Climate and large-sized trees, but not diversity, drive above-ground biomass in subtropical forests

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ABSTRACT

Subtropical forests certainly contribute to terrestrial global carbon storage, but we have limited understanding about the relative amounts and of the drivers of above-ground biomass (AGB) variation in their region. Here we assess the spatial distribution and drivers of AGB in 119 sites across the South American subtropical forests. We applied a structural equation modelling approach to test the causal relationships between AGB and environmental (climate and soil), structural (proportion of large-sized trees) and community (functional and species diversity and composition) variables. The AGB on subtropical forests is on average 246 Mg ha^{-1}. Biomass stocks were driven directly by temperature annual range and the proportion of large-sized trees, whilst soil texture, community mean leaf nitrogen content and functional diversity had no predictive power. Temperature annual range had a negative effect on AGB, indicating that communities under strong thermal amplitude across the year tend to accumulate less AGB. The positive effect of large-sized trees indicates that mature forests are playing a key role in the long-term persistence of carbon storage, as these large trees account for 64% of total biomass stored in these forests. Our study reinforces the importance of structurally complex subtropical forest remnants for maximising carbon storage, especially facing future climatic changes predicted for the region.

1. Introduction

Forests are an essential component of the global carbon cycle, being responsible for storing a substantial amount of carbon as living above-ground biomass (hereafter, AGB) (Fahey et al., 2010; Pan et al., 2013). However, carbon storage capacity varies greatly across forests. Tropical forests are able to stock ca. 56% of global plant biomass (Pan et al., 2011; Sullivan et al., 2020), two times more than temperate forests (Fotis et al., 2017). In order to predict the future of the global carbon stocks, we need to understand the drivers behind this variation in AGB. Forest biomass is expected to be affected direct and indirectly by climatic conditions and soil, through effects of forest structure, and species composition and traits (Fig. 1; Poorter et al., 2017, 2015). Ground-based studies on forest structure are still limited for particular ecosystems,
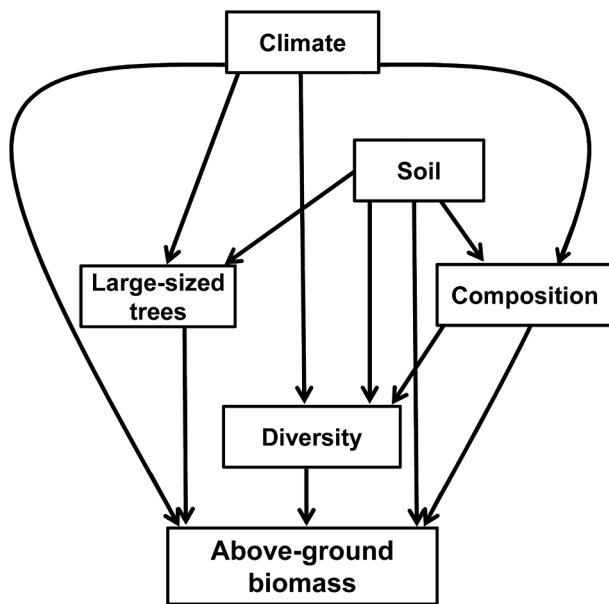
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Fig. 1. Conceptual framework showing the expected relationships of distinct sets of factors – climate, soil, large-sized trees, diversity, and composition – on above-ground biomass. Climate is represented by temperature and rainfall variables. Soil is represented by fertility and texture variables. Large-sized trees represent a proportion of large trees in the forest communities. Diversity is represented by both species and functional diversity. Composition is represented by tree species and functional composition.

hampering our understanding of the distribution and mechanism behind the variation in AGB. This is the case for subtropical forests, one of the most threatened ecosystems in the world (FAO and UNEP, 2020), found in China and the Neotropics. AGB in these forests have been assessed only by a few studies (Ali and Yan, 2017a; Li et al., 2018), and never in South America.

Climate effects on AGB are largely observed across many forest ecosystems (Sullivan et al., 2020; Vilanova et al., 2018). Within tropical forests temperature seems to be negative related to AGB (Ali et al., 2019a), due to the negative effects of high temperatures on plant metabolism, by increasing respiration rates (Álvarez-Dávila et al., 2017; Sullivan et al., 2020). Thus, it may represent a stressful condition, especially when accounting for the minimum temperatures or higher temperature annual ranges. In addition to temperature, water availability is also an important driver of AGB, which tends to peak under intermediate rainfall conditions, as a combination of the absence of extreme droughts, and low levels of light limitation due to cloud cover under high rainfall conditions (Poorter et al., 2015; Vilanova et al., 2018).

Soil texture and fertility are the main edaphic factors for limiting AGB and forest dynamics in the tropics, especially due to the importance of soil texture for water retention, and fertility due to soil phosphorous content (Quesada et al., 2012; van der Sande et al., 2017b). Soil fertility was found to be negatively related to AGB in Asian subtropical forests, acting as an environmental filter for nutrient-poor tolerant species (Ali and Yan, 2017a), and modulating the structure and dynamics in South American subtropical forests (Bordin and Müller, 2019). Soil texture is strongly related to water holding capacity, which is greater in clay-rich soils (Quesada et al., 2012), also playing a key role in maintaining ecosystem processes and AGB stocks (Castilho et al., 2006).

Variation in climatic and edaphic conditions are also expected to affect the tree sizes in forest ecosystems (Slik et al., 2013). For instance, large-sized trees are more often exposed to higher solar radiation (Pinho et al., 2020), and are sensitive to water deficit (Bennett et al., 2015). Large trees are an important driver of forest structure (Bastin et al., 2018, 2015; Lutz et al., 2018; Slik et al., 2013), and account for the

largest amount of AGB in forest communities, potentially overruling the effect of remaining trees (Ali et al., 2019b). Large-diameter trees are often related to old-growth forests, as they take a longer time to grow and develop (Lindenmayer et al., 2012). Therefore, mature forests have an essential function in maintaining carbon stocks due to the higher proportion of large-sized trees.

Climatic and edaphic conditions may also have indirect effects on AGB by acting as environmental filters for community structuring (Ali et al., 2019c; Quesada et al., 2012; Rezende et al., 2015; Slik et al., 2010), and by imposing physiological limitations to the distribution of species (Esquivel-Muelbert et al., 2017; Marcilio-Silva et al., 2017; Peña-Claros et al., 2012). These limitations are then translated in variations in species composition and their functional trait values across climatic gradients (Asefa et al., 2017; Bruelheide et al., 2018). Functional traits are morpho-physio-phenological features of plants that affect their fitness (Violle et al., 2007). The dominant trait value within an ecological community is expected to be related to the environmental conditions experienced by that community, varying along the acquisitive-conservative spectrum of strategies (Garnier et al., 2004; Lavorel and Garnier, 2002). An acquisitive strategy is frequently represented by investments on leaf traits to improve light assimilation, via higher mean values of specific leaf area (SLA) or leaf nitrogen content (LNC) (Wright et al., 2004), while a conservative strategy is often represented by greater investments in structures, via higher values of leaf dry-matter content (LDMC) and wood density (WD) (Chave et al., 2009; Wright et al., 2004). Following the mass-ratio hypothesis (Garnier et al., 2004; Grime, 1977), the functional composition of the dominant species often influence AGB by improving in resources acquisition in tropical rain forests (van der Sande et al., 2017a), or resources conservation in drier forests (Prado-Junior et al., 2016). However, subtropical forests have a mixture of distinct elements of tree species (e.g. seasonal and evergreen, tropical and austral origins), which often co-dominate the ecological communities, thus the effect of functional composition on biomass is still poorly understood (Ali and Yan, 2017b; Souza and Longhi, 2019).

Diversity of species and functional traits are also expected to have a positive effect on AGB (Cardinale et al., 2007; Poorter et al., 2017, 2015). Diversity is thought to affect biomass stocks as a consequence of niche complementarity, where a greater number of species allow for greater partitioning in resources use among coexisting species (Diaz and Cabido, 2001). However, the relationship between diversity and carbon stocks has not been observed across large spatial scales (Chisholm et al., 2013; Finegan et al., 2015; Sullivan et al., 2017). Moreover, species and functional diversity are related to community species composition, thus increasing complexity in relationships between diversity and biomass across spatial and temporal scales. For instance, forests with the high dominance of one or a few species may have greater AGB despite lower observed niche complementarity (Marimon et al., 2014).

In the Neotropical region in particular, we have a limited understanding of what drives the biomass variation at higher latitudes (Alves et al., 2010; Poorter et al., 2017; Rosenfield and Souza, 2013; Vieira et al., 2011). The South American subtropical forests correspond to the second largest remnant of this forest type (FAO, 2012). These subtropical forests differ from tropical forests in terms of climatic seasonality, which is characterised by great temperature variations across the year with hot summer and cold winters (Rosenfield et al., 2019), while precipitation is well distributed across the year without the presence of marked dry period (Oliveira-Filho et al., 2014). This region experiences high biotic and abiotic heterogeneity, due to high environmental variation and diverse floristic origins that influence plant strategies (Rezende et al., 2015), even along short distances (Rosenfield et al., 2019). Therefore, we expect AGB within these forests to be driven by a different set of drivers when compared to those controlling the variation of AGB at lower latitudes, with temperature playing a greater role than precipitation. The lack of understanding of the ecological patterns within these unique highly diverse forests makes studying subtropical

forests crucial for understanding the role of this climate in determining AGB.

In this study, we determined the above-ground biomass stocks of subtropical forests in Southern Brazil. We further tested the predictive power of climatic variables, edaphic conditions, large-sized trees, composition, and diversity in driving AGB in subtropical forests. To evaluate the drivers of biomass stocks we used a conceptual model (Fig. 1), and tested whether (1) climatic conditions are able to predict - directly or indirectly - AGB; (2) edaphic factors are determining AGB in terms of texture or fertility, directly limiting the biomass or filtering out species or traits which in turn affect AGB; (3) large-sized trees determine biomass stocks; (4) community composition and diversity, in terms of species and functional traits, affect AGB in subtropical forests.

2. Material and methods

2.1. Study area

We investigated trends in above-ground biomass by analysing forest inventories in subtropical forests in Southern Brazil. Our database comprehends 119 sites with different sampling efforts (mean sampled area: 0.25 ha; see Appendix A for details), established in old-growth forests, with some minor level of past human disturbances, such as cattle grazing and potential selective logging (but not clear cutting; Fig. 2). The sites cover different forest types across the subtropical forests in the southern portion of Brazilian Atlantic Forest and Pampean forests (Holdridge, 1947; Oliveira-Filho et al., 2014), including the Araucaria forests (mixed forests with large dominance of the Gymnosperm *Araucaria angustifolia*), Seasonal forests and Atlantic moist forests (see Fig. 2; Appendix B). The Pampean forests are located in a grassland

matrix (often called Pampa biome), with forested areas along riverine and hillslope areas. For our study, we selected just forest plots along hillslope areas, which have similar species composition to Seasonal forests (Oliveira-Filho et al., 2014). All sites are distributed along a climatic and edaphic gradient (Appendix C).

2.2. Forest inventory data and AGB estimations

In each of our sampling sites, all alive trees with 10 cm of diameter at breast height (dbh) or greater had their diameter measured and their height estimated by eye, or laser tap. All trees were identified to the species level.

To estimate AGB we used the pantropical allometric equation proposed by Chave et al. (2014) (Eq. (1)):

$$AGB = 0.0673(WDdbh^2H)^{0.976} \tag{1}$$

where H represents tree height (m), and WD represents the wood density of the species (g cm^{-3}). Wood density information was obtained from regional (Missio et al., 2017; Oliveira et al., 2019) and global databases (Chave et al., 2009; Zanne et al., 2009). Total AGB per hectare was calculated as the sum of the above-ground biomass of all trees in each site and dividing by the area of the site in hectares (AGB, Mg ha^{-1}). In order to obtain an accurate measure per site, we used the average AGB across multiple censuses whenever possible (see Appendix A). Biomass was estimated by using the 'computeAGB' function, package *BIOMASS* (Réjou-Méchain et al., 2017).

