

REVIEW ARTICLE

Biomass and carbon stocks in restored Atlantic Forests: a systematic review

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In restored tropical forests, a better understanding of biomass and carbon estimation methods is needed—especially biomass assessment, allometric equation choice, and the influence of local conditions. Understanding these factors is critical given forests' role in sequestering and storing atmospheric carbon. We conducted a systematic review on the state of the art in estimating plant biomass and carbon storage in restored forests within the Atlantic Forest. We examined the biomass measurement methods, the factors influencing biomass productivity, and estimated the time required for restored forests to attain biomass levels observed in conserved forests. For each study, we investigated: (1) how biomass stocks were assessed; (2) the allometric equations used for estimation; (3) and the restoration techniques applied alongside the biotic and abiotic conditions at each site. We also examined whether local climatic conditions, forest age, and the number of planted species influenced biomass accumulation. Despite the limited number of studies assessing carbon stocks in restored Atlantic Forests, publications have increased recently. However, the equations used to estimate carbon stocks were mainly adjusted to young forests (5–17 years). Moreover, studies lack a standardized protocol for converting biomass into carbon, and few assessing root biomass. We found that age is the key factor explaining biomass accumulation. Finally, our projections indicate forests over 25 years of restoration likely exhibit plant biomass similar to conserved forests. Still, different protocols and equations for estimating plant biomass accumulation may lead to under- or overestimates compared to the projections presented here.

Key words: allometric equations, bibliometric analysis, carbon stock, ecosystem services, forest restoration

Implications for Practice

- Using equations inappropriate for forest age, tree composition, or local wood density reduces the reliability of biomass estimates.
- Biomass assessments that neglect root biomass, disregard wood density, or rely on different and inconsistent allometric equations may inaccurately estimate carbon storage in restored forests.
- Establishing a consistent database with information on carbon conversion for different species and ages can provide more reliable results on forest carbon stocks.
- Forest age is the primary factor influencing biomass and carbon stocks, with Atlantic Forest restoration sites older than 25 years approaching the biomass levels of conserved forests.
- Biomass accumulation over the years can be projected and leveraged to access the carbon credit potential of restoration projects.

successional trajectory (Holl 2017). Several sources of error can bias the estimates of biomass accumulation in restoration systems (Baker et al. 2004; Chave et al. 2004; Gardon et al. 2020). Sources of error can arise from the quality of inventory data (e.g. tree measurements and the representativeness of the sampled area), the use of inappropriate allometric equations/models (e.g. those based on few trees and small samples), and the non-use or misuse of wood density values, which vary widely among species and sites, but enhance the robustness and reliability of plant biomass estimates (Chave et al. 2004; Flores & Coomes 2011).

Studies estimating biomass accumulation in forest systems have also predominantly focused on the aboveground portion (Azevedo et al. 2018; Brancalion et al. 2019; Arcanjo &

Author contributions: GJM, VLE conceived the idea and designed the study; GLM collected the data; GJM, CSB, DSP performed the analysis; DSP validated the results; all authors wrote and edited the manuscript.

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doi: 10.1111/rec.70231

Supporting information at:

<http://onlinelibrary.wiley.com/doi/10.1111/rec.70231/supinfo>

Introduction

In tropical regions, forest restoration serves as a conservation strategy to restore ecological functions, such as biomass and carbon accumulation (Chazdon 2008; Locatelli et al. 2015; James et al. 2018). Nevertheless, the role of restored forests in sequestering atmospheric carbon through biomass storage over time is complex, as various abiotic and biotic factors influence their

Torezan 2022), often overlooking the belowground component (i.e. roots), which is crucial for achieving a comprehensive and accurate estimate of the total biomass in a given forest system (Nogueira Junior 2010; Gatto et al. 2014). Furthermore, different allometric equations use different variables to estimate the productivity of restored forests (e.g. whether plant height is included or not), which can lead to disparities in biomass estimates (Brown 1997; Baker et al. 2004; Chave et al. 2004, 2014; Van Breugel 2007). However, a comprehensive review of the methods employed to estimate biomass stocks in many tropical forests, such as the Atlantic Forest, is still lacking.

The Atlantic Forest of Brazil is renowned as the oldest and most latitudinally expansive forest in South America, spanning latitudes from 3 to 31°S (Ribeiro et al. 2009). Its long evolutionary history and high latitudinal range have facilitated numerous interactions with adjacent and non-adjacent ecosystems, including the African, Andean, and Amazonian flora (Joly et al. 2014), resulting in an impressive number of 20,000 plant species, with 44% of them being endemic (Silva & Casteletti 2003; Mittermeier et al. 2004). Recognized for its exceptional species richness and high levels of endemism, the Atlantic Forest has been identified as one of the world's top biodiversity hotspots for conservation priorities (Myers et al. 2000). However, as primarily situated along the Brazilian Atlantic coast, anthropogenic pressures dating back to the 1500s have reduced the Atlantic Forest to less than 16% of its original extent (Ribeiro et al. 2009). The remaining fragments consist mostly of small, isolated patches located outside protected areas, rendering them highly vulnerable to ongoing human impacts (Ribeiro et al. 2009).

Although the Atlantic Forest is under significant pressure from human activities and land use changes, it accommodates approximately 65% of Brazil's population and plays a crucial role in providing ecosystem services for human well-being (Joly et al. 2014). In this context, various restoration initiatives are underway to connect and expand fragmented protected areas (Rodrigues et al. 2009; Oliveira & Engel 2017). Yet, the accuracy of estimates regarding the effectiveness of these restoration endeavors in terms of restoring forests structurally and functionally, and enhancing the ecosystem services they provide, remains largely unexplored (DeLuca et al. 2010; Viani et al. 2017; Ballarin et al. 2024). For instance, while the impact of restoration practices on biomass accumulation in the Atlantic Forest has been assessed (Gardon et al. 2020; Zanini et al. 2021), discrepancies in biomass estimation methods—such as whether or not to account for wood density and the use of different allometric equations—may have resulted in significantly different biomass estimates. Such unresolved issues hinder the development of standardized protocols for biomass assessment in restored tropical forests.

Numerous factors can influence the dynamics of biomass accumulation in forests undergoing restoration (Gardon et al. 2020). For example, it is established that the rate of biomass accumulation in restored forests is influenced by topographic features (e.g. elevation; Tiwari et al. 2022), climatic variables (e.g. temperature and precipitation; Peichl & Arain 2007; Zhang & Liang 2014; Wang et al. 2016), age (Gardon et al. 2020), and plant community composition (Pontes et al. 2019; Gardon et al. 2020; Capellesso

et al. 2021). While the Atlantic Forest occupies a central position in the neotropical ecological restoration agenda (Araújo et al. 2018; Brancalion et al. 2019; Arcanjo & Torezan 2022), with restoration sites of different ages, strategies, and designs across a spectrum of climatic and topographic contexts, there is still no synthesis available to: (1) determine the current state of research dedicated to estimating biomass in this ecosystem, (2) identify general patterns in carbon stocks under different ecological conditions, (3) forecast the effectiveness of restored forests in replenishing carbon levels compared to conserved forests through standardized protocols, and (4) compare methods employed to assess biomass stocks in restored sites with biomass projected from conserved reference forests within different biotic and abiotic contexts. These gaps need to be addressed as the role of tropical forests in carbon sequestration has received increasing attention from researchers and decision-makers in recent years (IPCC 2007; Palmer 2016; Lewis et al. 2019).

We undertook a systematic review that focused on: (1) summarizing the main methods and equations used in scientific studies to estimate plant biomass and carbon stocks in restored forest ecosystems within the Atlantic Forest, and (2) investigating the influence of various historical (e.g. age and type of restoration), biogeographic (e.g. latitude), climatic (e.g. temperature and precipitation), and biotic (e.g. plant species richness) factors on biomass and carbon accumulation in these sites undergoing restoration. Additionally, we (3) estimated the time required for tree biomass in restored forests to attain values commensurate with those observed in conserved native forests. Using this estimate as a threshold, we then (4) compared how different methods employed to assess plant biomass consistently under- or overestimate biomass stocks relative to our projections.

Methods

Search Protocol

Our search protocol focused on collecting all studies addressing biomass and carbon stocks in restoration systems within the Atlantic Forest, and included scientific papers, dissertations, and theses. We included dissertations and theses in our review, recognizing that some may remain unpublished but are likely to explore previously unstudied restoration sites, thereby increasing the spatial coverage of the data collected. We excluded reviews, meta-analyses, perspectives, and studies using geographic information systems as they lacked data on tree species composition and did not assess in situ biomass accumulation. We only considered studies conducted within the Brazilian Atlantic Forest that assessed carbon and plant biomass stocks in actively restored areas of known age. Secondary forests (i.e. naturally regenerated) were excluded due to uncertainty regarding their exact age, which could lead to potential pre-existing biomass accumulation at the onset of the carbon stock assessment.

