.15	40.38	4.37	56.12
2004	1	***Anadenanthera peregrina*** (Ana_per)	65	4.8	4.8	18.05	18.05	18.17	18.17
2004	2	***Piptadenia gonoacantha*** (Pip_gon)	79	5.83	10.64	16.44	34.48	16.55	34.73
2004	3	***Machaerium stipitatum*** (Mac_sti)	53	3.91	14.55	10.34	44.82	10.41	45.14
2004	4	*Allophylus edulis* (All_edu)	44	3.25	17.8	4.71	49.53	4.74	49.88
2004	5	*Trichilia lepidota* (Tri_lep)	101	7.46	25.26	3.77	53.29	3.79	53.68
2011	1	***Anadenanthera peregrina*** (Ana_per)	48	3.81	3.81	19.03	19.03	17.53	17.53
2011	2	***Piptadenia gonoacantha*** (Pip_gon)	52	4.13	7.94	16.39	35.42	15.1	32.63
2011	3	***Machaerium stipitatum*** (Mac_sti)	41	3.25	11.19	10.06	45.47	9.27	41.89
2011	4	***Allophylus edulis*** (All_edu)	42	3.33	14.52	6.72	52.19	6.19	48.08
2011	5	*Trichilia lepidota* (Tri_lep)	104	8.25	22.78	4.84	57.03	4.46	52.54
2017	1	***Anadenanthera peregrina*** (Ana_per)	61	4.37	4.37	20.41	20.41	17.98	17.98
2017	2	***Piptadenia gonoacantha*** (Pip_gon)	43	3.08	7.44	16.58	36.99	14.6	32.58
2017	3	***Allophylus edulis*** (All_edu)	43	3.08	10.52	7.73	44.72	6.81	39.38
2017	4	***Machaerium stipitatum*** (Mac_sti)	39	2.79	13.31	7.35	52.07	6.48	45.86
2017	5	*Trichilia lepidota* (Tri_lep)	117	8.38	21.69	5.63	57.69	4.95	50.81

The carbon dominant species are given in bold.

N°Sp.: species number; Species: abbreviation of each 5 most carbon dominant species; Ab: abundance; %Ab: relative abundance; %Ab.Ac.: accumulated relative abundance; AGC: aboveground carbon; AGC.Ac.: aboveground carbon accumulated; %AGC: proportion of aboveground carbon; % AGC.Ac.: proportion of aboveground carbon accumulated.

(Lohbeck et al. 2016; Phillips et al. 2019). Our results showed that despite the low proportion of dominant species, these present large-sized individuals with maximum size (expressed as CWM of D_{max}) compared to carbon non-dominant species with smaller-sized individuals. These few dominant species with large-sized individuals could play a more prominent role in AGB stock than those abundant smaller-sized individuals. Previous studies have shown this positive relationship between the maximum stem diameter and CWM of wood density and AGB, confirming that high AGB is associated with large-diameter trees (Ali et al. 2019; Rodrigues et al. 2019; Villa, Ali, et al. 2020). Moreover, this observed pattern in our study probably explains the more conservative trait values (increasing the community WD with time) and ecosystem functioning stabilization during late-secondary succession (Poorter et al. 2019). This relationship between the CWM of wood density and D_{max} and AGC may explain the importance of slow-growing and shade-tolerant species during late-secondary succession (Poorter et al. 2019, Villa, Ali, et al. 2020).