Analysis related to above-ground biomass in inventory plots with different sample sizes, especially smaller plots, may present a large variation to the overall biomass estimates. We tested the need for
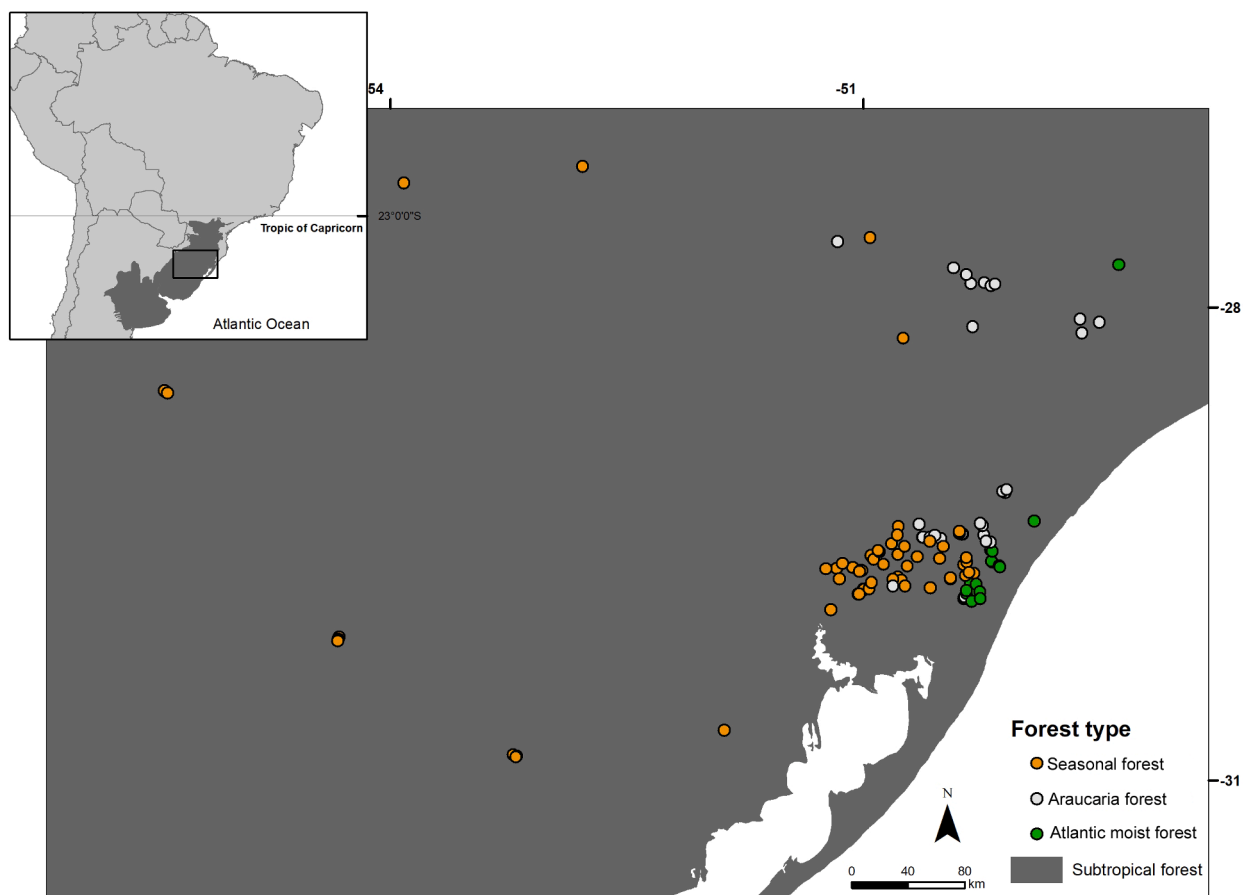

Fig. 2. Distribution of South American subtropical forests, with the location of the 119 study sites. The forest types (i.e. Atlantic moist forest, Araucaria and Seasonal forests) are also shown as the color of points.

corrections and further implementation of weights in our analysis following the protocol from Lewis et al. (2009). This analysis showed the need to account for the plot area in our analyses by including the cubic root of the sampling area as weights in our models (Appendix A).

2.3. Climatic and edaphic variables

All climatic variables were obtained at the WorldClim database (grid cells of 30′, i.e. 1 km resolution) (Fick and Hijmans, 2017). The climatic variables selected for predictive analysis were the minimum temperature of the coldest month (°C), temperature annual range (°C) and mean annual precipitation (mm). We selected these variables based on Rezende et al. (2015), which describes the strong climatic filter in subtropical forests, mainly related to high humidity and low winter temperatures. Across our study sites, the mean annual precipitation varies from 1704 to 2206 mm yr^{-1}, the minimum temperature of the coldest month varies between 6 and 9.4 °C, the mean annual temperature varies from 11 to 20 °C, and the temperature annual range varies between 16.3 and 23.2 °C.

Information on edaphic conditions were based on clay content (%) and cation exchange capacity (CEC, cmolc/kg, both at 15 cm depth), which were available at the global soil database SoilGrids (grid cells of 1 km resolution) (Hengl et al., 2017). Soil clay content characterises the soil texture, and CEC is a proxy for soil fertility, as it provides information on available ions for plant use. The study sites show soil CEC ranging from 16 to 24 cmol kg^{-1}, while soil clay content ranged from 33 to 44%.

2.4. Functional traits

Functional traits were collected and measured following standardized protocols (Pérez-Harguindeguy et al., 2013). The traits measured in our study were specific leaf area (SLA, cm^2 g^{-1}), leaf dry-matter content (LDMC, mg g^{-1}), leaf nitrogen content (LNC, %), and wood density (WD, g cm^{-3}). Both high values of SLA and LNC are related to species that invest in resources acquisition, while higher values of LDMC and WD are related to species that invest in resources conservation (see Appendix D for details). We used species leaf trait values for 90% of species; when species value was unavailable, we used genus or family means. Species trait values are derived from regional collections, from the database of Plant Ecology Lab of the Federal University of Rio Grande do Sul (also available at TRY database; Kattge et al., 2020) and from specialized databases (Chave et al., 2009; Missio et al., 2017; Oliveira et al., 2019).

2.5. Diversity and composition metrics

We used metrics associated with species and functional traits described above. We described taxonomic richness using rarefied species richness, to control for the different number of stems found in our sites. Thirty-nine individuals was our reference for the rarefied richness, as it was the minimum number of individuals found amongst our plots. For each site, we determined the number of tree species in the stand and based on the number of individuals we calculated the Simpson's species diversity index. The species composition was represented by the first axis of an ordination analysis, obtained through a non-metric multidimensional scaling (NMDS) on a species basal area matrix, after Hellinger transformation (Appendix E). These analyses were performed using the functions 'rarefy', 'diversity' and 'metaMDS', package *vegan* (Oksanen et al., 2019).

Functional diversity was obtained using Rao's quadratic entropy (Botta-Dukát, 2005) considering the Euclidean distance among species using the four traits (SLA, LDMC, LNC, and WD). Functional composition was estimated using community-weighted mean (CWM, Garnier et al. (2004)) for each trait. Both CWM and functional diversity were calculated using the community matrix described by species basal area. We calculated both metrics using 'dbFD' function, *FD* package (Laliberté

et al., 2015).

2.6. Large-sized trees

Our conceptual model included the proportion of large-sized trees as a driver of above-ground biomass in subtropical forests. Within each plot, medium-large diameter trees (trees ≥30 cm dbh) were selected and turned into a proportion, representing the state of each site in terms of the large-sized trees.

2.7. Data analysis

We developed structural equation models (SEMs) to evaluate the multiple relationships of biotic and abiotic factors and above-ground biomass, based on the conceptual framework presented in Fig. 1. This approach allows us to estimate direct and indirect correlations among variables, and also to select the best statistically accepted model (Shipley, 2016). We evaluated the direct and indirect effects of climatic and edaphic variables and the direct effect of large-sized trees, composition, and diversity on AGB. Indirect effects were quantified through the interaction between the direct effect of a given predictor (e.g., climatic variable) on a mediator (e.g., diversity metric), and the direct effect of a given mediator on above-ground biomass (Fig. 1).

Prior to applying the SEM, we used multiple regression analyses followed by model selection, to pre-select the best subset of variables from the diversity and composition components. The model selection was performed using the 'dredge' function (*MuMIn* package, Bartón (2012)), and all subset models with the Akaike Information Criterion (AIC) ≤ 2 were selected (Burnham and Anderson, 2002). When models were equally supported, we selected the model with the higher AIC weight (see Appendix F for model selection results). We also evaluated the presence of spatial autocorrelation on AGB, by using generalized least-squares models (Beale et al., 2010), applying the maximum likelihood fitting method ('gls' function, *nlme* package (Pinheiro et al., 2020). We fitted models (AGB ~ predictor variables) among sites with and without spherical autocorrelation structure (i.e. local X and Y coordinate), and selected the model with the lowest AIC (Ali and Yan, 2017a; Chisholm et al., 2013). This diagnosis showed no significant spatial structure on AGB; therefore, this was not included in the SEM analyses (Appendix F).

After the composition and diversity variable selection previously described, we tested between 18 candidate SEM models considering climatic variables (minimum temperature of the coldest month, temperature annual range or mean annual precipitation), soil variables (fertility: CEC or texture: clay content), large-sized trees, functional diversity, and CWM of traits (SLA, LNC and LDMC). As we were interested in characterising the general patterns across the region, we controlled for the effect of the different forest types (i.e., Atlantic moist forest, Seasonal, or Araucaria forest), by including it as random effect (Appendix G). The candidate SEMs were developed using the 'psem' function from the *piecewiseSEM* package (Liefecheck, 2015), which allows for evaluation of both fixed and random factors on the response variable. In order to access the potential differences in biomass stocks among forest types in subtropical forests (i.e. Atlantic moist forest, Araucaria and Seasonal forests), we fitted an Analysis of Variance (ANOVA), using 'aov' function.

For each endogenous variable in SEM, we evaluated the R^2 marginal (R^2m, related to fixed effect variance), and R^2 conditional (R^2c; related to both fixed and random effect variance). All variables were standardized to mean zero and unit variance to allow direct comparisons ('decostand' function, *vegan* package). All well-fitted SEM models ($P \geq 0.05$) were subjected to a model selection following the lowest AIC value. All analyses were conducted at R environment for statistical computing (R Core Team, 2020).

3. Results

The above-ground biomass stocks across the subtropical forests evaluated in this study were on average 246.5 Mg ha^{-1} ($\pm$sd 105.1 Mg ha^{-1}; weighted mean AGB: 231.6 Mg ha^{-1}), ranging from 80.9 Mg ha^{-1} to 539.5 Mg ha^{-1}. When analysing by forest types, we found no difference between the AGB stocks (Fig. 3).

The best SEM to understand the drivers of biomass stocks across subtropical forests includes temperature annual range, soil texture, large-sized trees, functional diversity, and CWM of leaf nitrogen content (LNC) (Fig. 4). Large-sized trees and temperature annual range are the two most important variables explaining AGB (significant correlations of 0.62 and −0.28, respectively; Fig. 4, Fig. 5d and e). On the other hand, soil texture, LNC and functional diversity have no effect in AGB (Fig. 4). However, functional diversity is positively predicted by temperature annual range, leaf nitrogen content and soil texture (indirectly, via LNC; Fig. 5a, b, and c, see Appendix H for details). All the relationships established according to SEM are shown in Fig. 4, and the corresponding explained variance is presented in Table 1. The random effect, expressed through R^{2}c indicates the potential influence spread throughout the forest types, by controlling the relationship among the predictor variables, but not overall AGB.

4. Discussion

The South American subtropical forests have the capacity of storing a great amount of biomass, equivalent to tropical forests, but here the climatic drivers of AGB stocks differ from those observed in lower latitudes. Above-ground biomass was strongly explained by the proportion of large-sized trees ($\geq$30 cm dbh) in forest communities, and temperature annual range. The importance of such forest structural feature on biomass stocks reinforces the needs for protection of the old-growth remnants across these endangered subtropical forests.

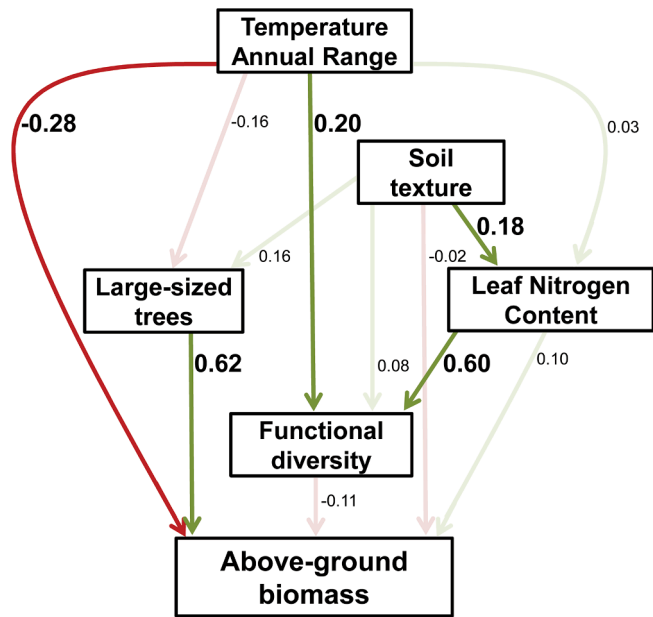### 4.1. Above-ground biomass stocks in subtropical forests

Our results support the great capacity of subtropical forests in storing biomass. The AGB stocked in South American subtropical forests here studied is within the range of tropical dry forests in Brazil (Prado-Junior et al., 2016), higher than temperate forests (Fotis et al., 2017), but lower than tropical Amazon forest and pan-tropical estimations (Castilho et al., 2006; Sullivan et al., 2020). We highlight that South American subtropical forests store twice as much AGB than Asian subtropical forests (Zhang et al., 2019).

Field estimations shown here are a valuable contribution to our understanding of global estimates of biomass stocks. Avitabile et al. (2016), in a great effort for providing global estimations of above-ground biomass, developed a pan-tropical biomass map combining two locally calibrated and high-resolution biomass maps. However, no field-based AGB information was used for the estimations in this region. It led to an underestimation of AGB stocks in these forests (about half of the mean AGB estimated for the same areas in this study, i.e. 140 Mg ha^{-1}). Our findings should be used to improve future global biomass estimates, providing a broader cover of distribution of AGB in subtropical forests.