We searched the Scopus, Web of Science, and Google Scholar databases for all available years (until December 2022). We selected studies that assessed carbon and biomass stocks in restoration sites, using the following keywords: “biomass” and “carbon” alongside: “restoration”, “recovery”,

“regeneration”, “re-sprout”, and “reforest”. These terms were included in the title, abstract, and/or keywords of publications, in both English and Portuguese (Fig. S1). We attempted to be as inclusive as possible, as standardization of restoration terminology is still in progress (McDonald et al. 2016).

Data Compilation

We compiled metadata on the publication year, research location (i.e. longitude, latitude, and elevation), local climatic conditions, physiognomy type, and the size and the age of the restoration system for each study included in the database. We used WorldClim 2 to assess the mean annual temperature and cumulative annual precipitation as representatives of the local climatic conditions (Fick & Hijmans 2017). Additionally, we recorded the minimum size of plants selected for biomass calculation, the number of plant species used during restoration implementation, the number of current plant species, the experimental design adopted, whether biomass and carbon stocks were compared between restored and adjacent native forests, and the restoration technique used during system implementation (e.g. planting and seeding).

Furthermore, we accessed the protocols employed to estimate tree biomass and carbon stocks. We extracted the following metrics: (1) type of measurement (e.g. aboveground and/or belowground—root biomass); (2) method of measurement (e.g. destructive or non-destructive); (3) allometric equations used to estimate biomass (i.e. literature source or locally adjusted); (4) inclusion of wood density in the equations; (5) the source of wood density used in the equations (e.g. literature or locally measured); (6) whether carbon stock was estimated by converting biomass into carbon; and (7) the metric used to convert biomass to carbon. We considered destructive carbon estimation methods to be those that involve ground-truthing by harvesting and weighing tree organs to directly measure biomass, whereas non-destructive methods were considered to be those that use allometric equations and indirect measurements for estimation.

Data Analysis

We tested whether historical (e.g. age), biogeographic (e.g. latitude and elevation), climatic (e.g. temperature and precipitation), and biotic factors (e.g. plant species richness) influence biomass and carbon accumulation in Atlantic Forest sites undergoing restoration. This also allowed us to estimate the time interval required for restored forests to reach biomass levels similar to those of conserved native reference forests. Using this estimate, we compared whether the type and method of measurement, the allometric equation used, and the inclusion of wood density consistently under- or overestimated biomass stocks relative to our projections.

To assess whether historical, biogeographic, climatic, and biotic variables influence biomass production in actively restored Atlantic Forest sites, we included only those studies ($n = 29$) from our database that provided the necessary information on local, biotic, and abiotic conditions for each site ($n = 104$). We then assessed the effects of these variables using

linear mixed models with the log-transformed biomass accumulated at each site as the response variable fitted against all predictor factors (i.e. temperature, precipitation, elevation, forest age, and plant species richness). For forest age, we included linear, quadratic, and cubic terms to capture potential non-linear relationships, as biomass stocks do not increase linearly over time. We log-transformed precipitation and elevation to account for scale differences and to improve the model fit. We also included the study identity as a random effect, because studies used different protocols to estimate biomass stocks and often examined multiple restoration sites. We used the corrected Akaike Information Criterion for small sample sizes (AICc) to identify the best model based on the lowest AICc obtained, comparing the full model (all predictor factors) to all other models, including possible combinations of predictors. Additionally, we assessed the relative importance (Σwi) of each predictor variable to the explanatory power of the model (Burnham & Anderson 2004) using the function “model.sel” in the *MuMIn* R package (Barton 2012). According to Symonds and Moussalli (2011), Σwi values represent the probability that a given particular predictor variable is included in the best-fit model. Because this analysis focused on restoration sites with specific spatial locations, we used univariate spline correlograms to assess the efficiency of each model in dealing with spatial autocorrelation and partial Mantel correlograms to assess the significance of spatial autocorrelation across 13 distance classes. Spatial autocorrelation analysis was performed using the R packages *spdep* (Bivand 2014) and *mpmcorrelogram* (Matesanz et al. 2011). Finally, we assessed the variance inflation factor (VIF) between predictors to test for collinearity using the *car* R package (Fox & Weisberg 2019).

To estimate the time interval required for restored forests to attain biomass stocks similar to those of conserved native reference forests, we compiled data from research previously identified in this study, specifically focusing on those that compared the restored area with the native reference forest ($n = 5$). In addition, we identified pertinent studies from the same databases and selected 11 sites with forest areas larger than 50 ha, resulting in a total of 16 studies that evaluated biomass stocks in ($n = 24$) native reference forests, including ($n = 14$). Seasonal Semideciduous Forests and ($n = 10$) Dense Rainforests (Table S1). Biomass data (Mg/ha) were recorded for each reference native forest, from which the mean and standard deviation values of biomass accumulation were calculated. Using an interpolation method, we determined the age (i.e. time in years) at which restored forests are expected to attain mean and standard deviation values comparable to those observed in conserved reference forests. We then calculated the residuals between predicted and observed biomass values at the same forest age for each study. These residuals represent the deviation of observed biomass in restored forests from our predictions for that age, based on native reference forests. Because the studies used different protocols for biomass assessment, we built four linear models, each with residuals as the response variable, to determine whether different aspects within these protocols led to under- or overestimates relative to our predictions. The fixed factors in each model were: type and method of biomass measurement (1), allometric equations (2), inclusion of wood density (3), and tree

sampling criteria based on diameter at breast height (DBH) (4), with each factor being used in a separate model. These factors represented different aspects within the protocols used by researchers to calculate biomass stocks. Differences were tested using a Tukey post hoc test with the *emmeans* R package (Lenth 2016).

Results

Out of 681 studies identified in our search protocol, 34 met the inclusion criteria and were thus included in this review (Table S2; Fig. S1). These studies were published between 2010 and 2022, with a notable increase in the cumulative number of publications after 2018, while the restoration projects spanned recovery periods ranging from 1.4 to 53 years (Fig. 1). Study sites spanned a wide elevational range (0–1550 m) and were conducted in only two distinct phytophysiognomies, with the Seasonal Semideciduous Forest receiving greater attention (28 studies—82%) than the Dense Rainforest (6—18%; Fig. 1B–D). There was a disproportionate

concentration of studies in the southeastern region, with comparatively fewer studies conducted in the southern- and northernmost regions of the Atlantic Forest. Restored sites ranged in size from 0.2 to 1519 ha, but most of the studies were conducted on sites smaller than 50 ha (26–76%). While site ages ranged up to 53 years, the majority of studies (26–74%) focused on sites with less than 15 years of restoration.

Nearly a half of the studies monitored plants DBH ≥ 5 cm (14–42%). Only three publications evaluated the herbaceous/shrub layer, with biomass accumulation in this compartment ranging from 0.20 to 10.62 Mg/ha. Only 12 studies (35%) implemented some form of experimental design, testing different spacings while assessing species growth rates. The remaining studies (22–65%) adopted a standardized spacing of 3×2 m among trees. Moreover, while most studies provided information on the number of species initially planted (28–82%), only 13–38% tracked the current status of plant species richness. Out of the 34 studies, 33 (97%) used seedling planting as the restoration technique, of which five (15%) also used direct