In this sense, large-sized trees have been shown to drive variation in biomass since those store high quantities of carbon in tropical forests (Bastin et al. 2015; Fauset et al. 2015; Poulsen et al. 2020). Despite storing higher amounts of AGC, these trees with high CWM of D_{max} values are found in low abundance (Fauset et al. 2015; Rodrigues et al. 2019a). This result showed that the ecosystem functioning is mainly determined by the functional traits of the CD species despite species richness and abundance. Hence, the results found in our research are in agreement with the mass-ratio hypothesis (Grime 1998; Villa, Ali, et al. 2020). However, in the northeastern patch, several CD species are also dominant in terms of abundance. Thus, these species can also be considered oligarchs in relation to abundance in this patch. Therefore,

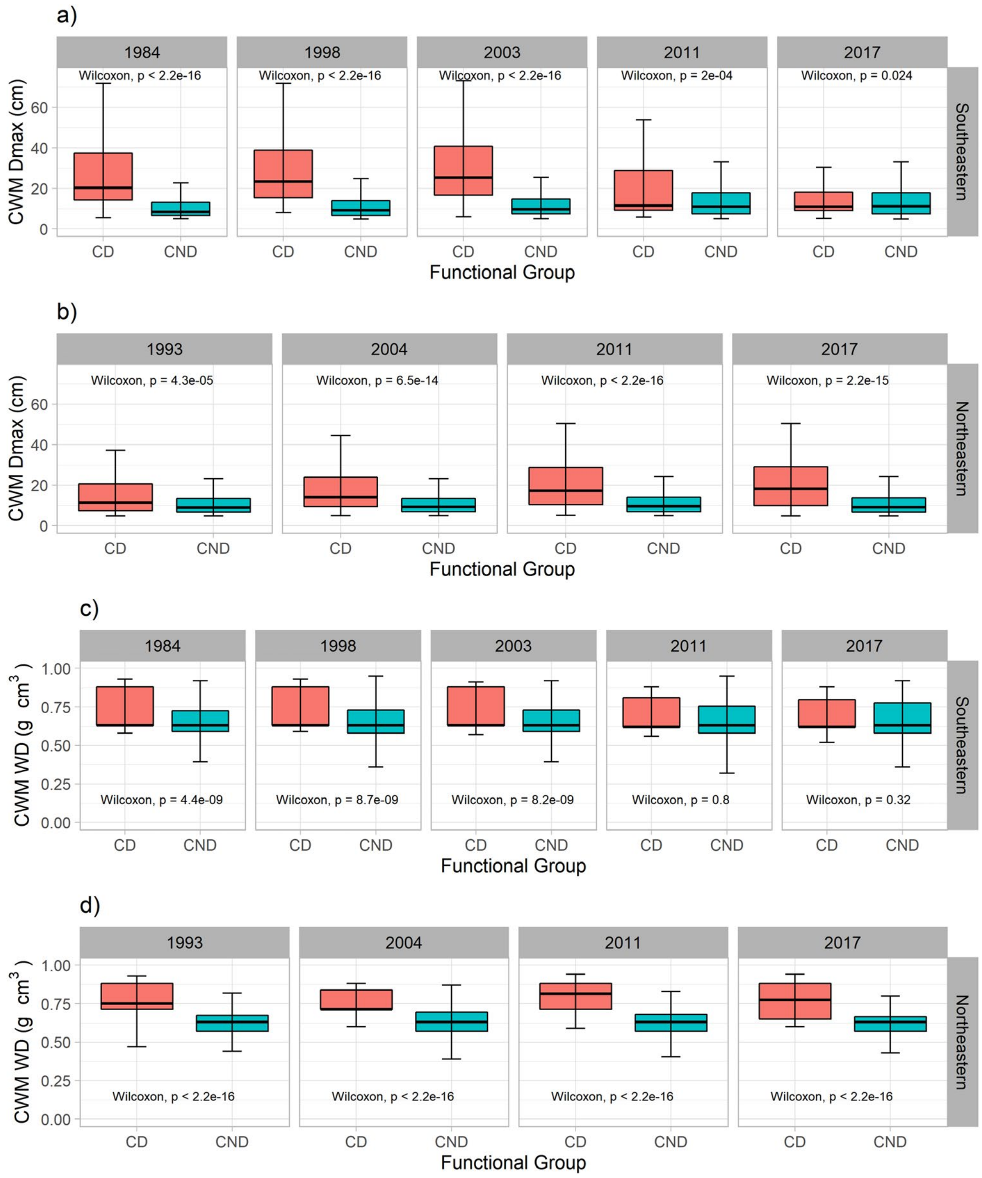

Figure 4. The relative importance of CWM of the functional traits maximum stem diameter (D_{max}) (A, B) and wood density – WD (C, D) of carbon dominant species (CD) and carbon non-dominant species (CND) in all stand age and patches with different topographic conditions studied. CD corresponds to the CWM of the traits of the species that accumulate approximately 50% of the total AGC stock, while CND corresponds to the CWM of the traits of other species in the community.