The mean AGB stored in these forests does not vary across forest types (i.e. Atlantic moist forest, Araucaria and Seasonal forests), indicating the major influence of large-sized trees and temperature annual
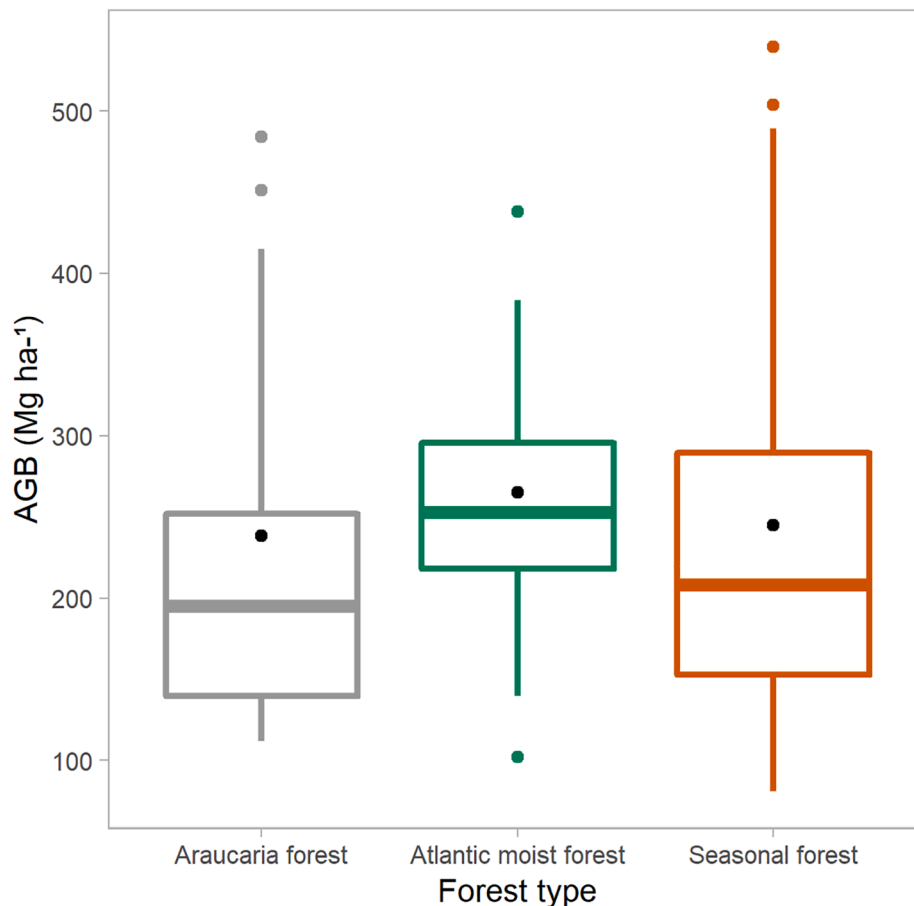
Fig 3. Above-ground biomass (AGB) among forest types across South American subtropical forests (i.e. Atlantic moist forest, Araucaria forest, and Seasonal forest). Boxplots show the AGB variation, and the black points inside the boxplots show the weighted mean values of AGB per forest type.

Fig 4. Structural equation model explaining the above-ground biomass across South American subtropical forests. Here we show effects of temperature annual range, soil texture, large-sized trees, functional composition (CWM of leaf nitrogen content), and functional diversity on AGB of subtropical forests. Standardized coefficients with significant levels are represented by green or red colours (positive and negative effect, respectively), non-significant relationships are expressed by light green or red colours, and no arrows mean that the relationship was not included in the model. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

range over the geographical gradient marked by significant differences in floristic, structure, and plant strategies between these forest types (Oliveira-Filho et al., 2014; Rosenfield et al., 2019). Moreover, as the Brazilian Atlantic Forest experienced historical devastation (Ribeiro et al., 2009), related to deforestation for timber products, crop plantations and pastures (Fonseca, 1985), and also selective logging, the structure and AGB stocks of current remnants are potentially distinct from former pristine forests. Nevertheless, the key role of these forests in maintaining carbon stocks, by preventing emissions derived from deforestation and forest degradation, reinforces the priority for habitat protection and sustainable management of the complex and heterogeneous subtropical forests (Bergamin et al., 2017).

4.2. Temperature annual range and large-sized trees drive AGB variation

Temperature annual range is an important variable associated to biomass stocks in subtropical climatic conditions, as shown for AGB in our results. Temperature is frequently associated with plant metabolism, which is related to growth and respiration rates, further affecting forest productivity and carbon storage (Ballantyne et al., 2017; Vilanova et al., 2018). Recent reports have indicated the thermal sensitivity of tropical forests, which is closely related to higher maximum temperatures, which affects the potential carbon stocks of these forests (Sullivan et al., 2020). The negative effect of temperature annual range on above-ground

Table 1
Variance explained by fixed (R^2m) and fixed + random (R^2c) effects of relationships established in the structural equation model presented in Fig. 1.

Response variable	R^2m	R^2c
Large-sized trees	0.05	0.07
Functional diversity	0.27	0.29
Leaf nitrogen content	0.01	0.34
Above-ground biomass	0.36	0.36
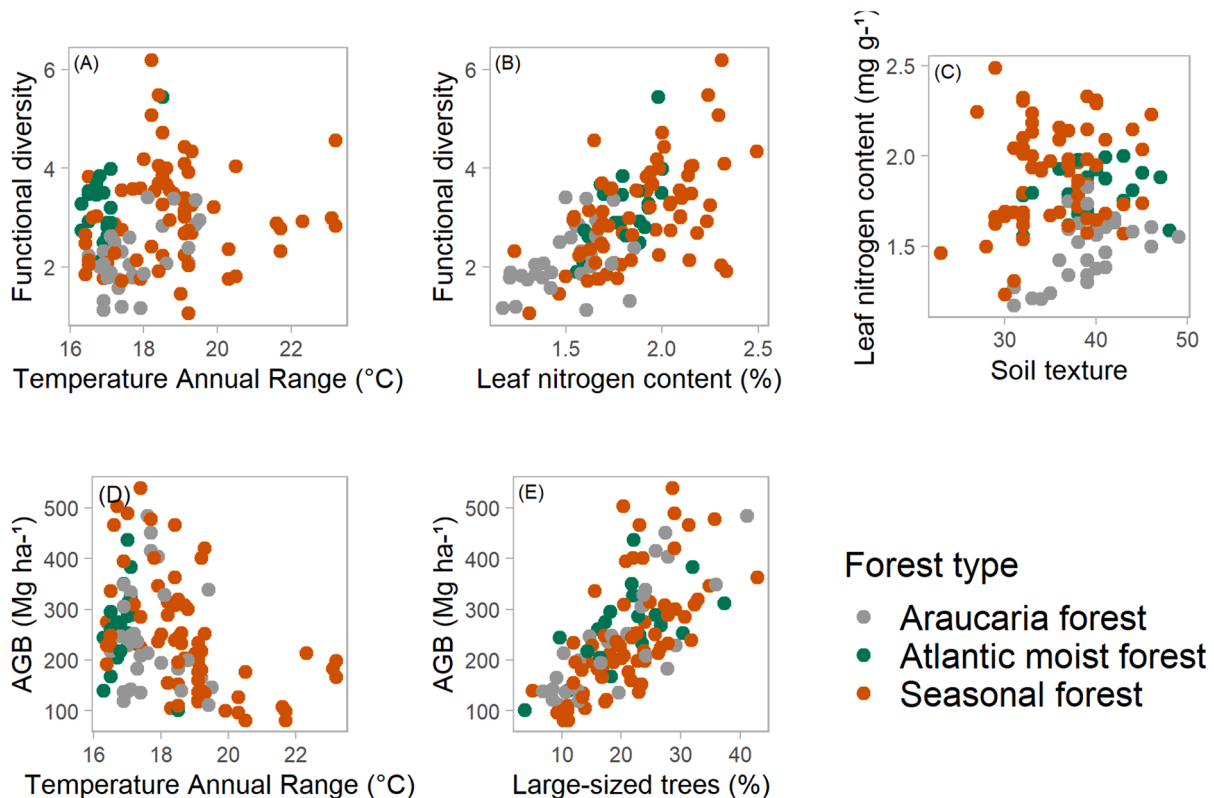
Fig 5. Significant bivariate relationships for hypothesized causal paths used in the structural equation model shown in Fig. 4.

biomass observed in the present study may be related to a stressful environmental condition for trees, associated with the great thermal amplitude along the year (Oliveira-Filho et al., 2014; Oliveira-Filho and Fontes, 2000). For instance, these tree species must invest more resources to tolerate the environmental change instead of biomass storage. This is likely to be related to Seasonal forest's species, which are subjected to a deciduous condition during the winter time and to high transpiration rates during hot summers, leading to a higher investment in leaves and metabolism maintenance than AGB. Additionally, Araucaria forests are under the influence of cold winters with frequent frost and cloud conditions, which limit productivity through photosynthesis constrains, contrasting with hot summer periods.

We show that large-size trees are an important predictor of AGB, as expected. Similarly to our results, large-sized trees are related to higher AGB stocks in tropical forests (Poorter et al., 2015; Slik et al., 2013), reflecting their capacity for storing great amounts of biomass per stem. Also, large trees account for 64% of the AGB in these forests, about 158 Mg ha^{-1} on average (see Appendix I), reinforcing their importance for the global carbon cycle. This result further reflects the importance of the conservation of large-diameter trees, and the maintenance and conservation of old-growth forests (Lutz et al., 2018). Large trees also play a key role in creating habitat conditions for epiphytic flora, contributing for litter production, nesting sites, and microclimatic environments for arthropod species (Lindenmayer et al., 2012; Lohbeck et al., 2015). Therefore, conserving old-growth forests not only guarantees greater carbon stocks (due to large-sized trees protection), but also promotes the conservation of biodiversity at the most diverse trophic levels.

Large trees are often more susceptible to atmospheric drought (Ali et al., 2019b), due to higher evaporative demands (Bennett et al., 2015), especially in higher temperatures. Such relationship of large trees and temperature annual range shed light on the importance of climatic variables in subtropical forests structure (Ali et al., 2019c), and on biomass storage, as evidenced here. On the other hand, potential extreme climatic events derived from future climate changes in this subtropical region, such as increasing in temperature, precipitation and extreme events, may have a strong negative impact on the forest biomass stocks and accumulation capacity (Baker et al., 2004; Souza and Longhi, 2019). These changes in climate may lead to higher tree mortality rates, and the further consequences in forest dynamics are related to faster carbon sequestration of young trees, but an overall lower carbon storage due to the increase in mortality rates in extreme events (Aleixo et al., 2019; Brienen et al., 2015).

4.3. Soil, diversity, and composition do not predict AGB in subtropical forests

We did not find a relationship between soil texture and AGB for the set of studied subtropical forests, but soil texture is positively related to AGB in tropical forests (Castilho et al., 2006). As our result is associated with clay content, it may indicate that AGB is not constrained by soil moisture in subtropical forests. Nevertheless, temperature annual range and soil texture (indirectly via LNC), positively affects functional diversity of these forest communities. This result indicates that environmental conditions imposed by higher temperature variability and potential soil water availability on species traits shape the diversity of traits in these forest communities (Bruelheide et al., 2018). Such conditions may maximise trait values for resources acquisition strategies in this condition (e.g. more photosynthetically efficient leaves, as there was a positive relationship between LNC and diversity). Regardless of the influence of soil, climate and LNC on functional diversity, diversity itself did not explain the AGB in subtropical forests, as previously reported for tropical forests (Finegan et al., 2015; Sullivan et al., 2017). This might be related to a potential saturation of niche complementarity effects in old-growth forests (Lasky et al., 2014).

Despite of the absence of relationship among functional traits and AGB, these variables are often good predictors of forest dynamics and

AGB stocks (Finegan et al., 2015; Prado-Junior et al., 2016). For instance, higher mean LNC values in communities is potentially related to investments in resources acquisition, which may in turn lead to higher AGB along the time (Wright et al., 2004). Also, wood density is an important component to account for forest AGB (Baker et al., 2004). Surprisingly, we found that WD had no influence on the spatial variation of AGB across subtropical forests. This might be explained by the negative relationship between large-sized trees and community mean wood density (Appendix S9), with sites that had a greatest proportion of large trees also having lower community means of WD. For instance, these trees may be old and senescent trees, being remaining in old-growth forests. However, these large trees might be replaced along local forest dynamics (e.g. gap dynamics), as higher mortality rates are associated to big trees in subtropical forests (Bordin and Müller, 2019; Ma et al., 2016), influencing the biomass stocks in the long-term ecosystem functioning. Our data also show a negative relationship between mean individual basal area and stem density (Appendix I), suggesting that we have a range in the development characteristics of studied forest remnants, which can be related to the historical selective logging experienced by these forests in the past (Fonseca, 1985). Thus, some of these subtropical forests may have stocked more biomass in the past and, if competition processes are acting now on communities with high density of trees (i.e., self-thinning, see Pillet et al. (2018)), they have a greater potential for storing biomass in the future, when achieving a more mature state.

5. Conclusions

The South American subtropical forests have a great capacity to store AGB, which is strongly influenced by the climate and forest structure. The negative effect of temperature annual range shows that forest communities experiencing stable temperatures throughout the year contribute greatly to the AGB stocks in this region. Additionally, structurally complex forests with large-sized trees play a key role in the long-term persistence of carbon storage, and ecosystem processes maintenance. It reinforces the importance of preserving old-growth forests (Pyles et al., 2018), and of protecting regenerating secondary forests (Capellesso et al., 2020), by allowing them to achieve complex structures in order to maximize the carbon stocks in these forests, especially facing future climatic changes predicted for this region.