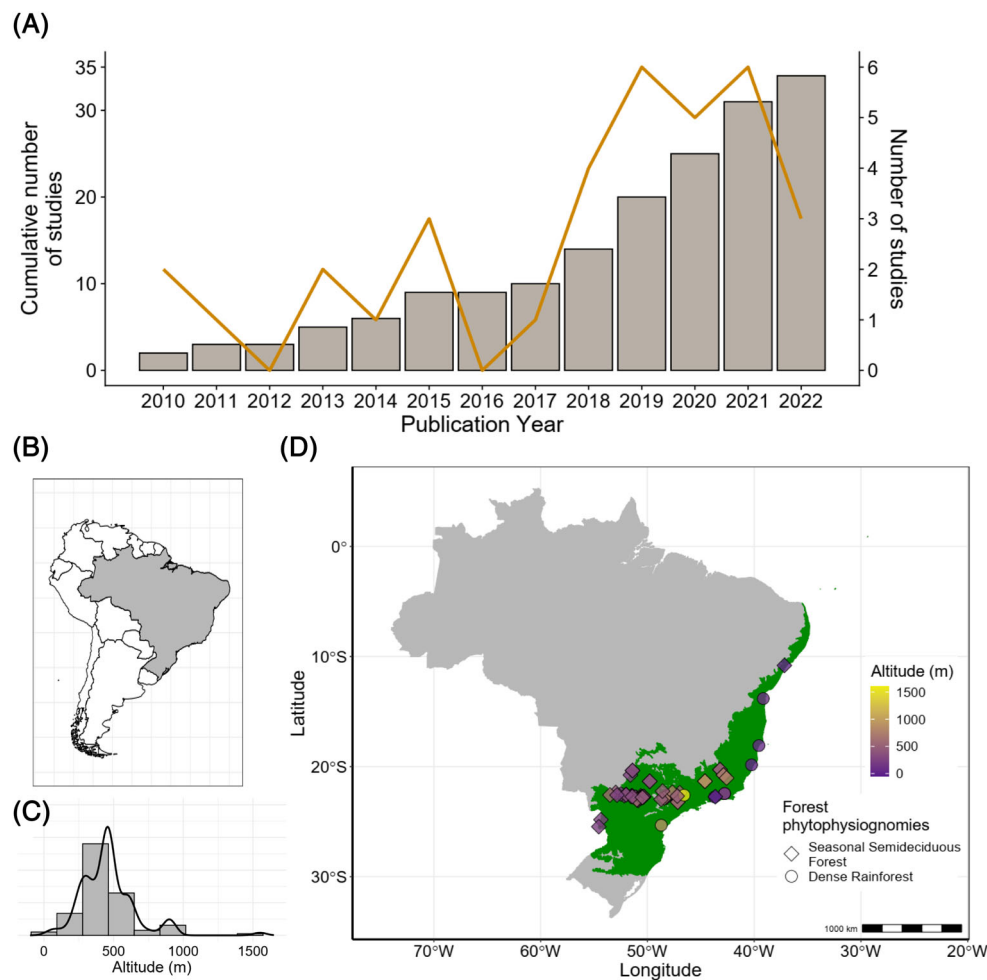


Figure 1. Number of publications assessing biomass and carbon stocks in the Atlantic Forest of Brazil. The left and right y-axes show the cumulative number of studies and the number of studies per year, respectively (A). The green polygon shows the theoretical distribution of the Atlantic Forest biome within Brazil and the points the location of restoration projects (B–D) and their respective elevations (C). Color gradients represent elevation, while point shapes depict different forest phytophysiognomies within the Atlantic Forest (in green; D).

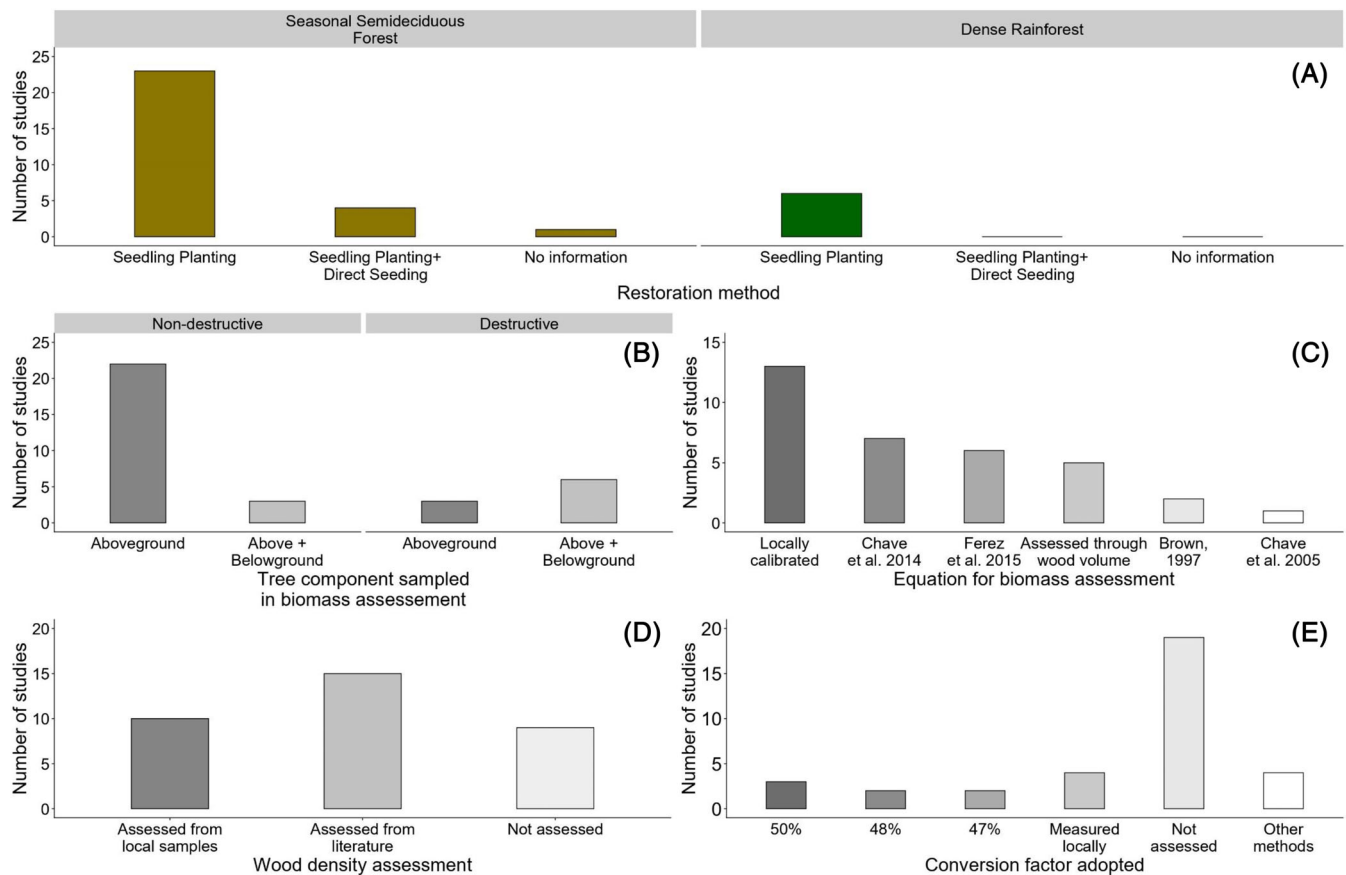


Figure 2. Protocol for estimating biomass and carbon stock in Atlantic Forest within Brazil. Restoration techniques employed according to Atlantic Forest phytophysiognomy (A). Assessed compartments for estimating biomass accumulation (B). Number of studies regarding the use of allometric equations for biomass estimation (C). Number of studies regarding methods used to determine wood density for use in the allometric equation (D). Number of studies converting biomass into carbon and the method employed for conversion (E).

seeding (Fig. 2A). Only one publication did not mention the technique used. Finally, only 11 studies (32%) compared biomass stock between restored and native reference forests.

The non-destructive method was the most frequently used to estimate biomass stocks among the studies analyzed (25 studies—74%; Fig. 2B). The focus was on aboveground biomass assessment, but biomass stocks varied widely among studies (ranging from 2 to 360 Mg/ha). Furthermore, sites with contrasting aboveground biomass accumulations did not necessarily differ in age. For example, the aboveground biomass in 12-year-old restored forests ranged from 11.25 to 192 Mg/ha. However, older restoration systems have generally accumulated more biomass over the years. For example, only seven out of 21 restored forests that accumulated more than 150 Mg/ha of biomass were less than 15 years. Only nine studies (26%) considered belowground biomass. They reported accumulations ranging from 2.1 to 28.63 Mg/ha, representing $(23 \pm 3.4\%)$ of the total forest biomass. Six out of these nine studies (17%) used the destructive method to estimate biomass in this component.

Only 13 studies (38%) used locally adjusted allometric equations to assess biomass stocks, and the remaining (21 studies—62%) used equations from the literature, with the most

commonly used equations being those of Chave et al. (2014) and Ferez et al. (2015), in seven (21%) and six (18%) studies, respectively (Fig. 2C). Furthermore, most of the studies (25–74%) included wood density in the allometric equations, but only 10 (38%) measured wood density on local trees (Fig. 2D). The Global Wood Density Database was the most commonly used data source by studies that obtained wood density externally (seven studies—21%), and four (12%) relied on Chave et al. (2005). Fifteen (44%) studies converted biomass into carbon. The assumed conversion factor ranged from 41 to 50% of the plant biomass (Fig. 2E).

Biomass accumulation in restored sites within the Atlantic Forest was only explained by forest age ($r^2 = 0.84$; $p < 0.001$; Fig. 3; and Table S3, Figs. S3 & S4 for relationships with all predictors). Based on the interpolation method, we estimated that biomass accumulation in restored forests approached the minimal value of conserved reference forests in 24.45 years, reaching an accumulated biomass of 193.11 ± 11.74 Mg/ha. Biomass accumulation increased until 40 years, reaching its maximum at 43 years (306.70 ± 26.79 Mg/ha), after which tends to stabilize, reaching values close to those observed in conserved native forests (294.032 ± 15.04 Mg/ha; Fig. 4A).