here we do not intend to dismiss the importance of abundant species in relation to dominant, as these, together with the dominant species, participate in multiple ecosystem functions and maintain biodiversity (Ali et al. 2019, 2020). This premise is fundamental in programs focused on carbon-diversity cobenefits, especially considering heterogeneity within forests (Matos et al. 2020). In addition, it is extremely relevant to consider our results in forest recovery and conservation programs. Since the anthropogenic disturbances affect tree communities in Atlantic Forests (Matos et al. 2020), changes in species richness and, consequently, relative abundance and dominance, can also affect ecosystems' stability (Hillebrand et al. 2008). These disturbances can have negative effects because the loss of a single dominant species has several negative consequences for forest functioning (Bradford and Murphy 2019).

Our study showed that topographical conditions and stand age shape tree community composition changes, species richness, abundance and CD species in a second-growth Atlantic Forest. Furthermore, we showed that CWM of functional traits values of WD and D_{max} of CD species determine AGC stock, agreeing with the mass ratio hypothesis. Therefore, our study reveals that both trait functional composition and taxonomic identity across CD species shape AGC stock in our studied forests. We reported a stabilization of the dominant species and families along late-secondary succession, with *A. peregrina* being the main CD species. In addition, we emphasize the relevance of the trait-based approach to understanding forest functioning and trait functional composition, and taxonomic identity (role of key species) for the carbon storage, recovery and increase of the threatened Atlantic Forest.

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Author contributions

ACR, PMV and AVN conceived and designed the study. ACR and PMV analyzed the data. ACR wrote the manuscript with input from FSC, CEMT, PMV, LPG, JAAMN and AVN. All authors contributed substantially to the writing and revision of the manuscript.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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References

Ali A, Lin S-L, He J-K, Kong F-M, Yu J-H, Jiang H-S. 2019. Big-sized trees overrule remaining trees' attributes and species richness as determinants of aboveground biomass in tropical forests. Glob Chang Biol. 25(8):2810–2824.

Ali A, Mattsson E, Nissanka SP, Wang LQ. 2020. Topmost trees and foremost species underlie tropical forest structure, diversity and biomass through opposing mechanisms. For Ecol Manag. 473:118299.

Ali A, Yan E-R, Chang SX, Cheng J-Y, Liu X-Y. 2017. Community-weighted mean of leaf traits and divergence of wood traits predict aboveground biomass in secondary subtropical forests. Sci Total Environ. 574:654–662.

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G. 2013. Köppen's climate classification map for Brazil. Meteorol Z. 22(6):711–728.

APG IV. 2016. An update of the Angiosperm Group classification for the orders and families of flowering plants: APG IV. Bot J Linn Soc. 141:399–436.

Avila-Diaz A, Justino F, Lindemann DS, Rodrigues JM, Ferreira GR. 2020. Climatological aspects and changes in temperature and precipitation extremes in Viçosa-Minas Gerais. An Acad Bras Cienc. 92(2):e20190388.

Bastin JF, Barbier N, Réjou-Méchain M, Fayolle A, Gourlet-Fleury S, Maniatis D, de Haulleville T, Baya F, Beeckman H, Beina D, et al. 2015. Seeing Central African forests through their largest trees. Sci Rep. 5:13156.

Bradford M, Murphy HT. 2019. The importance of large-diameter trees in the wet tropical rainforests of Australia. PLoS One. 14(5):e0208377.