Quantifying the biomass stocks in subtropical forests is essential for understanding the potential of these forests to mitigate future carbon emissions. Future work based on long-term monitoring, should assess how these stocks vary over time. The maintenance of long-term plots is crucial for understanding forest dynamics and the potential carbon sink of these forest (Phillips et al., 1998), especially in the understudied subtropical forests (Bordin and Müller, 2019).

CRediT authorship contribution statement

Kauane Maiara Bordin: Conceptualization, Data curation, Methodology, Formal analysis, Funding acquisition, Writing - original draft. **Adriane Esquivel-Muelbert:** Conceptualization, Methodology, Supervision, Writing - original draft. **Rodrigo Scarton Bergamin:** Data curation, Writing - review & editing. **Joice Klipel:** Data curation, Writing - review & editing. **Rayana Caroline Picolotto:** Data curation, Writing - review & editing. **Marcelo Araújo Frangipani:** Data curation. **Katia Janaina Zanini:** Data curation. **Marcus Vinicius Cianciaruso:** Methodology, Funding acquisition, Writing - review & editing. **João André Jarenkow:** Data curation, Writing - review & editing. **Cristiane Follmann Jurinitz:** Data curation, Writing - review & editing. **Martin Molz:** Data curation, Writing - review & editing. **Pedro Higuchi:** Data curation, Writing - review & editing. **Ana Carolina Silva:** Data curation, Writing - review & editing. **Sandra Cristina Müller:** Conceptualization, Methodology, Supervision, Funding acquisition, Writing - original draft.

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.

Authors' contributions

KMB, AE-M and SCM conceived the ideas and designed methodology; KMB, RSB, JK, RCP, MAF, KJZ, JAJ, CFJ, MM, PH and ACS collected the data; KMB analysed the data; KMB led the writing of the manuscript with the contributions from AE-M and SCM, and RSB, JK, RCP, MVC, JAJ, CFJ, MM, PH and ACS contributed to the drafts.

Data availability

Part of the forest inventory data can be accessed through ForestPlots database (www.forestplots.net). Data for the analyses are available as a ForestPlots.net data package at http://doi.org/10.5521/Forestplots.net/2021_1.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119126.

References

Aleixo, I., Norris, D., Hemerik, L., Barbosa, A., Prata, E., Costa, F., Poorter, L., 2019. Amazonian rainforest tree mortality driven by climate and functional traits. Nat. Clim. Chang. 9, 384–388. https://doi.org/10.1038/s41558-019-0458-0.

Ali, A., Lin, S.L., He, J.K., Kong, F.M., Yu, J.H., Jiang, H.S., 2019a. Elucidating space, climate, edaphic, and biodiversity effects on aboveground biomass in tropical forests. L. Degrad. Dev. 30, 918–927. https://doi.org/10.1002/ldr.3278.

Ali, A., Lin, S.L., He, J.K., Kong, F.M., Yu, J.H., Jiang, H.S., 2019b. Big-sized trees overrule remaining trees' attributes and species richness as determinants of aboveground biomass in tropical forests. Glob. Chang. Biol. 25, 2810–2824. https://doi.org/10.1111/gcb.14707.

Ali, A., Lin, S.L., He, J.K., Kong, F.M., Yu, J.H., Jiang, H.S., 2019c. Climate and soils determine aboveground biomass indirectly via species diversity and stand structural complexity in tropical forests. For. Ecol. Manage. 432, 823–831. https://doi.org/10.1016/j.foreco.2018.10.024.

Ali, A., Yan, E.R., 2017a. Functional identity of overstorey tree height and understorey conservative traits drive aboveground biomass in a subtropical forest. Ecol. Indic. 83, 158–168. https://doi.org/10.1016/j.ecolind.2017.07.054.

Ali, A., Yan, E.R., 2017b. Relationships between biodiversity and carbon stocks in forest ecosystems: a systematic literature review. Trop. Ecol. 58, 1–14.

Álvarez-Dávila, E., Cayuela, L., González-Caro, S., Aldana, A.M., Stevenson, P.R., Phillips, O., Cogollo, Á., Peñuela, M.C., Von Hildebrand, P., Jiménez, E., Melo, O., Londoño-Vega, A.C., Mendoza, I., Velásquez, O., Fernández, F., Serna, M., Velázquez-Rua, C., Benítez, D., Rey-Benayas, J.M., 2017. Forest biomass density across large climate gradients in northern South America is related to water availability but not with temperature. PLoS One 12, 1–16. https://doi.org/10.1371/journal.pone.0171072.

Alves, L.F., Vieira, S.A., Scaranello, M.A., Camargo, P.B., Santos, F.A.M., Joly, C.A., Martinelli, L.A., 2010. Forest structure and live aboveground biomass variation along an elevational gradient of tropical Atlantic moist forest (Brazil). For. Ecol. Manage. 260, 679–691. https://doi.org/10.1016/j.foreco.2010.05.023.

Asefa, M., Cao, M., Zhang, G., Ci, X., Li, J., Yang, J., 2017. Environmental filtering structures tree functional traits combination and lineages across space in tropical tree assemblages. Sci. Rep. 7, 1–11. https://doi.org/10.1038/s41598-017-00166-z.

Avitabile, V., Herold, M., Heuvelink, G.B.M., Lewis, S.L., Phillips, O.L., Asner, G.P., Armston, J., Ashton, P.S., Banin, L., Bayol, N., Berry, N.J., Boeckx, P., de Jong, B.H. J., Devries, B., Girardin, C.A.J., Kearsley, E., Lindsell, J.A., Lopez-Gonzalez, G., Lucas, R., Malhi, Y., Morel, A., Mitchard, E.T.A., Nagy, L., Qie, L., Quinones, M.J., Ryan, C.M., Ferry, S.J.W., Sunderland, T., Laurin, G.V., Gatti, R.C., Valentini, R., Verbeeck, H., Wijaya, A., Willcock, S., 2016. An integrated pan-tropical biomass map using multiple reference datasets. Glob. Chang. Biol. 22, 1406–1420. https://doi.org/10.1111/gcb.13139.

Baker, T., Phillips, O.L., Malhi, Y., Almeida, S., Arroyo, L., Di Fiore, A., Erwin, T., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Pitman, N.C.A., Silva, J.N.M., Vásquez Martínez, R., 2004. Increasing biomass in Amazonian forest plots. Philos. Trans. R. Soc. B Biol. Sci. 359, 353–365. https://doi.org/10.1098/rstb.2003.1422.

Ballantyne, A., Smith, W., Anderegg, W., Kauppi, P., Sarmiento, J., Tans, P., Shevliakova, E., Pan, Y., Poulter, B., Anav, A., Friedlingstein, P., Houghton, R., Running, S., 2017. Accelerating net terrestrial carbon uptake during the warming hiatus due to reduced respiration. Nat. Clim. Chang. 7, 148–152. https://doi.org/10.1038/nclimate3204.

Bartón, K., 2012. MuMIn: multi-model inference.

Bastin, J., Barbier, N., Réjou-Méchain, M., Fayolle, A., Gourlet-Fleury, S., Maniatis, D., De Haulleville, T., Baya, F., Beeckman, H., Beina, D., Couteron, P., Chuyong, G., Dauby, G., Doucet, J.L., Droissart, V., Dufrène, M., Ewango, C., Gillet, J.F., Gonmadje, C.H., Hart, T., Kavali, T., Kenfack, D., Libalah, M., Malhi, Y., Makana, J. R., Pélissier, R., Ploton, P., Serckx, A., Sonké, B., Stevart, T., Thomas, D.W., De Cannière, C., Bogaert, J., 2015. Seeing Central African forests through their largest trees. Sci. Rep. 5, 1–8. https://doi.org/10.1038/srep13156.

Bastin, J., Rutishauser, E., Kellner, J.R., Saatchi, S., Pélissier, R., Hérault, B., Slik, F., Bogaert, J., De Cannière, C., Marshall, A.R., Poulsen, J., Alvarez-Loyayza, P., Andrade, A., Angbonga-Basia, A., Araujo-Murakami, A., Arroyo, L., Ayyappan, N., de Azevedo, C.P., Banki, O., Barbier, N., Barroso, J.G., Beeckman, H., Bitariho, R., Boeckx, P., Boehning-Gaese, K., Brandão, H., Brearley, F.Q., Breuer Ndoundou Hockemba, M., Brienen, R., Camargo, J.L.C., Campos-Arceiz, A., Cassart, B., Chave, J., Chazdon, R., Chuyong, G., Clark, D.B., Clark, C.J., Condit, R., Honorio Coronado, E.N., Davidar, P., de Haulleville, T., Descroix, L., Doucet, J.L., Dourdain, A., Droissart, V., Duncan, T., Silva Espejo, J., Espinosa, S., Farwig, N., Fayolle, A., Feldpausch, T.R., Ferraz, A., Fletcher, C., Gajapersad, K., Gillet, J.F., Amaral, I.L. do, Gonmadje, C., Grogan, J., Harris, D., Herzog, S.K., Homeier, J., Hubau, W., Hubbell, S.P., Hufkens, K., Hurtado, J., Kamdem, N.G., Kearsley, E., Kenfack, D., Kessler, M., Labrière, N., Laumonier, Y., Laurance, S., Laurance, W.F., Lewis, S.L., Libalah, M.B., Ligot, G., Lloyd, J., Lovejoy, T.E., Malhi, Y., Marimon, B.S., Marimon Junior, B.H., Martin, E.H., Matius, P., Meyer, V., Mendoza Bautista, C., Monteagudo-Mendoza, A., Mtui, A., Neill, D., Parada Gutierrez, G.A., Pardo, G., Parren, M., Parthasarathy, N., Phillips, O.L., Pitman, N.C.A., Ploton, P., Ponette, Q., Ramesh, B.R., Razafimahaimodison, J.C., Réjou-Méchain, M., Rolim, S.G., Romero-Saltos, H., Rossi, L.M.B., Spironello, W.R., Rovero, F., Saner, P., Sasaki, D., Schulze, M., Silveira, M., Singh, J., Sist, P., Sonke, B., Soto, J.D., de Souza, C.R., Stropp, J., Sullivan, M.J. P., Swanepoel, B., Steege, H. ter, Terborgh, J., Texier, N., Toma, T., Valencia, R., Valenzuela, L., Ferreira, L.V., Valverde, F.C., Van Andel, T.R., Vasque, R., Verbeeck, H., Vivek, P., Vleminckx, J., Vos, V.A., Wagner, F.H., Warsudi, P.P., Wortel, V., Zagt, R.J., Zebaze, D., 2018. Pan-tropical prediction of forest structure from the largest trees. Glob. Ecol. Biogeogr. 27, 1366–1383. https://doi.org/10.1111/geb.12803.

Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J., Elston, D.A., 2010. Regression analysis of spatial data. Ecol. Lett. 13, 246–264. https://doi.org/10.1111/j.1461-0248.2009.01422.x.

Bennett, A.C., McDowell, N.G., Allen, C.D., Anderson-Teixeira, K.J., 2015. Larger trees suffer most during drought in forests worldwide. Nat. Plants 1, 1–5. https://doi.org/10.1038/nplants.2015.139.

Bergamin, R.S., Bastazini, V.A.G., Vélez-Martin, E., Debastiani, V., Zanini, K.J., Loyola, R., Müller, S.C., 2017. Linking beta diversity patterns to protected areas: lessons from the Brazilian Atlantic Rainforest. Biodivers. Conserv. 26, 1557–1568. https://doi.org/10.1007/s10531-017-1315-y.

Bordin, K.M., Müller, S.C., 2019. Drivers of subtropical forest dynamics: the role of functional traits, forest structure and soil variables. J. Veg. Sci. 30, 1164–1174. https://doi.org/10.1111/jvs.12811.

Botta-Dukát, Z., 2005. Rao's quadratic entropy as a measure of functional diversity based on multiple traits. J. Veg. Sci. 16, 533–540. https://doi.org/10.1111/j.1654-1103.2005.tb02393.x.

Brienen, R.J.W., Phillips, O.L., Feldpausch, T.R., Gloor, E., Baker, T.R., Lloyd, J., Lopez-Gonzalez, G., Monteagudo-Mendoza, A., Malhi, Y., Lewis, S.L., Vásquez Martinez, R., Alexiades, M., Álvarez Dávila, E., Alvarez-Loayza, P., Andrade, A., Aragaõ, L.E.O.C., Araujo-Murakami, A., Arets, E.J.M.M., Arroyo, L., Aymard C, G.A., Bánki, O.S., Baraloto, C., Barroso, J., Bonal, D., Boot, R.G.A., Camargo, J.L.C., Castilho, C. V.,

Chama, V., Chao, K.J., Chave, J., Comiskey, J.A., Cornejo Valverde, F., Da Costa, L., De Oliveira, E.A., Di Fiore, A., Erwin, T.L., Fauset, S., Forsthofer, M., Galbraith, D.R., Grahame, E.S., Groot, N., Hérault, B., Higuchi, N., Honorio Coronado, E.N., Keeling, H., Killeen, T.J., Laurance, W.F., Laurance, S., Licona, J., Magnussen, W.E., Marimon, B.S., Marimon-Junior, B.H., Mendoza, C., Neill, D.A., Nogueira, E.M., Núñez, P., Pallqui Camacho, N.C., Parada, A., Pardo-Molina, G., Peacock, J., Penã-Claros, M., Pickavance, G.C., Pitman, N.C.A., Poorter, L., Prieto, A., Quesada, C.A., Ramírez, F., Ramírez-Angulo, H., Restrepo, Z., Roopsind, A., Rudas, A., Salomaõ, R. P., Schwarz, M., Silva, N., Silva-Espejo, J.E., Silveira, M., Stropp, J., Talbot, J., Ter Steege, H., Teran-Aguilar, J., Terborgh, J., Thomas-Caesar, R., Toledo, M., Torello-Raventos, M., Umetsu, R.K., Van Der Heijden, G.M.F., Van Der Hout, P., Guimarães Vieira, I.C., Vieira, S.A., Vilanova, E., Vos, V.A., Zagt, R.J., 2015. Long-term decline of the Amazon carbon sink. Nature 519, 344–348. https://doi.org/10.1038/na ture14283.

Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jiménez-Alfaro, B., Hennekens, S.M., Botta-Dukát, Z., Chytrý, M., Field, R., Jansen, F., Kattge, J., Pillar, V.D., Schrodt, F., Mahecha, M.D., Peet, R.K., Sandel, B., van Bodegom, P., Altman, J., Alvarez-Dávila, E., Arfin Khan, M.A.S., Attorre, F., Aubin, I., Baraloto, C., Barroso, J.G., Bauters, M., Bergmeier, E., Biurrun, I., Bjorkman, A.D., Blonder, B., Čarni, A., Cayuela, L., Černý, T., Cornelissen, J.H.C., Craven, D., Dainese, M., Derroire, G., De Sanctis, M., Díaz, S., Doležal, J., Farfan-Rios, W., Feldpausch, T.R., Fenton, N.J., Garnier, E., Guerin, G.R., Gutiérrez, A.G., Haider, S., Hattab, T., Henry, G., Hérault, B., Higuchi, P., Hölzel, N., Homeier, J., Jentsch, A., Jürgens, N., Kącki, Z., Karger, D.N., Kessler, M., Kleyer, M., Knollová, I., Korolyuk, A.Y., Kühn, I., Laughlin, D.C., Lens, F., Loos, J., Louault, F., Lyubenova, M.I., Malhi, Y., Marcenò, C., Mencuccini, M., Müller, J.V., Munzinger, J., Myers-Smith, I.H., Neill, D. A., Niinemets, Ü., Orwin, K.H., Ozinga, W.A., Penuelas, J., Pérez-Haase, A., Petřík, P., Phillips, O.L., Pärtel, M., Reich, P.B., Römermann, C., Rodrigues, A.V., Sabatini, F.M., Sardans, J., Schmidt, M., Seidler, G., Silva Espejo, J.E., Silveira, M., Smyth, A., Sporbert, M., Svenning, J.C., Tang, Z., Thomas, R., Tsiripidis, I., Vassilev, K., Violle, C., Virtanen, R., Weiher, E., Welk, E., Wesche, K., Winter, M., Wirth, C., Jandt, U., 2018. Global trait–environment relationships of plant communities. Nat. Ecol. Evol. 2, 1906–1917. https://doi.org/10.1038/s41559-018-0699-8.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel Inference: a practical information-theoretic approach, second ed., Ecological Modelling. https://doi.org/10.1016/j.ecolmodel.2003.11.004.

Capellesso, E.S., Cequinel, A., Marques, R., Marques, M.C.M., 2020. Temporal and environmental correlates of carbon stocks in a regenerating tropical forest. Appl. Veg. Sci. 23, 353–362. https://doi.org/10.1111/avsc.12487.

Cardinale, B.J., Wright, J.P., Cadotte, M.W., Carroll, I.T., Hector, A., Srivastava, D.S., Loreau, M., Weis, J.J., 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. Proc. Natl. Acad. Sci. U. S. A. 104, 18123–18128. https://doi.org/10.1073/pnas.0709069104.

Chave, J., Réjou-Méchain, M., Búrquez, A., Chidumayo, E., Colgan, M.S., Delitti, W.B.C., Duque, A., Eid, T., Fearnside, P.M., Goodman, R.C., Henry, M., Martínez-Yrízar, A., Mugasha, W.A., Muller-Landau, H.C., Mencuccini, M., Nelson, B.W., Ngomanda, A., Nogueira, E.M., Ortiz-Malavassi, E., Pélissier, R., Ploton, P., Ryan, C.M., Saldarriaga, J.G., Vieilledent, G., 2014. Improved allometric models to estimate the aboveground biomass of tropical trees. Glob. Chang. Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629.

de Castilho, C.V., Magnusson, W.E., de Araújo, R.N.O., Luizão, R.C.C., Luizão, F.J., Lima, A.P., Higuchi, N., 2006. Variation in aboveground tree live biomass in a central Amazonian Forest: effects of soil and topography. For. Ecol. Manage. 234, 85–96. https://doi.org/10.1016/j.foreco.2006.06.024.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G., Zanne, A.E., 2009. Towards a worldwide wood economics spectrum. Ecol. Lett. 12, 351–366. https://doi.org/10.1111/j.1461-0248.2009.01285.x.

Chisholm, R.A., Muller-Landau, H.C., Abdul Rahman, K., Bebber, D.P., Bin, Y., Bohlman, S.A., Bourg, N.A., Brinks, J., Bunyavejchewin, S., Butt, N., Cao, H., Cao, M., Cárdenas, D., Chang, L.W., Chiang, J.M., Chuyong, G., Condit, R., Dattaraja, H.S., Davies, S., Duque, A., Fletcher, C., Gunatilleke, N., Gunatilleke, S., Hao, Z., Harrison, R.D., Howe, R., Hsieh, C.F., Hubbell, S.P., Itoh, A., Kenfack, D., Kiratiprayoon, S., Larson, A.J., Lian, J., Lin, D., Liu, H., Lutz, J.A., Ma, K., Malhi, Y., Mcmahon, S., Mcshea, W., Meegaskumbura, M., Mohd. Razman, S., Morecroft, M.D., Nytch, C.J., Oliveira, A., Parker, G.G., Pulla, S., Punchi-Manage, R., Romero-Saltos, H., Sang, W., Schurman, J., Su, S.H., Sukumar, R., Sun, I.F., Suresh, H.S., Tan, S., Thomas, D., Thomas, S., Thompson, J., Valencia, R., Wolf, A., Yap, S., Ye, W., Yuan, Z., Zimmerman, J.K., 2013. Scale-dependent relationships between tree species richness and ecosystem function in forests. J. Ecol. 101, 1214–1224. https://doi.org/10.1111/1365-2745.12132.

Diaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16, 646–655. https://doi.org/10.1016/S0169-5347(01)02283-2.

Esquivel-Muelbert, A., Baker, T.R., Dexter, K.G., Lewis, S.L., ter Steege, H., Lopez-Gonzalez, G., Monteagudo Mendoza, A., Brienen, R., Feldpausch, T.R., Pitman, N., Alonso, A., van der Heijden, G., Peña-Claros, M., Ahuite, M., Alexiaides, M., Álvarez Dávila, E., Murakami, A.A., Arroyo, L., Aulestia, M., Balslev, H., Barroso, J., Boot, R., Cano, A., Chama Moscoso, V., Comiskey, J.A., Cornejo, F., Dallmeier, F., Daly, D.C., Dávila, N., Duivenvoorden, J.F., Duque Montoya, A.J., Erwin, T., Di Fiore, A., Fredericksen, T., Fuentes, A., García-Villacorta, R., Gonzales, T., Guevara Andino, J. E., Honorio Coronado, E.N., Huamantupa-Chuquimaco, I., Killeen, T.J., Malhi, Y., Mendoza, C., Mogollón, H., Jørgensen, P.M., Montero, J.C., Mostacedo, B., Nauray, W., Neill, D., Vargas, P.N., Palacios, S., Palacios Cuenca, W., Pallqui Camacho, N.C., Peacock, J., Phillips, J.F., Pickavance, G., Quesada, C.A., Ramírez-Angulo, H., Restrepo, Z., Reynel Rodriguez, C., Paredes, M.R., Sierra, R., Silveira, M.,

Stevenson, P., Stropp, J., Terborgh, J., Tirado, M., Toledo, M., Torres-Lezama, A., Umaña, M.N., Urrego, L.E., Vasquez Martinez, R., Gamarra, L.V., Vela, C.I.A., Vilanova Torre, E., Vos, V., von Hildebrand, P., Vriesendorp, C., Wang, O., Young, K. R., Zartman, C.E., Phillips, O.L., 2017. Seasonal drought limits tree species across the Neotropics. Ecography (Cop.) 40, 618–629. https://doi.org/10.1111/ecog.01904.

Fahey, T.J., Woodbury, P.B., Battles, J.J., Goodale, C.L., Hamburg, S.P., Ollinger, S.V., Woodall, C.W., 2010. Forest carbon storage: ecology, management, and policy. Front. Ecol. Environ. 8, 245–252. https://doi.org/10.1890/080169.

FAO, 2012. Global ecological zones for FAO forest reporting: 2010 Update, Food and Agriculture Organization of the United Nations.

FAO, UNEP, 2020. The State of the World's Forests 2020. Forests, biodiversity and people. Rome. https://doi.org/10.4060/ca8642en.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37, 4302–4315. https://doi.org/10.1002/joc.5086.

Finegan, B., Peña-Claros, M., Oliveira, A. De, Ascarrunz, N., Casanoves, F., Bret-harte, M. S., Carre, G., Velepucha, P.E., Fernandez, F., Licona, J.C., Lorenzo, L., Negret, B.S., Vaz, M., Poorter, L., 2015. Does functional trait diversity predict above-ground biomass and productivity of tropical forests? Testing three alternative hypotheses. J. Ecol. 191–201 https://doi.org/10.1111/1365-2745.12346.

da Fonseca, G.A.B., 1985. The vanishing Brazilian Atlantic forest. Biol. Conserv. 34, 17–34. https://doi.org/10.1016/0006-3207(85)90055-2.

Fotis, A.T., Murphy, S.J., Ricart, R.D., Krishnadas, M., Whitacre, J., Wenzel, J.W., Queenborough, S.A., Comita, L.S., 2017. Above-ground biomass is driven by mass-ratio effects and stand structural attributes in a temperate deciduous forest. J. Ecol. 106, 561–570. https://doi.org/10.1111/1365-2745.12847.

Garnier, E., Cortez, J., Billes, G., Laure-Navas, M., 2004. Plant functional markers capture ecosystem properties. Ecology 85, 2630–2637. https://doi.org/10.1890/03-0799.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169–1194.

Hengl, T., De Jesus, J.M., Heuvelink, G.B.M., Gonzalez, M.R., Kilibarda, M., Blagotić, A., Shangguan, W., Wright, M.N., Geng, X., Bauer-Marschallinger, B., Guevara, M.A., Vargas, R., MacMillan, R.A., Batjes, N.H., Leenaars, J.G.B., Ribeiro, E., Wheeler, I., Mantel, S., Kempen, B., 2017. SoilGrids250m: global gridded soil information based on machine learning. PLoS ONE. https://doi.org/10.1371/journal.pone.0169748.

