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ECOSYSTEMS

Carbon stock in aboveground biomass and necromass in the Atlantic Forest: an analysis of data published between 2000 and 2021

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Abstract: Synthesising knowledge on carbon stocks is an essential tool for understanding the potential of forests to store carbon and its drivers. However, such a synthesis needs to be constructed for the Atlantic Forest due to various methodological approaches and biogeographic heterogeneity. Thus, here we conducted a bibliographic search (2000 to 2021) on carbon stocks in the biomass and necromass of Atlantic Forest ecosystems to understand the variation in stocks and their explanatory variables. Drivers included spatial (altitude, forest size) and climatic (precipitation and temperature) variables, and successional stages. Based on the information in 46 articles, biomass exhibited the highest carbon stock (96%), in Mature Forests (MF), with an average of 125.34±40.3 MgC.ha^{-1}, whereas Secondary Forests (SF) stored 82.7±38.2 MgC.ha^{-1}. The carbon in the necromass varied from 1.63 to 11.47 MgC.ha^{-1}, with SF exhibiting 3.90±2.73 MgC.ha^{-1} and MF 4.31±2.82 MgC.ha^{-1}. Only average annual precipitation and successional stage positively explained the carbon in Atlantic Forest. This research clarifies the function and potential of Atlantic Forest fragments for storing carbon and reinforces need for conserving mature forest patches throughout the biome since one hectare of mature forest can store almost twice as much carbon as one hectare of secondary young patches.

Key words: Tropical Forest, carbon estimates, dead organic matter, litter, climate, disturbance.

INTRODUCTION

Tropical forests occupy 45% of the world's forests and play a multiplicity of roles, including the maintenance of biodiversity and provision of ecosystem services, as well as the associated benefits for human well-being (Keenan et al. 2015, FAO 2020). These forests are amongst the most complex and diverse ecosystems globally, exhibiting high densities and richness of tree species. The diversity of forms and functions of tropical forest communities allows a large amount of carbon to be stored in their compartments (Decuyper et al. 2018). The carbon reservoirs in forest ecosystems, as defined by The Intergovernmental Panel on Climate Change (IPCC 2006), include aboveground (trunks, branches and leaves) and belowground (roots) biomass and the dead aboveground matter, also known as necromass. The latter compartment includes fine litter (plant pieces with a diameter ≤10 cm) and coarse woody debris (diameter ≥ 10 cm), which can be further divided into standing dead trees and fallen trees and trunks (Higa 2014, Barbosa et al. 2017, Fonsêca et al. 2019).

Tree biomass accounts for the most considerable aboveground fraction of the carbon stored in forest ecosystems and is also the most studied (Pfeifer et al. 2015, Silva et al. 2018), second only to C stored in the soil, which is three times greater than the amount stored in the vegetation (Scharleman et al. 2014). On the other hand, aboveground necromass is commonly neglected in forest studies, despite also comprising a significant fraction of the total carbon stocks in tropical forests. Aboveground necromass usually ranges between 10 to 20% (Houghton et al. 2001), although it can reach up to 40% of the total stocks (Palace et al. 2012). Belowground biomass (roots), although acknowledged as contributing a considerable portion of the total biomass and carbon, is rarely assessed, as its quantification is time-consuming and demands high costs (Diniz et al. 2015). Thus, belowground biomass and carbon are most often estimated from the root-to-shoot ratio of trees using the conversion factor of 0.24, indicated for all tropical forests (Cairns et al. 1997) and recommended by the IPCC (2006).

Undeniably, thorough assessments of tropical forests biomass and necromass storage are required to understand forest ecosystem dynamics and functioning. In addition, we must comprehend the drivers that explain the amount of carbon stored in each compartment. However, in some tropical forests, such as the Brazilian Atlantic Forest, there has been great difficulty in systematising information about the potential of forests to store carbon in biomass and necromass and the pattern of this storage throughout the biome (Vieira et al. 2008, Anderson-Teixeira et al. 2016). Located mainly in Brazil, the Atlantic Forest is a global priority for biodiversity conservation (Mittermeier et al. 1997). It holds exceptional species diversity and endemism levels, housing approximately 20,000 species, of which at least 6,000 are endemic (Marques & Grelle 2021). The Atlantic Forest domain includes a series of vegetation types (Silva et al. 2017), mainly due to significant geographical differences within its distribution associated with climate variation, which resulted in the development of different plant communities (Stehmann et al. 2009). As a result, diverse formations are found, comprising Dense Ombrophilous, Open and Mixed Forests, as well as Seasonal Semideciduous and Deciduous forests - which originally represented approximately 85% of this phytogeographic domain's coverage (IBGE 2019). It is currently considered one of the five most important biodiversity hotspots on the planet and a priority area for conserving biodiversity and ecosystem services (Marques & Grelle 2021). Nonetheless, the Atlantic Forest continues to suffer from widespread habitat loss.