Chao A, Gotelli NJ, Hsieh TC, Sander EL, Ma KH, Colwell RK, Ellison AM. 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr. 84(1):45–67.

Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, Fölster H, Fromard F, Higuchi N, Kira T, et al. 2005. Tree allometry and improved estimation of carbon stocks and balance in tropical forests. Oecologia. 145(1):87–99.

Chave J, Coomes D, Jansen S, Lewis SL, Swenson NG, Zanne AE. 2009. Towards a worldwide wood economics spectrum. Ecol Lett. 12(4):351–366.

Clarke KR. 1993. Non-parametric multivariate analyses of changes in community structure. Austral Ecol. 18(1):117–143.

Colwell RK, Chao A, Gotelli NJ, Lin S-Y, Mao CX, Chazdon RL, Longino JT. 2012. Models and estimators linking individual-based and sample-based rarefaction, extrapolation and comparison of assemblages. J Plant Ecol. 5(1):3–21.

Conti G, Díaz S. 2013. Plant functional diversity and carbon storage - an empirical test in semi-arid forest ecosystems. J Ecol. 101(1):18–28.

Crawley MJ. 2012. The R Book. 2nd ed. London: Wiley.

De'ath G. 2002. Multivariate regression trees: a new technique for modeling species-environment relationships. Ecology. 83:1105–1117.

Del Peloso RV. 2012. [Dinâmica e sucessão de um fragmento de Floresta Atlântica] [master's thesis]. Viçosa, Brazil: Universidade Federal de Viçosa.

Fauset S, Johnson M, Gloor M, Baker TR, Monteagudo AM, Brienen RJW, Feldpausch TR, Lopez-Gonzalez G, Malhi Y, ter Steege H, et al. 2015. Hyperdominance in Amazonian Forest carbon cycling. Nat Commun. 6:6857.

Ferreira-Júnior WG, Silva A, Schaefer C, Meira Neto JAA, Dias A, Ignácio M, Medeiros M. 2007. Influence of soils and topographic gradients on tree species distribution in a Brazilian Atlantic tropical semideciduous forest. Edinburgh J Bot. 64(2):137–157.

Fotis AT, Murphy SJ, Ricart RD, Krishnadas M, Whitacre J, Wenzel JW, Queenborough SA, Comita LS. 2018. Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. J Ecol. 106(2):561–570.

Garnier E, Cortez J, Billès G, Navas M, Roumet C, Debussche M, Laurent G, Blanchard A, Aubry D, Bellmann A, et al. 2004. Plant functional markers capture ecosystem properties during secondary succession. Ecology. 85(9):2630–2637.

Garnier E, Lavorel S, Ansquer P, Castro H, Cruz P, Dolezal J, Eriksson O, Fortunel C, Freitas H, Golodets C, et al. 2007. Assessing the effects of land-use change on plant traits, communities and ecosystem functioning in grasslands: a standardized methodology and lessons from an application to 11 European sites. Ann Bot. 99(5):967–985.

Grime JP. 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. J Ecology. 86(6):902–910.

Guo Y, Wang B, Mallik AU, Huang F, Xiang W, Ding T, Wen S, Lu S, Li D, He Y, et al. 2016. Topographic species-habitat associations of tree species in a heterogeneous tropical karst seasonal rain forest, China. J Plant Ecol. 10(3):450–460.

Hillebrand H, Bennett DM, Cadotte MW. 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. Ecology. 89(6):1510–1520.

Hsieh TC, Ma KH, Chao A. 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol Evol. 7(12):1451–1456.

Jucker T, Bongalov B, Burslem DFRP, Nilus R, Dalponte M, Lewis SL, Phillips OL, Qie L, Coomes DA. 2018. Topography shapes the structure, composition and function of tropical forest landscapes. Ecol Lett. 21(7):989–1000.

Kahmen H, Faig W. 1988. Surveying. Berlin: Walter de Gruyter & Co.