Holdridge, L., 1947. Determination of world plant formations from simple climate data. Science (80-.) 105, 367–368.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P., Tautenhahn, S., Werner, G.D.A., Aakala, T., Abedi, M., Acosta, A.T.R., Adamidis, G.C., Adamson, K., Aiba, M., Albert, C.H., Alcántara, J.M., Alcázar C, C., Aleixo, I., Ali, H., Amiaud, B., Ammer, C., Amoroso, M.M., Anand, M., Anderson, C., Anten, N., Antos, J., Apgaua, D.M.G., Ashman, T.L., Asmara, D.H., Asner, G.P., Aspinwall, M., Atkin, O., Aubin, I., Baastrup-Spohr, L., Bahalkeh, K., Bahn, M., Baker, T., Baker, W.J., Bakker, J.P., Baldocchi, D., Baltzer, J., Banerjee, A., Baranger, A., Barlow, J., Barneche, D.R., Baruch, Z., Bastianelli, D., Battles, J., Bauerle, W., Bauters, M., Bazzato, E., Beckmann, M., Beeckman, H., Beierkuhnlein, C., Bekker, R., Belfry, G., Belluau, M., Beloiu, M., Benavides, R., Benomar, L., Berdugo-Lattke, M.L., Berenguer, E., Bergamin, R., Bergmann, J., Bergmann Carlucci, M., Berner, L., Bernhardt-Römermann, M., Bigler, C., Bjorkman, A.D., Blackman, C., Blanco, C., Blonder, B., Blumenthal, D., Bocanegra-González, K.T., Boeckx, P., Bohlman, S., Böhning-Gaese, K., Boisvert-Marsh, L., Bond, W., Bond-Lamberty, B., Boom, A., Boonman, C.C.F., Bordin, K., Boughton, E.H., Boukili, V., Bowman, D.M.J.S., Bravo, S., Brendel, M.R., Broadley, M.R., Brown, K.A., Bruelheide, H., Brumnich, F., Bruun, H.H., Bruy, D., Buchanan, S.W., Bucher, S.F., Buchmann, N., Buitenwerf, R., Bunker, D.E., Bürger, J., Burrascano, S., Burslem, D.F.R.P., Butterfield, B.J., Byun, C., Marques, M., Scalon, M.C., Caccianiga, M., Cadotte, M., Cailleret, M., Camac, J., Camarero, J.J., Campany, C., Campetella, G., Campos, J.A., Cano-Arboleda, L., Canullo, R., Carbognani, M., Carvalho, F., Casanoves, F., Castagneyrol, B., Catford, J.A., Cavender-Bares, J., Cerabolini, B.E.L., Cervellini, M., Chacón-Madrigal, E., Chapin, K., Chapin, F.S., Chelli, S., Chen, S.C., Chen, A., Cherubini, P., Chianucci, F., Choat, B., Chung, K.S., Chytrý, M., Ciccarelli, D., Coll, L., Collins, C.G., Conti, L., Coomes, D., Cornelissen, J. H.C., Cornwell, W.K., Corona, P., Coyea, M., Craine, J., Craven, D., Cromsigt, J.P.G. M., Csecserits, A., Cufar, K., Cuntz, M., da Silva, A.C., Dahlin, K.M., Dainese, M., Dalke, I., Dalle Fratte, M., Dang-Le, A.T., Danihelka, J., Dannoura, M., Dawson, S., de Beer, A.J., De Frutos, A., De Long, J.R., Dechant, B., Delagrange, S., Delpierre, N., Derroire, G., Dias, A.S., Diaz-Toribio, M.H., Dimitrakopoulos, P.G., Dobrowolski, M., Doktor, D., Dřevojan, P., Dong, N., Dransfield, J., Dressler, S., Duarte, L., Ducouret, E., Dullinger, S., Durka, W., Duursma, R., Dymova, O., E-Vojtkó, A., Eckstein, R.L., Ejtehadi, H., Elser, J., Emilio, T., Engemann, K., Erfanian, M.B., Erfmeier, A., Esquivel-Muelbert, A., Esser, G., Estiarte, M., Domingues, T.F., Fagan, W.F., Fagúndez, J., Falster, D.S., Fan, Y., Fang, J., Farris, E., Fazlioglu, F., Feng, Y., Fernandez-Mendez, F., Ferrara, C., Ferreira, J., Fidelis, A., Finegan, B., Firn, J., Flowers, T.J., Flynn, D.F.B., Fontana, V., Forey, E., Forgiarini, C., François, L., Frangipani, G., Frank, D., Frenette-Dussault, C., Freschet, G.T., Fry, E.L., Fyllas, N. M., Mazzochini, G.G., Gachet, S., Gallagher, R., Ganade, G., Ganga, F., García-Palacios, P., Gargaglione, V., Garnier, E., Garrido, J.L., de Gasper, A.L., Gea-Izquierdo, G., Gibson, D., Gillison, A.N., Giroldo, A., Glasenhardt, M.C., Gleason, S., Gliesch, M., Goldberg, E., Göldel, B., Gonzalez-Akre, E., Gonzalez-Andujar, J.L., González-Melo, A., González-Robles, A., Graae, B.J., Granda, E., Graves, S., Green, W.A., Gregor, T., Gross, N., Guerin, G.R., Günther, A., Gutiérrez, A.G., Haddock, L., Haines, A., Hall, J., Hambuckers, A., Han, W., Harrison, S.P., Hattingh, W., Hawes, J. E., He, T., He, P., Heberling, J.M., Helm, A., Hempel, S., Hentschel, J., Hérault, B., Hereş, A.M., Herz, K., Heuertz, M., Hickler, T., Hietz, P., Higuchi, P., Hipp, A.L., Hirons, A., Hock, M., Hogan, J.A., Holl, K., Honnay, O., Hornstein, D., Hou, E., Hough-Snee, N., Hovstad, K.A., Ichie, T., Igić, B., Illa, E., Isaac, M., Ishihara, M., Ivanov, L., Ivanova, L., Iversen, C.M., Izquierdo, J., Jackson, R.B., Jackson, B., Jactel,

H., Jagodzinski, A.M., Jandt, U., Jansen, S., Jenkins, T., Jentsch, A., Jespersen, J.R. P., Jiang, G.F., Johansen, J.L., Johnson, D., Jokela, E.J., Joly, C.A., Jordan, G.J., Joseph, G.S., Junaedi, D., Junker, R.R., Justes, E., Kabzems, R., Kane, J., Kaplan, Z., Kattenborn, T., Kavelenova, L., Kearsley, E., Kempel, A., Kenzo, T., Kerkhoff, A., Khalil, M.I., Kinlock, N.L., Kissling, W.D., Kitajima, K., Kitzberger, T., Kjøller, R., Klein, T., Kleyer, M., Klimešová, J., Klipel, J., Kloeppel, B., Klotz, S., Knops, J.M.H., Kohyama, T., Koike, F., Kollmann, J., Komac, B., Komatsu, K., König, C., Kraft, N.J. B., Kramer, K., Kreft, H., Kühn, I., Kumarathunge, D., Kuppler, J., Kurokawa, H., Kurosawa, Y., Kuyah, S., Laclau, J.P., Lafleur, B., Lallai, E., Lamb, E., Lamprecht, A., Larkin, D.J., Laughlin, D., Le Bagousse-Pinguet, Y., le Maire, G., le Roux, P.C., le Roux, E., Lee, T., Lens, F., Lewis, S.L., Lhotsky, B., Li, Y., Li, X., Lichstein, J.W., Liebergesell, M., Lim, J.Y., Lin, Y.S., Linares, J.C., Liu, C., Liu, D., Liu, U., Livingstone, S., Llusià, J., Lohbeck, M., López-García, Á., Lopez-Gonzalez, G., Lososová, Z., Louault, F., Lukács, B.A., Lukeš, P., Luo, Y., Lussu, M., Ma, S., Maciel Rabelo Pereira, C., Mack, M., Maire, V., Mäkelä, A., Mäkinen, H., Malhado, A.C.M., Mallik, A., Manning, P., Manzoni, S., Marchetti, Z., Marchino, L., Marcilio-Silva, V., Marcon, E., Marignani, M., Markesteijn, L., Martin, A., Martínez-Garza, C., Martínez-Vilalta, J., Mašková, T., Mason, K., Mason, N., Massad, T.J., Masse, J., Mayrose, I., McCarthy, J., McCormack, M.L., McCulloh, K., McFadden, I.R., McGill, B.J., McPartland, M.Y., Medeiros, J.S., Medlyn, B., Meerts, P., Mehrabi, Z., Meir, P., Melo, F.P.L., Mencuccini, M., Meredieu, C., Messier, J., Mészáros, I., Metsaranta, J., Michaletz, S.T., Michelaki, C., Migalina, S., Milla, R., Miller, J.E.D., Minden, V., Ming, R., Mokany, K., Moles, A.T., Molnár, A., Molofsky, J., Molz, M., Montgomery, R.A., Monty, A., Moravcová, L., Moreno-Martínez, A., Moretti, M., Mori, A.S., Mori, S., Morris, D., Morrison, J., Mucina, L., Mueller, S., Muir, C.D., Müller, S.C., Munoz, F., Myers-Smith, I.H., Myster, R.W., Nagano, M., Naidu, S., Narayanan, A., Natesan, B., Negoita, L., Nelson, C.R., Neuschulz, E.L., Ni, J., Niedrist, G., Nieto, J., Niinemets, Ü., Nolan, R., Nottebrock, H., Nouvellon, Y., Novakovskiy, A., Nystuen, K.O., O'Grady, A., O'Hara, K., O'Reilly-Nugent, A., Oakley, S., Oberhuber, W., Ohtsuka, T., Oliveira, R., Öllerer, K., Olson, M.E., Onipchenko, V., Onoda, Y., Onstein, R.E., Ordonez, J., Osada, N., Ostonen, I., Ottaviani, G., Otto, S., Overbeck, G.E., Ozinga, W.A., Pahl, A.T., Paine, C.E.T., Pakeman, R.J., Papageorgiou, A.C., Parfionova, E., Pärtel, M., Patacca, M., Paula, S., Paule, J., Pauli, H., Pausas, J.G., Peco, B., Penuelas, J., Perea, A., Peri, P.L., Petisco-Souza, A.C., Petraglia, A., Petritan, A.M., Phillips, O. L., Pierce, S., Pillar, V.D., Pisek, J., Pomogaybin, A., Poorter, H., Portsmuth, A., Poschlod, P., Potvin, C., Pounds, D., Powell, A.S., Power, S.A., Prinzing, A., Puglielli, G., Pyšek, P., Raevel, V., Rammig, A., Ransijn, J., Ray, C.A., Reich, P.B., Reichstein, M., Reid, D.E.B., Réjou-Méchain, M., de Dios, V.R., Ribeiro, S., Richardson, S., Riibak, K., Rillig, M.C., Riviera, F., Robert, E.M.R., Roberts, P., Robroek, B., Roddy, A., Rodrigues, A.V., Rogers, A., Rollinson, E., Rolo, V., Römermann, C., Ronzhina, D., Roscher, C., Rosell, J.A., Rosenfield, M.F., Rossi, R., Roy, D.B., Royer-Tardif, S., Rüger, N., Ruiz-Peinado, R., Rumpf, S.B., Rusch, G.M., Ryo, M., Sack, L., Saldaña, A., Salgado-Negret, B., Salguero-Gomez, R., Santa-Regina, I., Santacruz-García, A.C., Santos, J., Sardans, J., Schamp, B., Scherer-Lorenzen, M., Schleuning, M., Schmid, B., Schmidt, M., Schmitt, S., Schneider, J. V., Schowanek, S.D., Schrader, J., Schrodt, F., Schuldt, B., Schurr, F., Selaya Garvizu, G., Semchenko, M., Seymour, C., Sfair, J. C., Sharpe, J.M., Sheppard, C.S., Sheremetiev, S., Shiodera, S., Shipley, B., Shovon, T. A., Siebenkäs, A., Sierra, C., Silva, V., Silva, M., Sitzia, T., Sjöman, H., Slot, M., Smith, N.G., Sodhi, D., Soltis, D., Soltis, P., Somers, B., Sonnier, G., Sørensen, M.V., Sosinski, E.E., Soudzilovskaia, N.A., Souza, A.F., Spasojevic, M., Sperandii, M.G., Stan, A.B., Stegen, J., Steinbauer, K., Stephan, J.G., Sterck, F., Stojanovic, D.B., Strydom, T., Suarez, M.L., Svenning, J.C., Svitková, I., Svitok, M., Svoboda, M., Swaine, E., Swenson, N., Tabarelli, M., Takagi, K., Tappeiner, U., Tarifa, R., Tauugourdeau, S., Tavsanoglu, C., te Beest, M., Tedersoo, L., Thiffault, N., Thom, D., Thomas, E., Thompson, K., Thornton, P.E., Thuiller, W., Tichý, L., Tissue, D., Tjoelker, M.G., Tng, D.Y.P., Tobias, J., Török, P., Tarin, T., Torres-Ruiz, J.M., Tóthmérész, B., Treurnicht, M., Trivellone, V., Trolliet, F., Trotsiuk, V., Tsakalos, J. L., Tsiripidis, I., Tysklind, N., Umehara, T., Usoltsev, V., Vadeboncoeur, M., Vaezi, J., Valladares, F., Vamosi, J., van Bodegom, P.M., van Breugel, M., Van Cleemput, E., van de Weg, M., van der Merwe, S., van der Plas, F., van der Sande, M.T., van Kleunen, M., Van Meerbeek, K., Vanderwel, M., Vanselow, K.A., Vårhammar, A., Varone, L., Vasquez Valderrama, M.Y., Vassilev, K., Vellend, M., Veneklaas, E.J., Verbeeck, H., Verheyen, K., Vibrans, A., Vieira, I., Villacís, J., Violle, C., Vivek, P., Wagner, K., Waldram, M., Waldron, A., Walker, A.P., Waller, M., Walther, G., Wang, H., Wang, F., Wang, W., Watkins, H., Watkins, D., Weber, U., Weedon, J.T., Wei, L., Weigelt, P., Weiher, E., Wells, A.W., Wellstein, C., Wenk, E., Westoby, M., Westwood, A., White, P.J., Whitten, M., Williams, M., Winkler, D.E., Winter, K., Womack, C., Wright, I.J., Wright, S.J., Wright, J., Pinho, B.X., Ximenes, F., Yamada, T., Yamaji, K., Yanai, R., Yankov, N., Yguel, B., Zanini, K.J., Zanne, A.E., Zelený, D., Zhao, Y.P., Zheng, Jingming, Zheng, Ji, Ziemińska, K., Zirbel, C.R., Zizka, G., Zo-Bi, I. C., Zotz, G., Wirth, C., 2020. TRY plant trait database – enhanced coverage and open access. Glob. Chang. Biol. 26, 119–188. https://doi.org/10.1111/gcb.14904.

Laliberté, E., Legendre, P., Shipley, B., 2015. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Packag. Version 1.0-12.

Lasky, J.R., Uriarte, M., Boukili, V.K., Erickson, D.L., John Kress, W., Chazdon, R.L., 2014. The relationship between tree biodiversity and biomass dynamics changes with tropical forest succession. Ecol. Lett. 17, 1158–1167. https://doi.org/10.1111/ele.12322.

Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. Funct. Ecol. 16, 545–556.

Lewis, S.L., Lopez-Gonzalez, G., Sonké, B., Affum-Baffoe, K., Baker, T.R., Ojo, L.O., Phillips, O.L., Reitsma, J.M., White, L., Comiskey, J.A., Djuikouo, K.M.N., Ewango, C.E.N., Feldpausch, T.R., Hamilton, A.C., Gloor, M., Hart, T., Hladik, A., Lloyd, J., Lovett, J.C., Makana, J.R., Malhi, Y., Mbago, F.M., Ndangalasi, H.J., Peacock, J., Peh, K.S.H., Sheil, D., Sunderland, T., Swaine, M.D., Taplin, J.,

Taylor, D., Thomas, S.C., Votere, R., Wöll, H., 2009. Increasing carbon storage in intact African tropical forests. Nature 457, 1003–1006. https://doi.org/10.1038/nature07771.