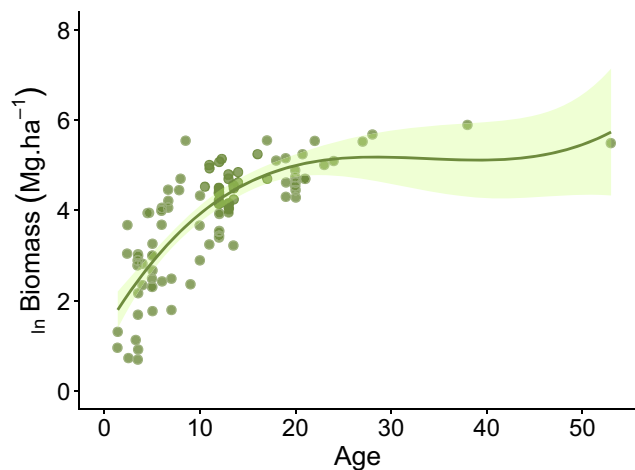


Figure 3. Relationship between forest age and biomass stock (Mg/ha) in Atlantic Forest restoration sites. The fitted curve, based on a linear mixed model, represents a polynomial relationship between observed biomass accumulation and forest age at restoration sites. Green points indicate biomass stocks measured at each restoration site.

Predictor variables showed low levels of collinearity ($VIF > 1.81$). Spatial autocorrelation did not affect our model, and partial Mantel correlograms indicated low levels of autocorrelation with only two out of 13 distance classes showing some autocorrelation (Fig. S2).

Type of study, that is, aboveground and/or belowground ($F_{[1,102]} = 6.16$); and measurement methods, that is, destructive or non-destructive ($F_{[1,102]} = 3.66$) influenced biomass estimates ($r^2 = 0.09$), with non-destructive methods that assessed both above and belowground compartments tending to underestimate biomass stocks. The destructive method generally provided results closer to the estimates in this study (Fig. 4B). Furthermore, allometric equations used to assess biomass yielded different biomass stocks ($F_{[4,99]} = 14.42$, $r^2 = 0.37$, $p < 0.001$), with the equations from Brown (1997) generally overestimating biomass, while other equations from the literature and locally calibrated equations yielded biomass stocks closer to our projections (Fig. 4C). Equations that included wood density generally yielded results more aligned with our projections than those that omitted wood density ($F_{[2,101]} = 9.32$, $r^2 = 0.16$, $p < 0.001$), which tended to overestimate biomass (Fig. 4D). Finally, no differences were found between studies with different tree sampling criteria ($F_{[3,100]} = 1.91$, $r^2 = 0.05$, $p = 0.13$; Fig. 4E).

Discussion

Forest restoration projects require long periods of time to restore the structure and functioning of ecosystems, and the recovery of biomass stocks is a slow process. Even when appropriate techniques are adopted, it usually takes several decades for restored areas to reach biomass levels similar to those of preserved natural forests (Jucker et al. 2020). This is associated with several factors, such as the initial species composition, proximity to natural fragments, soil conditions, history of land use, and also the

effects of climate change, which can alter the dynamics of species growth and succession (Crouzeilles et al. 2016; Feeley et al. 2020). We have found few studies assessing biomass stocks in restored Atlantic Forest. Although the restoration projects reviewed span recovery periods of up to 53 years, the studies were published between 2010 and 2022, underscoring that research on this topic is still recent. A notable increase in publication frequency after 2018 suggests a growing interest in understanding biomass recovery in this important ecosystem. However, even though the Atlantic Forest encompasses a large latitudinal range of Brazil, studies were mainly concentrated in the southeastern region, showing a strong geographical bias. Therefore, the exploration of new sites within the Atlantic Forest domain may be crucial to promote a more robust understanding of the effects of climatic conditions and local environmental characteristics on the productivity of restored sites. This is particularly important given that vegetation types within this forest domain vary with latitude, which may reflect differences in ecosystem function and productivity. For example, assessments of biomass and carbon stocks in restored Subtropical Forests (*Araucaria* forests) in the southernmost region and Deciduous Forests in the northernmost region have not yet been conducted, which impairs a holistic perspective regarding the carbon storage potential of restored sites within these phytophysiognomies. Therefore, understanding the differences in the structure, function, and productivity of restored sites located in different parts of the Atlantic Forest could help to create a coherent management plan to support the best strategies for restored forests with different plant profiles (Pontes et al. 2019).

In addition to climate and edaphic factors, the legacy of previous land use profoundly influences the trajectory and outcomes of forest restoration (Crouzeilles et al. 2016; Jakovac et al. 2021). For example, sites formerly subjected to intensive agriculture or cattle ranching often experience soil compaction, nutrient depletion, and altered microbial communities, all of which can delay biomass accumulation and hinder forest recovery (Krause et al. 2016; Parré et al. 2023). Furthermore, the proximity of restoration sites to conserved forest fragments plays a crucial role by facilitating ecological processes that underlie forest regeneration (Chazdon & Uriarte 2016; Ballarin et al. 2022). Consequently, both land use history and the surrounding landscape matrix must be taken into account when interpreting variations in biomass stocks across restored areas, thereby justifying the exploration of new sites that vary in these factors.

Root biomass has been overlooked in biomass assessments of restored forests. This trend also extends to other Brazilian biomes (Gardon et al. 2020), compromising the accuracy of estimates. Biomass estimates that do not consider the belowground compartment are biased because root biomass represents a significant proportion of the total biomass, ranging from 19.8% (Nogueira Junior 2010) to 33% of it (Ferez et al. 2015), depending on the species studied. As a result, biomass assessments that do not take into account the biomass from the belowground compartment may underestimate it by 1.7 Mg/ha (Ferez et al. 2015) to 38 Mg/ha (Watzlawick et al. 2003), depending on the age, composition of the plant community, and the management system adopted. We posit that this underestimation

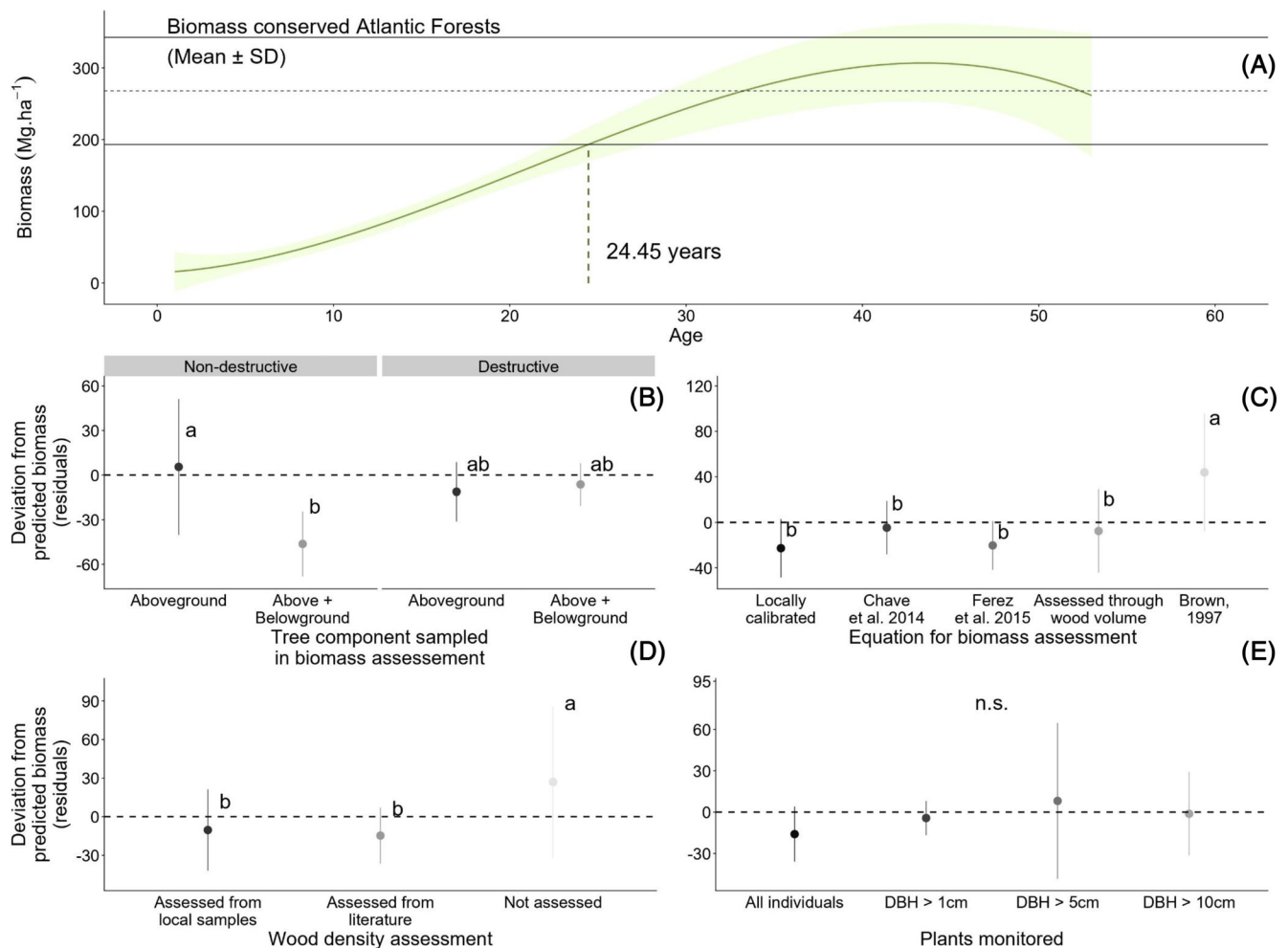


Figure 4. Predictions of biomass accumulation according to forest age and comparison of different methodological approaches used to assess biomass stocks in Atlantic Forest restored sites. Restored forests tend to achieve biomass stocks comparable to those observed in conserved forests at 24.45 years (vertical dashed green line; A). Black dashed and solid lines represent the mean ($\pm$ SD) of biomass stocks in conserved reference forests, respectively. Different methodological approaches to assess biomass accumulation in restoration sites may under- or overestimate biomass stock. Destructive methods generally yield biomass estimates more closely aligned with predictions based on forest age (B). Using the allometric equations proposed by Brown (1997) tends to overestimate biomass stock (C). Similarly, omitting wood density in equations results in overestimated values (D). Finally, no significant differences were observed among biomass assessments based on different DBH thresholds used as tree sampling criteria (E).