Kearsley E, Hufkens K, Verbeeck H, Bauters M, Beeckman H, Boeckx P, Huygens D. 2019. Large-sized rare tree species contribute disproportionately to functional diversity in resource acquisition in African tropical forest. Ecol Evol. 9(8):4349–4361.

Laliberté E, Legendre P. 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology. 91(1):299–305.

Larsen DR, Speckman PL. 2004. Multivariate regression trees for analysis of abundance data. Biometrics. 60(2):543–549.

Lohbeck M, Poorter L, Lebrija-Trejos E, Martínez-Ramos M, Meave JA, Paz H, Pérez-García EA, Romero-Pérez IE, Tauro A, Bongers F. 2013. Successional changes in functional composition contrast for dry and wet tropical forest. Ecology 94(6):1211–1216.

Lohbeck M, Poorter L, Martínez-Ramos M, Bongers F. 2015. Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. Ecology 96(5):1242–1252.

Lohbeck M, Bongers F, Martinez-Ramos M, Poorter L. 2016. The importance of biodiversity and dominance for multiple ecosystem functions in a human-modified tropical landscape. Ecology. 97(10):2772–2779.

Magurran AE. 2004. Measuring biological diversity. 1st ed. Oxford: Blackwell Science.

Matos FAR, Magnago LFS, Aquila Chan Miranda C, de Menezes LFT, Gastauer M, Safar NVH, Schaefer CEGR, da Silva MP, Simonelli M, Edwards FA, et al. 2020. Secondary forest fragments offer important carbon and biodiversity cobenefits. Glob Chang Biol. 26(2):509–522.

Mattsson E, Ostwald M, Wallin G, Nissanka SP. 2016. Heterogeneity and assessment uncertainties in forest characteristics and biomass carbon stocks: important considerations for climate mitigation policies. Land Use Policy. 59:84–94.

Morera-Beita A, Sánchez D, Wanek W, Hofhansl F, Werner H, Chacón-Madrigal E, Montero-Muñoz JL, Silla F. 2019. Beta diversity and oligarchic dominance in the tropical forests of Southern Costa Rica. Biotropica. 51(2):117–128.

Morlon H, White EP, Etienne RS, Green JL, Ostling A, Alonso D, Enquist BJ, He F, Hurlbert A, Magurran AE, et al. 2009. Taking species abundance distributions beyond individuals. Ecol Lett. 12(6):488–501.

Nychka D, Furrer R, Paige J, Sain S. 2017. "fields: Tools for spatial data." R package version 12.3. https://github.com/NCAR/Fields.

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, et al. 2018. 'Vegan': Community Ecology Package. R package version 2.4-6. [accessed 2020 June 8]; https://cran.r-project.org/web/packages/vegan/vegan.pdf.

Pebesma EJ. 2004. Multivariable geostatistics in S: The gstat package. Comput Geosci. 30(7):683–691.

Phillips OL, Sullivan MJP, Baker TR, Monteagudo Mendoza A, Vargas PN, Vásquez R. 2019. Species matter: wood density influences tropical forest biomass at multiple scales. Surv Geophys. 40(4):913–935.

Poorter L, Rozendaal DMA, Bongers F, de Almeida-Cortez JS, Almeyda Zambrano AM, Álvarez FS, Andrade JL, Villa LFA, Balvanera P, Becknell JM, et al. 2019. Wet and dry tropical forests show opposite successional pathways in wood density but converge over time. Nat Ecol Evol. 3(6):928–934.

Poulsen JR, Medjibe VP, White LJT, Miao Z, Banak-Ngok L, Beirne C, Clark CJ, Cuni-Sanchez A, Disney M, Doucet J-L, et al. 2020. Old growth Afrotropical forests critical for maintaining forest carbon. Global Ecol Biogeogr. 29(10):1785–1798.

Prado-Junior JA, Schiavini I, Vale VS, Arantes CS, van der Sande MT, Lohbeck M, Poorter L. 2016. Conservative species drive biomass productivity in tropical dry forests. J Ecol. 104(3):817–827.