Li, Y., Tian, D., Yang, H., Niu, S., 2018. Size-dependent nutrient limitation of tree growth from subtropical to cold temperate forests. Funct. Ecol. 32, 95–105. https://doi.org/10.1111/1365-2435.12975.

Liefecheck, J.S., 2015. piecewiseSEM: piecewise structural equation modelling in r for ecology, evolution, and systematics. Methods Ecol. Evol. 7, 573–579.

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Global decline in large old trees. Science (80-.) 338, 1305–1306. https://doi.org/10.1126/science.1231070.

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, 1242–1252. https://doi.org/10.1890/14-0472.1.

Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., Anderson-Teixeira, K.J., Andrade, A., Baltzer, J., Becker, K.M.L., Blomdahl, E.M., Bourg, N.A., Bunyavejchewin, S., Burslem, D.F.R.P., Cansler, C.A., Cao, K., Cao, M., Cárdenas, D., Chang, L.W., Chao, K.J., Chao, W.C., Chiang, J.M., Chu, C., Chuyong, G.B., Clay, K., Condit, R., Cordell, S., Dattaraja, H.S., Duque, A., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Freund, J.A., Giardina, C., Germain, S.J., Gilbert, G.S., Hao, Z., Hart, T., Hau, B.C.H., He, F., Hector, A., Howe, R.W., Hsieh, C.F., Hu, Y.H., Hubbell, S.P., Inman-Narahari, F.M., Itoh, A., Janík, D., Kassim, A.R., Kenfack, D., Korte, L., Král, K., Larson, A.J., Li, Y. De, Lin, Y., Liu, S., Lum, S., Ma, K., Makana, J.R., Malhi, Y., McMahon, S.M., McShea, W.J., Memiaghe, H.R., Mi, X., Morecroft, M., Musili, P.M., Myers, J.A., Novotny, V., de Oliveira, A., Ong, P., Orwig, D.A., Ostertag, R., Parker, G.G., Patankar, R., Phillips, R.P., Reynolds, R., Sack, L., Song, G. Z.M., Su, S.H., Sukumar, R., Sun, I.F., Suresh, H.S., Swanson, M.E., Tan, S., Thomas, D.W., Thompson, J., Uriarte, M., Valencia, R., Vicentini, A., Vrška, T., Wang, X., Weiblen, G.D., Wolf, A., Wu, S.H., Xu, H., Yamakura, T., Yap, S., Zimmerman, J.K., 2018. Global importance of large-diameter trees. Glob. Ecol. Biogeogr. 27, 849–864. https://doi.org/10.1111/geb.12747.

Ma, L., Lian, J., Lin, G., Cao, H., Huang, Z., Guan, D., 2016. Forest dynamics and its driving forces of sub-tropical forest in South China. Sci. Rep. 6, 1–10. https://doi.org/10.1038/srep22561.

Marcilio-Silva, V., Zwiener, V.P., Marques, M.C.M., 2017. Metacommunity structure, additive partitioning and environmental drivers of woody plants diversity in the Brazilian Atlantic Forest. Divers. Distrib. 23, 1110–1119. https://doi.org/10.1111/ddi.12616.

Marimon, B.S., Marimon-Junior, B.H., Feldpausch, T.R., Oliveira-Santos, C., Mews, H.A., Lopez-Gonzalez, G., Lloyd, J., Franczak, D.D., de Oliveira, E.A., Maracahipes, L., Miguel, A., Lenza, E., Phillips, O.L., 2014. Disequilibrium and hyperdynamic tree turnover at the forest-cerrado transition zone in southern Amazonia. Plant Ecol. Divers. 7, 281–292. https://doi.org/10.1080/17550874.2013.818072.

Missio, F.D.F., Da Silva, A.C., Higuchi, P., Longhi, S.J., Brand, M.A., Rios, P.D., Rosa, A. D., Buzzi Junior, F., Bento, M.A., Gonçalves, D.A., Loebens, R., Pscheidt, F., 2017. Functional traits of tree species in a fragment of Araucaria forest in Lages, Santa Catarina state. Cienc. Florest. 27, 215–224. https://doi.org/10.5902/1980509826460.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., Mcglinn, D., Minchin, P. R., O'hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Szoecs, E., Maintainer, H.W., 2019. Package "vegan": Community Ecology Package 2, 1–297.

Oliveira-Filho, A.T., Budke, J.C., Jarenkow, J.A., Eisenlohr, P.V., Neves, D.R.M., 2014. Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. J. Plant Ecol. 8, 242–260. https://doi.org/10.1093/jpe/rtt058.

Oliveira-Filho, A.T., Fontes, M.A.L., 2000. Patterns of floristic differentiation among Atlantic forests in Southeastern Brazil and the influence of climate. Biotropica 32, 793–810. https://doi.org/10.1111/j.1744-7429.2000.tb00619.x.

Oliveira, L.Z., Uller, H.F., Klitzke, A.R., Eleotério, J.R., Vibrans, A.C., 2019. Towards the fulfillment of a knowledge gap: wood densities for species of the subtropical atlantic forest. Data 4, 1–10. https://doi.org/10.3390/data4030104.

Pan, Y., Birdsey, R.A., Fang, J., Houghton, R., Kauppi, P.E., Kurz, W.A., Phillips, O.L., Shvidenko, A., Lewis, S.L., Canadell, J.G., Ciais, P., Jackson, R.B., Pacala, S.W., McGuire, A.D., Piao, S., Rautiainen, A., Sitch, S., Hayes, D., 2011. A large and persistent carbon sink in the world's forests. Science (80-.) 333, 988–994. https://doi.org/10.1126/science.1201609.

Pan, Y., Birdsey, R.A., Phillips, O.L., Jackson, R.B., 2013. The structure, distribution, and biomass of the world's forests. Annu. Rev. Ecol. Evol. Syst. 44, 593–622. https://doi.org/10.1146/annurev-ecolsys-110512-135914.

Peña-Claros, M., Poorter, L., Alarcon, A., Blate, G., Choque, U., Fredericksen, T.S., Justiniano, M.J., Leaño, C., Licona, J.C., Pariona, W., Putz, F.E., Quevedo, L., Toledo, M., 2012. Soil effects on forest structure and diversity in a moist and a dry tropical forest. Biotropica 44. https://doi.org/10.1111/j.1744-7429.2011.00813.x.

Pérez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S.S., Cornwell, W.K.K., Craine, J.M.M., Gurvich, D.E.E., Urcelay, C., Veneklaas, E.J.J., Reich, P.B.B., Poorter, L., Wright, I.J.J., Etc., Ray, P., Etc., Díaz, S., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S.S., Cornwell, W.K.K., Craine, J.M.M., Gurvich, D.E.E., Urcelay, C., Veneklaas, E.J.J., Reich, P.B.B., Poorter, L., Wright, I.J.J., Ray, P., Enrico, L., Pausas, J.G., Vos, A.C. de, Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., Steege, H. ter, Heijden, M.G.A. van der, Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A.C., Aquino, S., Cornelissen, J.H.C., 2013. New Handbook for standardized measurment of plant functional traits worldwide. Aust. J. Bot. 61, 167–234. https://doi.org/10.1071/BT12225.

Phillips, O.L., Malhi, Y., Higuchi, N., Laurance, W.F., Nuñez, P.V., 1998. Changes in the carbon balance of tropical forests: evidence from long-term plots. Science (80-.) 439, 439. https://doi.org/10.1126/science.282.5388.439.

Pillet, M., Joetzjer, E., Belmin, C., Chave, J., Ciais, P., Dourdain, A., Evans, M., Hérault, B., Luyssaert, S., Poulter, B., 2018. Disentangling competitive vs. climatic drivers of tropical forest mortality. J. Ecol. 106, 1165–1179. https://doi.org/10.1111/1365-2745.12876.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., Heisterkamp, S., Van Willigen, B., 2020. nlme: Linear and Nonlinear Mixed Effects Models. R Packag. 1–336.

Pinho, B.X., Peres, C.A., Leal, I.R., Tabarelli, M., 2020. Critical role and collapse of tropical mega-trees: a key global resource, first ed, Advances in Ecological Research. Elsevier Ltd. https://doi.org/10.1016/bs.aecr.2020.01.009.

Poorter, L., van der Sande, M.T., Arets, E.J.M.M., Ascarrunz, N., Enquist, B., Finegan, B., Licona, J.C., Martínez-Ramos, M., Mazzei, L., Meave, J.A., Muñoz, R., Nytch, C.J., de Oliveira, A.A., Pérez-García, E.A., Prado-Junior, J., Rodríguez-Velázques, J., Ruschel, A.R., Salgado-Negret, B., Schiavini, I., Swenson, N.G., Tenorio, E.A., Thompson, J., Toledo, M., Uriarte, M., van der Hout, P., Zimmerman, J.K., Peña-Claros, M., 2017. Biodiversity and climate determine the functioning of Neotropical forests. Glob. Ecol. Biogeogr. 26, 1423–1434. https://doi.org/10.1111/geb.12668.

Poorter, L., van der Sande, M.T., Thompson, J., Arets, E.J.M.M., Alarcón, A., Álvarez-Sánchez, J., Ascarrunz, N., Balvanera, P., Barajas-Guzmán, G., Boit, A., Bongers, F., Carvalho, F.A., Casanoves, F., Cornejo-Tenorio, G., Costa, F.R.C., de Castilho, C.V., Duivenvoorden, J.F., Dutrieux, L.P., Enquist, B.J., Fernández-Méndez, F., Finegan, B., Gormley, L.H.L., Healey, J.R., Hoosbeek, M.R., Ibarra-Manríquez, G., Junqueira, A.B., Levis, C., Licona, J.C., Lisboa, L.S., Magnusson, W.E., Martínez-Ramos, M., Martínez-Yrizar, A., Martorano, L.G., Maskell, L.C., Mazzei, L., Meave, J. A., Mora, F., Muñoz, R., Nytch, C., Pansonato, M.P., Parr, T.W., Paz, H., Pérez-García, E.A., Rentería, L.Y., Rodríguez-Velazquez, J., Rozendaal, D.M.A., Ruschel, A. R., Sakschewski, B., Salgado-Negret, B., Schietti, J., Simões, M., Sinclair, F.L., Souza, P.F., Souza, F.C., Stropp, J., ter Steege, H., Swenson, N.G., Thonicke, K., Toledo, M., Uriarte, M., van der Hout, P., Walker, P., Zamora, N., Peña-Claros, M., 2015. Diversity enhances carbon storage in tropical forests. Glob. Ecol. Biogeogr. 24, 1314–1328. https://doi.org/10.1111/geb.12364.

Prado-Junior, J.A., Schiavini, I., Vale, V.S., Arantes, C.S., van der Sande, M.T., Lohbeck, M., Poorter, L., 2016. Conservative species drive biomass productivity in tropical dry forests. J. Ecol. 104, 817–827. https://doi.org/10.1111/1365-2745.12543.

Pyles, M.V., Prado-Junior, J.A., Magnago, L.F.S., de Paula, A., Meira-Neto, J.A.A., 2018. Loss of biodiversity and shifts in aboveground biomass drivers in tropical rainforests with different disturbance histories. Biodivers. Conserv. 27, 3215–3231. https://doi.org/10.1007/s10531-018-1598-7.

Quesada, C.A., Phillips, O.L., Schwarz, M., Czimczik, C.I., Baker, T.R., Patiño, S., Fyllas, N.M., Hodnett, M.G., Herrera, R., Almeida, S., Alvarez Dávila, E., Arneth, A., Arroyo, L., Chao, K.J., Dezzeo, N., Erwin, T., Di Fiore, A., Higuchi, N., Honorio Coronado, E., Jimenez, E.M., Killeen, T., Lezama, A.T., Lloyd, G., López-González, G., Luizão, F.J., Malhi, Y., Monteagudo, A., Neill, D.A., Núñez Vargas, P., Paiva, R., Peacock, J., Peñuela, M.C., Peña Cruz, A., Pitman, N., Priante Filho, N., Prieto, A., Ramírez, H., Rudas, A., Salomão, R., Santos, A.J.B., Schmerler, J., Silva, N., Silveira, M., Vásquez, R., Vieira, I., Terborgh, J., Lloyd, J., 2012. Basin-wide variations in Amazon forest structure and function are mediated by both soils and climate. Biogeosciences 9, 2203–2246. https://doi.org/10.5194/bg-9-2203-2012.

R Core Team, 2020. R: A language and environment for statistical computing. R Foundation for Statistical Computing [WWW Document]. https://www.r-project.org/.

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, 1163–1167. https://doi.org/10.1111/2041-210X.12753.

Rezende, V.L., Eisenlohr, P.V., Vibrans, A.C., de Oliveira-Filho, A.T., 2015. Humidity, low temperature extremes, and space influence floristic variation across an insightful gradient in the Subtropical Atlantic Forest. Plant Ecol. 216, 759–774. https://doi.org/10.1007/s11258-015-0465-9.

Ribeiro, M.C., Metzger, J.P., Martensen, A.C., Ponzoni, F.J., Hirota, M.M., 2009. The Brazilian Atlantic Forest: how much is left, and how is the remaining forest distributed? Implications for conservation. Biol. Conserv. 142, 1141–1153. https://doi.org/10.1016/j.biocon.2009.02.021.