could be much higher, given our limited understanding of the representation of root biomass for the majority of native species in the Atlantic Forest. Thus, assessing root biomass is critical not only for calibrating biomass stock assessments but also for advancing our understanding of the proportion of biomass that roots represent in various native tropical tree species, a dimension that remains largely unexplored. Nevertheless, we recognize that not all studies have well-developed allometric equations for estimating root biomass (Vieira et al. 2008) and that destructive method adjustment is time-consuming and costly (Chave et al. 2014). In this case, the use of the non-destructive method is a viable alternative to estimate root biomass, as it can be easily applied using variables such as DBH, height, or aerial biomass (Cairns et al. 1997; Nogueira Junior et al. 2014; Rasera 2019).

The most commonly used method for biomass estimation was the non-destructive approach, mainly employing locally calibrated equations or those developed by Chave et al. (2014). Most of the allometric equations retrieved from the literature were calibrated for tropical forests, but did not include sites from the Atlantic Forest, with the exception of Chave et al. (2014), which focused only on a coastal sandbank rainforest. This underscores the urgent need to develop equations that are specifically tailored to the Atlantic Forest domain. For example, coastal sandbank rainforests have different structural and functional characteristics in terms of tree architecture and biomass accumulation compared to Semideciduous Seasonal Forests and Dense Rainforests within the Atlantic Forest. Such differences may compromise indirect estimates for restored habitats that aim to restore tropical rainforests, rather than coastal sandbank rainforests.

Our results show that the use of inappropriate equations can lead to significant deviations from actual biomass stock values. In particular, we caution against using allometric models from the literature to infer biomass stocks, as different equations—particularly those omitting wood density or based on non-destructive methods that assess only the arboreal aboveground compartment—can yield results that deviate significantly from biomass projections. Such wide variations are undesirable in biomass assessments. For example, within the same site, different equations can yield aboveground biomass estimates ranging from 215 to 461 Mg/ha (Chave et al. 2004).

We show that few studies have adjusted allometric equations using the destructive method. However, these equations provide biomass estimates that are more consistent with the biomass accumulated over time in conserved forests. We argue that equations based on the destructive method provide more accurate biomass estimates because trees are harvested and their organs are weighed, avoiding the biases that occur when proxies such as tree height and DBH are used to infer biomass (Tavoni et al. 2007). For example, the floristic composition of restored forests typically differs from that of conserved forests (Suganuma & Durigan 2015), with early successional and fast-growing species (Rodrigues et al. 2011; Charles et al. 2018) being more prevalent in the early stages of succession in restored sites. As a result, the physical and chemical properties of tree wood may differ between conserved and restored forests. Relying on allometric equations based on non-destructive methods may overlook these *in situ* differences, potentially affecting biomass estimates (Baker et al. 2004). This highlights the importance of accounting for such differences when assessing ecological parameters in restored habitats.

However, because adjusting models using destructive methods is time-consuming and costly (Watzlawick et al. 2009; Chave et al. 2014), we recommend incorporating plant functional traits, such as wood density, to more accurately reflect biomass accumulation in restored sites. Incorporating wood density measurements into allometric equations is more consistent with our biomass projections. In fact, wood density emerges as a crucial factor in allometric equations to explain plant biomass (Baker et al. 2004; Goodman et al. 2013; Chave et al. 2014). For instance, most of the publications used wood density as an independent variable in their models. However, a significant proportion of studies relied solely on wood density data from existing literature databases. This approach can be challenging, as local wood density is strongly correlated with forest age and local environmental conditions (Baker et al. 2004; Swenson & Enquist 2007; Ribeiro et al. 2020). Although the Global Wood Density Database (Zanne et al. 2009) is a useful source, it has been recommended to estimate wood density *in situ* whenever possible, as even the same plant species can show strong disparities in wood density depending on its provenance, age, and local conditions (Savva et al. 2010; Pompa-Garcia & Venegas-Gonzalez 2016; Assad et al. 2020).

Some studies have employed allometric equations with varying ages, in which equations developed for 6-year-old forests were applied to estimate biomass in forests from 2.5 to 15 years old (Brancalion et al. 2019; Badari et al. 2020). This approach

can lead to erroneous biomass estimates (Mores 2024) as hypso-metric relationships (i.e. height/diameter) change with forest age (Jones et al. 2019). Therefore, greater rigor is needed in the selection of predictive models, with attention to the tree sizes used in equation fitting (Brown 1997; Chave et al. 2004).

Carbon content has generally been estimated at 50% of dry biomass (Shimamoto et al. 2014; Azevedo et al. 2018). However, the IPCC (2007) recommends 47%, and in our review, we found studies using values as low as 41.2% (Meira et al. 2020). This variability can lead to errors in carbon storage estimates, highlighting the importance of more accurate carbon assessments (Zanini et al. 2021). For example, inaccuracies in estimates of total carbon stocks could underestimate the stored value by about 6 t/ha in 21-year-old restored forests (Silva et al. 2015). On a global scale, a mere 1% deviation in carbon content from the standard 50% results in a difference equivalent to 7 billion tons (Jones & O'Hara 2016). We suggest that further research is needed, albeit costly, to assess the carbon content of native species at different ages. Such efforts would culminate in the creation of a database of carbon values for each species, similar to the wood density database (Zanne et al. 2009), providing more accurate carbon estimates by avoiding the use of fixed values that do not reflect the reality of forests.

An important aspect that deserves attention in our analysis is the predominant focus of studies on the tree component alone, as it represents the primary biomass stock. Nonetheless, herbs, shrubs, and lianas together can account for approximately 5.9% of the total biomass (Torres et al. 2013), while soil carbon and accumulated litter can represent 56.2 and 9.1%, respectively, of the total biomass stock of a given forest (Zanini et al. 2021). The relative contribution of these different ecosystem components is expected to be substantial in restored forests (Parré et al. 2023), potentially exceeding 50% of the total accumulated biomass (Nogueira Junior 2010; Zanini et al. 2021), and should not be overlooked.

Nevertheless, uncertainty in biomass assessments can arise even when only the tree component is considered. In our review, a significant proportion of studies did not follow the most commonly used size inclusion criteria of DBH ≥ 5 cm (Chave et al. 2014) when sampling trees to estimate biomass stock. Furthermore, we show that sampling all plant individuals or those with DBH greater than 1 cm to assess biomass stocks results in less variation in biomass estimates than using higher DBH thresholds as the sampling criteria. We suggest that selecting plants with a larger minimum inclusion diameter, along with allometric equations with parameters that are not locally calibrated and omitting wood density, may lead to under- or overestimation of total biomass accumulation. This is particularly relevant in young restoration sites, where small-sized young trees and the understory plant community contribute more significantly to the biomass stock and may have different wood physical and chemical properties compared to older and larger trees (Guerin et al. 2021; Arcanjo & Torezan 2022).

Age emerged as the primary factor explaining biomass stocks in Atlantic Forest restoration sites. Older forests generally have higher biomass due to the time required for ecological succession and the stronger relationship between ecosystem

functioning and tree growth in mature forests (Crouzeilles et al. 2016; Jucker et al. 2020). While existing studies highlight the influence of biodiversity on biomass stocks (Forrester 2014; Pontes et al. 2019; Capellesso et al. 2021) and suggest that higher temperature and precipitation promote greater vegetation biomass (Zhang & Liang 2014; Wang et al. 2016; Tiwari et al. 2022), our findings indicate that forest age serves as a reliable proxy for biomass stocks in the Atlantic Forest. However, as we found a geographic bias in our systematic review, we suggest that incorporating novel biomass assessments across different Atlantic Forest phytophysognomies will broaden the spatial scope of the analysis, potentially increasing the importance of climatic variables on biomass accumulation in restoration sites. This is particularly important given the predicted increase in temperature and the likelihood of extreme climate events due to climate change in Brazil (Ballarin et al. 2023), which may affect forest biomass accumulation and productivity in the future (Liu et al. 2014).