R Core Team. 2019. R version 3.6.0. Vienna, Austria: R Foundation for Statistical Computing.

Réjou-Méchain M, Tanguy A, Piponiot C, Chave J, Hérault B. 2017. Biomass: an R package for estimating above-ground biomass and its uncertainty in tropical forests. Methods Ecol Evol. 8(9):1163–1167.

Rodrigues AC, Villa PM, Ali A, Ferreira-Júnior W, Neri AN. 2020. Fine-scale habitat differentiation shapes the composition, structure and aboveground biomass but not species richness of a tropical Atlantic Forest. J For Res. 31(5):1599–1611.

Rodrigues AC, Villa PM, Neri AN. 2019. Fine-scale topography shape richness, community composition, stem and biomass hyperdominant species in Brazilian Atlantic Forest. Ecol Indic. 102:208–217.

Scarano FR, Ceotto P. 2015. Brazilian Atlantic Forest: impact, vulnerability, and adaptation to climate change. Biodivers Conserv. 24(9):2319–2331.

Terra MCNS, Santos RMS, Fontes MAL, Mello JM, Scolforo JRS, Gomide LR, P, Júnior JA, Schiavini I, ter Steege H. 2017. Tree dominance and diversity in Minas Gerais. Biodivers Conserv. 26(9):2133–2153.

Therneau T, Atkinson B, Ripley B. 2017. 'rpart': Recursive partitioning and regression trees. R package version 4.1-11. [accessed 2020 June 8]; https://CRAN.R-project.org/package=rpart.

Universidade Federal de Viçosa – UFV. 2020. Departamento de Engenharia Agrícola. Estação Climatológica Principal de Viçosa. Boletim meteorológico. 2020. Viçosa: UFV.

van der Sande MT, Arets EJMM, Peña-Claros M, de Avila AL, Roopsind A, Mazzei L, Ascarrunz N, Finegan B, Alarcón A, Cáceres-Siani Y, et al. 2016. Old-growth Neotropical forests are shifting in species and trait composition. Ecol Monogr. 86(2):228–243.

van der Sande MT, Arets EJMM, Peña-Claros M, Hoosbeek MR, Cáceres-Siani Y, van der Hout P, Poorter L. 2017. Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest. Funct Ecol. 32(2):461–474.

van der Sande MT, Peña-Claros M, Ascarrunz N, Arets EJMM, Licona JuanCarlos, Toledo M, Poorter L. 2017. Abiotic and biotic drivers of biomass change in a Neotropical forest. J Ecol. 105(5):1223–1234.

Villa PM, Martins SM, Rodrigues AC, Safar NVH, Bonilla MAC, Ali A. 2019. Testing species abundance distribution models in tropical forest successions: implications for fine-scale passive restoration. Ecol Eng. 135:28–35.

Villa PM, Ali A, Martins SV, Oliveira SN, Rodrigues AC, Teshome M, Carvalho FA, Heringer G, Gastauer M. 2020. Stand structural attributes and functional trait composition overrule the effects of functional divergence on aboveground biomass during Amazon forest succession. For Ecol Manag. 477:118481.

Villa PM, Martins SV, Oliveira SN, Rodrigues AC, Hernández EP, Kim D-G. 2020. Policy forum: Shifting cultivation and agroforestry in the Amazon: premises for REDD+. For Policy Econ. 118:102217.

Violle C, Navas ML, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! Oikos. 116(5):882–892.

Wang Q, Punchi-Manage R, Lu Z, Franklin SB, Wang Z, Li Y, Chi X, Bao D, Guo Y, Lu J, et al. 2016. Effects of topography on structuring species assemblages in a subtropical forest. J Plant Ecol. 10(3):440–449.

Yuan Z, Ali A, Jucker T, Ruiz-Benito P, Wang S, Jiang L, Wang X, Lin F, Ye J, Hao Z, et al. 2019. Multiple abiotic and biotic pathways shape biomass demographic processes in temperate forests. Ecology 100(5):e02650.