Rosenfield, M.F., Müller, S.C., Overbeck, G.E., 2019. Short gradient, but distinct plant strategies: the CSR scheme applied to subtropical forests. J. Veg. Sci. 30, 984–993. https://doi.org/10.1111/jvs.12787.

Rosenfield, M.F., Souza, A.F., 2013. Biomassa e carbono em florestas subtropicais: determinantes, métodos de quantificação e estimativas. Neotrop. Biol. Conserv. 8, 103–110. https://doi.org/10.4013/nbc.2013.82.06.

Shipley, B., 2016. Cause and Correlation in Biology: A User's Guide to Path Analysis, Structural Equations and Causal Inference With R, second ed. Cambridge University Press, Cambridge.

Slik, J.W.F., Aiba, S.I., Brearley, F.Q., Cannon, C.H., Forshed, O., Kitayama, K., Nagamasu, H., Nilus, R., Payne, J., Paoli, G., Poulsen, A.D., Raes, N., Sheil, D., Sidiyasa, K., Suzuki, E., van Valkenburg, J.L.C.H., 2010. Environmental correlates of tree biomass, basal area, wood specific gravity and stem density gradients in Borneo's tropical forests. Glob. Ecol. Biogeogr. 19, 50–60. https://doi.org/10.1111/j.1466-8238.2009.00489.x.

Slik, J.W.F., Paoli, G., Mcguire, K., Amaral, I., Barroso, J., Bastian, M., Blanc, L., Bongers, F., Boundja, P., Clark, C., Collins, M., Dauby, G., Ding, Y., Doucet, J.L., Eler, E., Ferreira, L., Forshed, O., Fredriksson, G., Gillet, J.F., Harris, D., Leal, M., Laumonier, Y., Malhi, Y., Mansor, A., Martin, E., Miyamoto, K., Araujo-Murakami, A., Nagamasu, H., Nilus, R., Nurtjahya, E., Oliveira, Á., Onrizal, O., Parada-Gutierrez, A., Permana, A., Poorter, L., Poulsen, J., Ramirez-Angulo, H., Reitsma, J., Rovero, F., Rozak, A., Sheil, D., Silva-Espejo, J., Silveira, M., Spironelo, W., ter Steege, H., Stevart, T., Navarro-Aguilar, G.E., Sunderland, T.,

Suzuki, E., Tang, J., Theilade, I., van der Heijden, G., van Valkenburg, J., Van Do, T., Vilanova, E., Vos, V., Wich, S., Wöll, H., Yoneda, T., Zang, R., Zhang, M.G., Zweifel, N., 2013. Large trees drive forest aboveground biomass variation in moist lowland forests across the tropics. Glob. Ecol. Biogeogr. 22, 1261–1271. https://doi.org/10.1111/geb.12092.

Souza, A.F., Longhi, S.J., 2019. Disturbance history mediates climate change effects on subtropical forest biomass and dynamics. Ecol. Evol. 1–16 https://doi.org/10.1002/ece3.5289.

Sullivan, M.J.P., Lewis, S.L., Affum-Baffoe, K., Castilho, C., Costa, F., Sanchez, A.C., Ewango, C.E.N., Hubau, W., Marimon, B., Monteagudo-Mendoza, A., Qie, L., Sonké, B., Martinez, R.V., Baker, T.R., Brienen, R.J.W., Feldpausch, T.R., Galbraith, D., Gloor, M., Malhi, Y., Aiba, S.-I., Alexiades, M.N., Almeida, E.C., Oliveira, E.A. de, Dávila, E.Á., Loayza, P.A., Andrade, A., Vieira, S.A., Aragão, L., Araujo-Murakami, A., Arets, E.J.M.M., Arroyo, L., Ashton, P., C., G.A., Baccaro, F.B., Banin, L.F., Baraloto, C., Camargo, P.B., Barlow, J., Barroso, J., Bastin, J.-F., Batterman, S.A., Beeckman, H., Begne, S.K., Bennett, A.C., Berenguer, E., Berry, N., Blanc, L., Boeckx, P., Bogaert, J., Bonal, D., Bongers, F., Bradford, M., Brearley, F.Q., Brncic, T., Brown, F., Burban, B., Camargo, J.L., Castro, W., Céron, C., Ribeiro, S.C., Moscoso, V.C., Chave, J., Chezeaux, E., Clark, C.J., Souza, F.C. de, Collins, M., Comiskey, J.A., Valverde, F.C., Medina, M.C., Costa, L. da, Dančák, M., Dargie, G.C., Davies, S., Cardozo, N.D., Thales de Haulleville, Medeiros, M.B. de, Pasquel, J. del A., Derroire, G., Fiore, A. Di, Doucet, J.-L., Dourdain, A., Droissart, V., Duque, L.F., Ekoungoulou, R., Elias, F., Erwin, T., Esquivel-Muelbert, A., Fauset, S., Ferreira, J., Llampazo, G.F., Foli, E., Ford, A., Gilpin, M., Hall, J.S., Hamer, K.C., Hamilton, A.C., Harris, D.J., Hart, T.B., Hédl, R., Herault, B., Herrera, R., Higuchi, N., Hladik, A., Eurídice Honorio Coronado, Huamantupa-Chuquimaco, I., Huasco, W.H., Jeffery, K.J., Jimenez-Rojas, E., Kalamandeen, M., Kamdem, M.-N., Kearsley, E., Umetsu, R.K., Khoon, L.K.K., Killeen, T., Kitayama, K., Klitgaard, B., Koch, A., Labrière, N., Laurance, W., Laurance, S., Leal, M.E., Levesley, A., Lima, A.J.N., Lisingo, J., Pontes-Lopes, A., Lopez-Gonzalez, G., Lovejoy, T., Lovett, J., Lowe, R., Magnusson, W.E., Malumbres-Olarte, J., Manzatto, Á., Jr., B.H.M., Marshall, A.R., Marthews, T., Reis, S.M. de A., Maycock, C., Melgaço, K., Mendoza, C., Metali, F., Mihindou, V., Milliken, W., Mitchard, E., Morandi, P.S., Mossman, H.L., Nagy, L., Nascimento, H., Neill, D., Nilus, R., Vargas, P.N., Palacios, W., Camacho, N.P., Peacock, J., Pendry, C., Mora, M.C.P., Pickavance, G.C., Pipoly, J., Pitman, N., Playfair, M., Poorter, L., Poulsen, J.R., Poulsen, A.D., Preziosi, R., Prieto, A., Richard Primack, Ramírez-Angulo, H., Reitsma, J., Réjou-Méchain, M., Correa, Z.R., Sousa, T.R. de, Bayona, L. R., Roopsind, A., Rudas, A., Rutishauser, E., Salim, K.A., Salomão, R.P., Schietti, J., Sheil, D., Silva, R.C., Espejo, J.S., Valeria, C.S., Silveira, M., Simo-Droissart, M., Simon, M.F., Singh, J., Shareva, Y.C.S., Stahl, C., Stropp, J., Sukri, R., Sunderland, T., Svátek, M., Swaine, M.D., Swamy, V., Taedoumg, H., Talbot, J., James Taplin, Taylor, D., Steege, H. ter, Terborgh, J., Thomas, R., Thomas, S.C., Torres-Lezama, A., Umunay, P., Gamarra, L.V., Heijden, G. van der, Hout, P. van der, Meer, P.J. van der, Nieuwstadt, M. van, Verbeeck, H., Vernimmen, R., Vicentini, A., Vieira, I.C.G., Torre, E.V., Vleminckx, J., Vos, V.A., Wang, O., White, L.J.T., Willcock, S., Woods, J.T., Wortel, V., Young, K., Zagt, R., Zemagho, L., Zuidema, P.A., Zwerts, J.A., Phillips, O. L., 2020. Long-term thermal sensitivity of Earth's tropical forests. Science (80-.). 368, 869–874.

Sullivan, M.J.P., Talbot, J., Lewis, S.L., Phillips, O.L., Qie, L., Begne, S.K., Chave, J., Cuni-Sanchez, A., Hubau, W., Lopez-Gonzalez, G., Miles, L., Monteagudo-Mendoza, A., Sonké, B., Sunderland, T., Ter Steege, H., White, L.J.T., Affum-Baffoe, K., Aiba, S.I., De Almeida, E.C., De Oliveira, E.A., Alvarez-Loayza, P., Dávila, E.Á., Andrade, A., Aragão, L.E.O.C., Ashton, P., Aymard, G.A., Baker, T.R., Balinga, M., Banin, L.F., Baraloto, C., Bastin, J.F., Berry, N., Bogaert, J., Bonal, D., Bongers, F., Brienen, R., Camargo, J.L.C., Cerón, C., Moscoso, V.C., Chezeaux, E., Clark, C.J., Pacheco, Á.C., Comiskey, J.A., Valverde, F.C., Coronado, E.N.H., Dargie, G., Davies, S.J., De Canniere, C., Djuikouo, M.N., Doucet, J.L., Erwin, T.L., Espejo, J.S., Ewango, C.E.N., Fauset, S., Feldpausch, T.R., Herrera, R., Gilpin, M., Gloor, E., Hall, J.S., Harris, D.J., Hart, T.B., Kartawinata, K., Kho, L.K., Kitayama, K., Laurance, S.G.W., Laurance, W. F., Leal, M.E., Lovejoy, T., Lovett, J.C., Lukasu, F.M., Makana, J.R., Malhi, Y., Marachipes, L., Marimon, B.S., Junior, B.H.M., Marshall, A.R., Morandi, P.S., Mukendi, J.T., Mukinzi, J., Nilus, R., Vargas, P.N., Camacho, N.C.P., Pardo, G., Peña-Claros, M., Pétronelli, P., Pickavance, G.C., Poulsen, A.D., Poulsen, J.R., Primack, R. B., Priyadi, H., Quesada, C.A., Reitsma, J., Réjou-Méchain, M., Restrepo, Z., Rutishauser, E., Salim, K.A., Salomão, R.P., Samsoedin, I., Sheil, D., Sierra, R., Silveira, M., Slik, J.W.F., Steel, L., Taedoumg, H., Tan, S., Terborgh, J.W., Thomas, S. C., Toledo, M., Umunay, P.M., Gamarra, L.V., Vieira, I.C.G., Vos, V.A., Wang, O., Willcock, S., Zemagho, L., 2017. Diversity and carbon storage across the tropical forest biome. Sci. Rep. 7, 1–12. https://doi.org/10.1038/srep39102.

van der Sande, M.T., Arets, E.J.M.M., Peña-Claros, M., Hoosbeek, M.R., Cáceres-Siani, Y., van der Hout, P., Poorter, L., 2017a. Soil fertility and species traits, but not diversity, drive productivity and biomass stocks in a Guyanese tropical rainforest. Funct. Ecol. https://doi.org/10.1111/1365-2435.12968.

van der Sande, M.T., Peña-Claros, M., Ascarrunz, N., Arets, E.J.M.M., Licona, J.C., Toledo, M., Poorter, L., 2017b. Abiotic and biotic drivers of biomass change in a Neotropical forest. J. Ecol. 105, 1223–1234. https://doi.org/10.1111/1365-2745.12756.

Vieira, S.A., Alves, L.F., Duarte-Neto, P.J., Martins, S.C., Veiga, L.G., Scaranello, M.A., Picollo, M.C., Camargo, P.B., do Carmo, J.B., Neto, E.S., Santos, F.A.M., Joly, C.A., Martinelli, L.A., 2011. Stocks of carbon and nitrogen and partitioning between above-and belowground pools in the Brazilian coastal Atlantic Forest elevation range. Ecol. Evol. 1, 421–434. https://doi.org/10.1002/ece3.41.

Vilanova, E., Ramírez-Angulo, H., Torres-Lezama, A., Aymard, G., Gámez, L., Durán, C., Hernández, L., Herrera, R., van der Heijden, G., Phillips, O.L., Ettl, G.J., 2018. Environmental drivers of forest structure and stem turnover across Venezuelan tropical forests. PLoS One 13. https://doi.org/10.1371/journal.pone.0198489.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., Garnier, E., 2007. Let the concept of trait be functional! Oikos 116, 882–892. https://doi.org/10.1111/j.2007.0030-1299.15559.x.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F., Cavender-Bares, J., Chapin, T., Cornelissen, J.H.C., Diemer, M., Flexas, J., Garnier, E., Groom, P.K., Gulias, J., Hikosaka, K., Lamont, B.B., Lee, T., Lee, W., Lusk, C., Midgley, J.J., Navas, M.-L., Niinemets, U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V.I., Roumet, C., Thomas, S.C., Tjoelker, M.G., Veneklaas, E.J., Villar, R., 2004. The worldwide leaf economics spectrum. Nature 428, 821–827. https://doi.org/10.1038/nature02403.

Zanne, A., Lopez-Gonzalez, G Coomes, D., Ilic, J., Jansen, S., Lewis, S., Miller, R., Swenson, N., Wiemann, M., Chave, J., 2009. Data from: Towards a worldwide wood economics spectrum [WWW Document]. Dryad Digit. Repos. https//doi.org/10.5061/dryad.234.

Zhang, R., Zhou, X., Ouyang, Z., Avitabile, V., Qi, J., Chen, J., Giannico, V., 2019. Estimating aboveground biomass in subtropical forests of China by integrating multisource remote sensing and ground data. Remote Sens. Environ. 232, 111341 https://doi.org/10.1016/j.rse.2019.111341.