Some restored forests have reached biomass levels close to 190 Mg/ha (Suganuma 2013; César et al. 2018; Guerin et al. 2021). We predict that after 25 years, the average biomass stock in restored forests will closely resemble that of conserved native forests, a trend observed in other local studies in the Atlantic Forest (Melo & Durigan 2006; Suganuma & Durigan 2015). However, after 40 years, we observed a stabilization of biomass stocks within restoration sites, which may be attributed to tree mortality from natural system exits or competition leading to self-thinning (Westoby 1984; Hood et al. 2018; Brown et al. 2019). However, it is important to note that, although the conserved forests used as reference sites are considered well conserved, the extent to which their history of past disturbance (e.g. timber exploitation) has influenced their current structure remains uncertain, which may have influenced biomass accumulation rates and the biomass predictions developed in our study.

In this study, we aimed to identify gaps and trends in biomass and carbon estimates in actively restored sites within the Atlantic Forest and suggest directions for future research. Our findings reveal several key trends in biomass studies in restoration systems: (1) Although the interest in the topic has increased significantly in recent years, the number of studies remains limited. (2) There is a significant geographic and physiognomic bias, with a concentration of studies in the Southeast Region and Semideciduous Seasonal Forests, limiting the ability to generalize biomass assessments across the Atlantic Forest. (3) Few studies have adjusted equations to estimate root biomass, which may lead to significant underestimation of total biomass. (4) The number of publications adjusting allometric equations using local wood density is relatively low, especially for older restored forests. (5) Forest age stands out as the most important proxy for inferring biomass stocks in the Atlantic Forest. Taken together, these results highlight the need for increased research on biomass and carbon stock estimation in restored Atlantic Forests, especially in regions outside the Southeast and under different environmental conditions. Future research should prioritize the use of locally calibrated equations for similar forests, incorporate local wood density data, and include root biomass estimates to improve the accuracy of biomass assessments.

Acknowledgments

We thank Coordenação de Aperfeiçoamento de Pessoal de Nível Superior—Brasil (Finance Code 001) for supporting G.J. M. PhD study. C.S.B. is associated with the Center for Research on Biodiversity Dynamics and Climate Change (CEPID FAPESP no. 2021/10639-5) through a postdoctoral research grant (FAPESP no. 2024/02640-1). The Article Processing Charge for the publication of this research was funded by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - Brasil (CAPES) (ROR identifier: 00x0ma614).

LITERATURE CITED

- Araújo EJGD, Loureiro GH, Sanquetta CR, Sanquetta MNI, Corte APD, Péllico Netto S, Behling A (2018) Allometric models to biomass in restoration areas in the Atlantic rain forest. *Floresta e Ambiente* 25:e20160193. <https://doi.org/10.1590/2179-8087.019316>
- Arcanjo FA, Torezan JMD (2022) Aboveground biomass accumulation and tree size distribution in seasonal Atlantic Forest restoration sites. *Restoration Ecology* 31:1–7. <https://doi.org/10.1111/rec.13669>
- Assad AAV, Ballarin AW, Freitas MLM, Longui EL (2020) Effect of provenances on wood properties of *Balfourodendron riedelianum*. *Madera y Bosques* 26:1–24. <https://doi.org/10.21829/myb.2020.2611905>
- Azevedo AD, Francelino MR, Camara R, Pereira MG, Leles PSS (2018) Estoque de carbono em áreas de restauração florestal da mata atlântica. *Floresta* 2:183–193. <https://doi.org/10.5380/rf.v48i2.54447>
- Badari CG, Bernardini LE, Almeida DRA, Brancalion PHS, César RG, Gutiérrez V, Chazdon RL, Gomes HB, Viani RAG (2020) Ecological outcomes of agroforests and restoration 15 years after planting. *Restoration Ecology* 28:1135–1144. <https://doi.org/10.1111/rec.13171>
- Baker TR, Philips OL, Malhi Y, Almeida S, Arroyo L, Di Fiore A, et al. (2004) Variation in wood density determines spatial patterns in Amazonian Forest biomass. *Global Change Biology* 5:545–562. <https://doi.org/10.1111/j.1365-2486.2004.00751.x>
- Ballarin AS, Sone JS, Gesualdo GC, Schwambach D, Reis A, Almagro A, Wendland EC (2023) CLIMBra-climate change dataset for Brazil. *Scientific Data* 10:47. <https://doi.org/10.1038/s41597-023-01956-z>
- Ballarin CS, Amorim FW, Watson DM, Fontúrbel FE (2024) The use and abuse of keystone plant species in restoration practices of terrestrial ecosystems. *Restoration Ecology* 32:e14030. <https://doi.org/10.1111/rec.14030>
- Ballarin CS, Hachuy-Filho L, Fontúrbel FE, Amorim FW (2022) Density-dependent effects on the reproductive outcome of a native tree at tropical restored habitats. *Forest Ecology and Management* 520:120391. <https://doi.org/10.1016/j.foreco.2022.120391>
- Barton K (2012) MuMIn: multi-model inference. R package version 1.7.2. <http://CRAN.R-project.org/package=MuMIn> (accessed 20 Apr 2025)
- Bivand RS (2014) SPDEP: spatial dependence: weighting schemes, statistics and models. R package v.0.5-74. <http://CRAN.R-project.org/package=spdep> (accessed 20 Apr 2025)
- Brancalion PHS, Campoe O, Mendes JCY, Noel C, Moreira GG, Melis JV, Stape JL, Guillemot J (2019) Intensive silviculture enhances biomass accumulation and tree diversity recovery in tropical forest restoration. *Ecological Applications* 29:1–12. <https://doi.org/10.1002/eap.1847>
- Brown GW, Murphy A, Fanson B, Tolma A (2019) The influence of different restoration thinning treatments on tree growth in a depleted forest system. *Forest Ecology and Management* 437:10–16. <https://doi.org/10.1016/j.foreco.2019.01.022>
- Brown S (1997) Estimating biomass and biomass change of tropical forests: a primer. For the Food and Agriculture Organization of the United Nations. FAO Forestry Paper. Food and Agriculture Organization of the United Nations, Rome, Italy

- Burnham KP, Anderson DR (2004) Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods & Research* 33:261–304. <https://doi.org/10.1177/0049124104268644>
- Cairns MA, Brown S, Helmer EH, Baumgardner GA (1997) Root biomass allocation in the world's upland forests. *Oecologia* 111:1–11. <https://doi.org/10.1007/s004420050201>
- Capellesso ES, Ceniuel A, Marques R, Sausen TL, Bayer C, Marques MCM (2021) Co-benefits in biodiversity conservation and carbon stock during forest regeneration in a preserved tropical landscape. *Forest Ecology and Management* 492:1–9. <https://doi.org/10.1016/j.foreco.2021.119222>
- César RG, Moreno VS, Coletta GD, Chazdon RL, Ferraz SFB, de Almeida DRA, Brancalion PHS (2018) Early ecological outcomes of natural regeneration and tree plantations for restoring agricultural landscapes. *Ecological Applications* 28:373–384. <https://doi.org/10.1002/eap.1653>
- Charles LS, Dwyer JM, Smith TJ, Connors S, Marchner P, Mayfield MM (2018) Species wood density and the location of planted seedlings drive early-stage seedling survival during tropical forest restoration. *Journal of Applied Ecology* 55:1009–1018. <https://doi.org/10.1111/1365-2664.13031>
- Chave J, Condit R, Aguilar S, Hernandez A, Lao S, Perez R (2004) Error propagation and scaling for tropical forest biomass estimates. *Philosophical Transactions of the Royal Society* 359:409–420. <https://doi.org/10.1098/rstb.2003.1425>
- Chave J, Andalo C, Brown S, Cairns MA, Chambers JQ, Eamus D, et al. (2005) Tree allometry and improved estimation of carbon stocks and balance in tropical forests. *Oecologia* 145:87–99. <https://doi.org/10.1007/s00442-005-0100-x>
- Chave J, Réjou-Méchain M, Búrquez A, Chidumayo E, Colga MS, Delitti WBC, et al. (2014) Improved allometric models to estimate the aboveground biomass of tropical trees. *Global Change Biology* 20:3177–3190. <https://doi.org/10.1111/gcb.12629>
- Chazdon RL (2008) Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science* 320:1458–1460. <https://doi.org/10.1126/science.1155365>
- Chazdon RL, Uriarte M (2016) Natural regeneration in the context of large-scale forest and landscape restoration in the tropics. *Biotropica* 48:709–715. <https://doi.org/10.1111/btp.12409>
- Crouzeilles R, Curran M, Ferreira MS, Lindenmayer DB, Grelle CE, Rey Benayas JM (2016) A global meta-analysis on the ecological drivers of forest restoration success. *Nature Communications* 7:11666. <https://doi.org/10.1038/ncomms11666>
- DeLuca TH, Aplet GH, Wilmer B, Burchfield J (2010) The unknown trajectory of forest restoration: a call for ecosystem monitoring. *Journal of Forestry* 108:288–295. <https://doi.org/10.1093/jof/108.6.288>
- Feeley KJ, Bravo-Avila C, Fadrique B, Perez TM, Zuleta D (2020) Climate-driven changes in the composition of New World plant communities. *Nature Climate Change* 10:965–970. <https://doi.org/10.1038/s41558-020-0873-2>
- Ferez APC, Campoe O, Mendes JCT, Stape JL (2015) Silvicultural opportunities for increasing carbon stock in restoration of Atlantic forests in Brazil. *Forest Ecology and Management* 350:40–45. <https://doi.org/10.1016/j.foreco.2015.04.015>
- Fick SE, Hijmans RJ (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37:4302–4315. <https://doi.org/10.1002/joc.5086>
- Flores O, Coomes DA (2011) Estimating the wood density of species for carbon stock assessments. *Methods in Ecology and Evolution* 2:214–220. <https://doi.org/10.1111/j.2041-210X.2010.00068.x>
- Forrester DI (2014) The spatial and temporal dynamics of species interactions in mixed-species forests: from pattern to process. *Forest Ecology and Management* 312:282–292. <https://doi.org/10.1016/j.foreco.2013.10.003>
- Fox J, Weisberg S (2019) *An R companion to applied regression*. 3rd ed. Sage, Thousand Oaks, California
- Gardon FR, Santos RF, Rodrigues RR (2020) Brazil's forest restoration, biomass and carbon stocks: a critical review of the knowledge gaps. *Forest Ecology and Management* 462:1–10. <https://doi.org/10.1016/j.foreco.2020.117972>
- Gatto A, Bussinguer AP, Ribeiro FC, Azevedo GB, Bueno MC, Monteiro MM, Souza PF (2014) Ciclagem e balanço de nutrientes no sistema solo-planta em um plantio de *Eucalyptus* sp., no Distrito Federal. *Revista Brasileira de Ciência do Solo* 38:879–887. <https://doi.org/10.1590/S0100-06832014000300019>
- Goodman RC, Phillips OL, Torres DC, Freitas L, Cortese ST, Monteagudo A, Baker TR (2013) Amazon palm biomass and allometry. *Forest Ecology and Management* 310:994–1004. <https://doi.org/10.1016/j.foreco.2013.09.045>
- Guerin N, Mendes FBG, Cianciaruso MV, Suganuma MS, Durigan G (2021) Pure or mixed plantings equally enhance the recovery of the Atlantic forest. *Forest Ecology and Management* 484:1–9. <https://doi.org/10.1016/j.foreco.2021.118932>
- Holl KD (2017) Restoring tropical forests from the bottom up. *Science* 355:455–456. <https://doi.org/10.1126/science.aam5432>
- Hood SM, Cluck DR, Jones BE, Pinnell S (2018) Radial and stand-level thinning treatments: 15-year growth response of legacy ponderosa and Jeffrey pine trees. *Restoration Ecology* 26:813–819. <https://doi.org/10.1111/rec.12638>
- IPCC (Intergovernmental Panel on Climate change) (2007) Impacts, adaptation and vulnerability. Contribution of working group II to the fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom
- Jakovac CC, Junqueira AB, Crouzeilles R, Peña-Claros M, Mesquita RC, Bongers F (2021) The role of land-use history in driving successional pathways and its implications for the restoration of tropical forests. *Biological Reviews* 96:1114–1134. <https://doi.org/10.1111/bvr.12694>
- James JN, Kates N, Kuhn CD, Littlefield CE, Miller CW, Bakker JD, Butman DE, Haugo RD (2018) The effects of forest restoration on ecosystem carbon in western North America: a systematic review. *Forest Ecology and Management* 429:625–641. <https://doi.org/10.1016/j.foreco.2018.07.029>
- Joly CA, Metzger JP, Tabarelli M (2014) Experiences from the Brazilian Atlantic Forest: ecological findings and conservation initiatives. *New Phytologist* 204:459–473. <https://doi.org/10.1111/nph.12989>
- Jones DA, O'Hara KL (2016) The influence of preparation method on measured carbon fractions in tree tissues. *Tree Physiology* 36:1177–1189. <https://doi.org/10.1093/treephys/tpw051>
- Jones IL, DeWalt SJ, Lopez OR, Bunnefeld L, Pattison Z, Dent DH (2019) Above- and belowground carbon stocks are decoupled in secondary tropical forests and are positively related to forest age and soil nutrients respectively. *Science of the Total Environment* 697:e133987. <https://doi.org/10.1016/j.scitotenv.2019.133987>
- Jucker T, Koricheva J, Finér L, Bouriaud O, Iacopetti G, Coomes DA (2020) Good things take time—diversity effects on tree growth shift from negative to positive during stand development in boreal forests. *Journal of Ecology* 108:2198–2211. <https://doi.org/10.1111/1365-2745.13464>
- Krause A, Pugh TA, Bayer AD, Lindeskog M, Arneth A (2016) Impacts of land-use history on the recovery of ecosystems after agricultural abandonment. *Earth System Dynamics* 7:745–766. <https://doi.org/10.5194/esd-7-745-2016>
- Lenth RV (2016) Least-squares means: the R package lsmeans. *Journal of Statistical Software* 69:1–33. <https://doi.org/10.18637/jss.v069.i01>
- Lewis SL, Wheeler CE, Mitchard ETA, Koch A (2019) Restoring natural forests is the best way to remove atmospheric carbon. *Nature* 568:5–28. <https://doi.org/10.1038/d41586-019-01026-8>
- Liu Y, Guirui Y, Wang Q, Zhang Y (2014) How temperature, precipitation and stand age control the biomass carbon density of global mature forests. *Global Ecology and Biogeography* 23:323–333. <https://doi.org/10.1111/geb.12113>
- Locatelli B, Catterall CP, Imbach P, Kumar C, Lasco R, Marín-Spiotta E, Mercer B, Powers JS, Schwartz N, Uriarte M (2015) Tropical reforestation and climate change: beyond carbon. *Restoration Ecology* 23:337–343. <https://doi.org/10.1111/rec.12209>
- Matesanz S, Gimeno TE, de la Cruz M, Escudero A, Valladares F (2011) Competition may explain the fine-scale spatial patterns and genetic structure of two co-occurring plant congeners. *Journal of Ecology* 99:838–848. <https://doi.org/10.1111/j.1365-2745.2011.01812.x>

- McDonald T, Gann G, Jonson J, Dixon K (2016) International standards for the practice of ecological restoration – including principles and key concepts. Society for Ecological Restoration, Washington, D.C.
- Meira ACS, Mello AA, Sanquetta CR, Ferreira RA (2020) Estimativas de biomassa e carbono em área de mata atlântica, implantada por meio de reflorestamento misto. *BIOFIX Scientific Journal* 5:130–134. <https://doi.org/10.5380/biofix.v5i1.67298>
- Melo ACG, Durigan G (2006) Fixação de carbono em reflorestamentos de matas ciliares no Vale do Paranapanema, SP, Brasil. *Scientia Forestalis* 71:149–154. <https://www.ipef.br/publicacoes/scientia/nr71/cap15.pdf> (accessed Apr 2024)
- Mittermeier RA, Gil PR, Hoffmann M, Pilgrim J, Brooks J, Mittermeier CG, Lamourux J, Fonseca GAB (2004) Hotspots revisited: earth's biologically richest and most endangered terrestrial ecoregions. Cermex, Washington, DC, USA
- Mores GJ (2024) Biomassa arbórea e carbono em áreas de restauração da Mata Atlântica. PhD dissertation. São Paulo State University Júlio de Mesquita Filho, Unesp, São Paulo, Brazil.
- Myers N, Mittermeier R, Mittermeier C, Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. *Nature* 403:853–858. <https://doi.org/10.1038/35002501>
- Nogueira Junior LR (2010) Estoque de carbono na fitomassa e mudanças nos atributos do solo em diferentes modelos de restauração da Mata Atlântica. PhD dissertation. São Paulo University, ESALQ, São Paulo, Brazil.
- Nogueira Junior LR, Engel VL, Parrotta JA, Melo ACGD, Ré DS (2014) Allometric equations for estimating tree biomass in restored mixed-species Atlantic Forest stands. *Biota Neotropica* 14:e20130084. <https://doi.org/10.1590/1676-06032013008413>
- Oliveira RE, Engel VL (2017) A restauração florestal na mata atlântica: três décadas em revisão. *Revista Ciência, Tecnologia & Ambiente* 5:40–48. <https://doi.org/10.4322/2359-6643.05101>
- Palmer MA (2016) Persistent and emerging themes in the linkage of theory to restoration practice. Pages 517–538. In: Palmer MA, Zedler JB, Falk DA (eds) *Foundations of restoration ecology*. Island Press, Washington, D.C. <https://doi.org/10.5822/978-1-61091-698-118>
- Parré FM, Loliola PP, Ballarin CS, Monquero PA (2023) Impact of invasive plant management on soil activity and litter decomposition in a tropical forest restoration. *Restoration Ecology* 31:e13906. <https://doi.org/10.1111/rec.13906>
- Peichl M, Arain MA (2007) Allometry and partitioning of above- and belowground tree biomass in an age-sequence of white pine forests. *Forest Ecology and Management* 253:68–80. <https://doi.org/10.1016/j.foreco.2007.07.003>
- Pompa-García M, Venegas-Gonzalez A (2016) Temporal variation of wood density and carbon in two elevational sites of *Pinus cooperi* in relation to climate response in northern Mexico. *PLoS One* 11:1–17. <https://doi.org/10.1371/journal.pone.0156782>
- Pontes DMF, Engel VL, Parrotta JA (2019) Forest structure, wood standing stock, and tree biomass in different restoration systems in the Brazilian Atlantic forest. *Forests* 10:1–18. <https://doi.org/10.3390/f10070588>
- Rasera S (2019) Biomassa e carbono no estrato arbóreo em área restaurada de Mata Atlântica. MSc dissertation. São Paulo University, ESALQ, São Paulo, Brazil.
- Ribeiro MDSB, Rodrigues SA, Ballarin AW (2020) Multivariate association of wood basic density with site and plantation variables in *Eucalyptus* spp. *Canadian Journal of Forest Research* 2:193–202. <https://doi.org/10.1139/cjfr-2019-0220>
- Ribeiro MC, Metzger JP, Martensen AC, Ponzoni FJ, Hirota MM (2009) The Brazilian Atlantic forest: how much is left, and how is the remaining forest distributed? Implications for conservation. *Biological Conservation* 142:1141–1153. <https://doi.org/10.1016/j.biocon.2009.02.021>
- Rodrigues RR, Gandolfi S, Nave AG, Aronson J, Barreto TE, Vidal CY, Brancalion PHS (2011) Large-scale ecological restoration of high-diversity tropical forests in SE Brazil. *Forest Ecology and Management* 261:1605–1613. <https://doi.org/10.1016/j.foreco.2010.07.005>
- Rodrigues RR, Lima RAF, Gandolfi S, Nave AG (2009) On the restoration of high diversity forests: 30 years of experience in the Brazilian Atlantic Forest. *Biological Conservation* 142:1242–1251. <https://doi.org/10.1016/j.biocon.2008.12.008>
- Savva Y, Koubaa A, Tremblay F, Bergeron Y (2010) Effects of radial growth, tree age, climate, and seed origin on wood density of diverse jack pine populations. *Trees* 24:53–65. <https://doi.org/10.1007/s00468-009-0378-0>
- Shimamoto CY, Botosso PC, Marques MC (2014) How much carbon is sequestered during the restoration of tropical forests? Estimates from tree species in the Brazilian Atlantic forest. *Forest Ecology and Management* 329:1–9. <https://doi.org/10.1016/j.foreco.2014.06.002>
- Silva HF, Ribeiro SC, Botelho AS, Faria RAVB, Teixeira MBR, Mello JM (2015) Estimativa do estoque de carbono por métodos indiretos em área de restauração florestal em Minas Gerais. *Scientia Forestalis* 43:943–953. <https://doi.org/10.18671/scifor.v43n108.18>
- Silva JMC, Casteleti CHM (2003) Status of the biodiversity of the Atlantic Forest of Brazil. Pages 43–59. In: Galindo-Leal C, Câmara IG (eds) *The Atlantic Forest of South America: biodiversity status, threats, and outlook*. Center for Applied Biodiversity Science and Island Press, Washington, D.C.
- Suganuma MS (2013) Trajetórias sucessionais e fatores condicionantes na restauração de matas ciliares em região de floresta estacional semidecidual. PhD dissertation. São Paulo University, São Carlos, Brazil.
- Suganuma MS, Durigan G (2015) Indicators of restoration success in riparian tropical forests using multiple reference ecosystems. *Restoration Ecology* 23:238–251. <https://doi.org/10.1111/rec.12168>
- Swenson NG, Enquist BJ (2007) Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. *American Journal of Botany* 94:451–459. <https://doi.org/10.3732/ajb.94.3.451>
- Symonds MR, Moussalli A (2011) A brief guide to model selection, multimodel inference and model averaging in behavioural ecology using Akaike's information criterion. *Behavioral Ecology and Sociobiology* 65:13–21. <https://doi.org/10.1007/s00265-010-1037-6>
- Tavoni M, Sohngen B, Bosetti V (2007) Forestry and the carbon market response to stabilize climate. *Energy Policy* 35:5346–5353. <https://doi.org/10.1016/j.enpol.2006.01.036>
- Tiwari RM, Liu J, Xie Y, Yao S, Liu S, Wu S, et al. (2022) Decoupling the impact of biodiversity and environmental factors on the biomass and biomass growth of trees in subtropical forests. *Journal of Plant Ecology* 16:1–15. <https://doi.org/10.1093/jpe/rtac040>
- Torres CMME, Jacovine LAG, Soares CPB, Oliveira Neto SN, Santos RD, Castro Neto F (2013) Quantificação de biomassa e estocagem de carbono em uma floresta estacional semidecidual, no parque tecnológico de Viçosa, MG. *Revista Árvore* 37:647–655. <https://doi.org/10.1590/S0100-6722013000400008>
- Van Breugel M (2007) Dynamics of secondary forests. PhD dissertation. C.T. de Wit Graduate School Production, Ecology & Resource Conservation, Wageningen University, Wageningen, The Netherlands.
- Viani RA, Holl KD, Padovezi A, Strassburg BB, Farah FT, Garcia LC, et al. (2017) Protocol for monitoring tropical forest restoration: perspectives from the Atlantic Forest restoration pact in Brazil. *Tropical Conservation Science* 10:1940082917697265. <https://doi.org/10.1177/1940082917697265>
- Vieira SA, Alves LF, Aidar M, Araújo LS, Baker T, Batista JLF, et al. (2008) Estimation of biomass and carbon stocks: the case of the Atlantic Forest. *Biota Neotropica* 8:21–29. <https://doi.org/10.1590/S1676-06032008000200001>
- Wang P, Heijmans MMPD, Mommer L, Ruyven JV, Maximov TC, Berendse F (2016) Belowground plant biomass allocation in tundra ecosystems and its relationship with temperature. *Environmental Research Letters* 11:e055003. <https://doi.org/10.1088/1748-9326/11/5/055003>
- Watzlawick LF, Sanquetta CR, Arce JE, Balbinot R (2003) Quantificação de biomassa total e carbono orgânico em povoamentos de *Araucaria angustifolia* (BERT.) O. Kuntze no sul do estado do Paraná, Brasil. *Revista Acadêmica: Ciências Agrárias e Ambientais* 1:63–68. <https://doi.org/10.7213/cienciaanimal.v1i2.14919>
- Watzlawick LF, Kirchner FF, Sanquetta CR (2009) Estimativa de biomassa e carbono em floresta com araucária utilizando imagens do satélite IKONOS II. *Ciência florestal* 19:169–181. <https://doi.org/10.5902/19805098408>

- Westoby M (1984) The self-thinning rule. Pages 167–225. In: Advances in ecological research. Vol 14. Academic Press. Cambridge, MA.
- Zanini AM, Mayrinck RC, Vieira SA, de Camargo PB, Rodrigues RR (2021) The effect of ecological restoration methods on carbon stocks in the Brazilian Atlantic Forest. *Forest Ecology and Management* 481:118734. <https://doi.org/10.1016/j.foreco.2020.118734>
- Zanne A, Lopez-Gonzalez G, Coomes DA, Llic J, Jansen S, Lewis SL, Miller RB, Swenson NG, Wiemann MC, Chave J (2009) Data from: towards a worldwide wood economics spectrum, Dryad, dataset. <https://doi.org/10.5061/dryad.234>
- Zhang Y, Liang S (2014) Changes in forest biomass and linkage to climate and forest disturbances over northeastern China. *Global Change Biology* 20: 2596–2606. <https://doi.org/10.1111/gcb.12588>

Coordinating Editor: Estefania P. Fernandez Barrancos

Supporting Information

The following information may be found in the online version of this article:

Table S1. List of data from selected native forests.

Table S2. List of data from publications selected in the databases.

Table S3. Values predicted by the model selected by the Akaike Information Criterion for the predictor variables.

Figure S1. Flowchart of the publication search protocol on biomass and carbon stocks in Atlantic Forest restoration systems.

Figure S2. Interpretation of model performance.

Figure S3. Correlation between biomass accumulation and all predictor variables.

Figure S4. Linear and non-linear relationships between variables.

Received: 24 June, 2024; First decision: 22 November, 2024; Revised: 2 July, 2025; Accepted: 29 September, 2025