The Atlantic Forest is highly fragmented, distributed as thousands of small forest remnants (Ribeiro et al. 2009a), and its remaining vegetation covers between 12.4% and 28% of the original area, depending on the forest size and the minimum degree of conservation considered (Rezende et al. 2018, SOS Mata Atlântica 2019). Forests remnants often occur in the steepest areas due to the difficulty of large-scale agricultural practices in such topographic conditions (Trindade et al. 2008). However, even in small fragments and young secondary vegetation patches, these forests exhibit complex floristic structures and compositions with a high potential for storing carbon (Vieira et al. 2008, Poorter et al. 2016).

The estimation of aboveground carbon stock depends directly on the assessment of biomass and necromass. In the case of the Atlantic Forest, investigators point out the main difficulties in understanding and searching for consistent estimates of carbon stocks for the biome: a vast array of spatial and temporal forest characteristics, such as size, conservation status, heterogeneity, and age; the lack of standardisation of sampling methods; and the absence of specific methods for biomass estimation applied to all forest types (Vieira et al. 2008, Fonsêca et al. 2019). For this biome, we can mention that the first synthesis of studies on biomass and carbon was published by Vieira et al. (2008), who reviewed estimation methods, and Alves et al. (2010), who provided the first extensive landscape-scale estimate available for AGB in the Brazilian Atlantic Forest. A third study was the carbon stock quantification in necromass for secondary forests in the State of Minas Gerais, prepared by Villanova et al. (2019).

The limited number of studies that provide a synthesis of carbon stocks in Atlantic Forests suggests that more research is needed to gather the type of information that will allow for consistent estimates and robust applications. Thus, this research aimed to review, analyse and update data on carbon stocks in the main aboveground reservoirs of the Atlantic Forest and evaluate the factors that influence carbon storage. The following questions were answered:

(i) How does the aboveground carbon stock vary in different successional stages in the Atlantic Forest?

(ii) Is there a relationship between carbon stock and climate conditions throughout the biome?

(iii) Are there differences in the carbon stocks of forest fragments at different altitudes and sizes?

We conducted a novel analysis based on a bibliographic search from 2000-2021 to answer these questions. As a result, this research provides the first comprehensive analysis to support public policies concerning carbon stocks in the Atlantic Forest at the biome level. It will facilitate decision-making in the search for mitigation measures for climate change and subsidise the implementation of carbon credit trading programs and incentives for restoring degraded forests.

MATERIALS AND METHODS

We prepared our dataset based on a systematic search of the literature and analysis of scientific articles published between 2000 and 2021 in Brazilian and international journals, available from the following search engines: SciELO platform (scielo.org/), Google Scholar (scholar.google.com.br/) and CAPES Portal (periodicos.capes.gov.br/). Additionally, the database prepared by De Lima et al. (2020) was consulted. In this search, we only considered the research carried out in Brazil for trees with a diameter at breast height (DBH) equal to or greater than 5 cm.

The search for articles was achieved following Boolean logic (OR/AND), using the following searching terms, in Portuguese (and English), with no language restrictions (Figure 1): biomassa (biomass) or/and necromassa (necromass), serapilheira (litter) or/and madeira morta (dead wood), and carbono (carbon). These terms mentioned above were combined with “Floresta Atlântica or/and Mata Atlântica” (“Atlantic Forest”), “floresta secundária” (“secondary forest”), “floresta madura” (“mature forest”), “cobertura da terra” and “uso da terra” (“land cover”, “land use”). Forests were categorised into two successional stages based on the research authors’ reports and structural information on the studied forests, synthesised as: Secondary Forest-SF (open forest formations with a predominance of shrubs and/or sparse trees, areas undergoing regeneration after abandonment and with a history of recent anthropic activities); and Mature Forest-MF (dense vegetation, with no record of clear-cutting, with tall trees of large diameters and continuous canopy).

The list of references obtained through this primary search was reviewed to identify additional relevant citations. Our dataset only

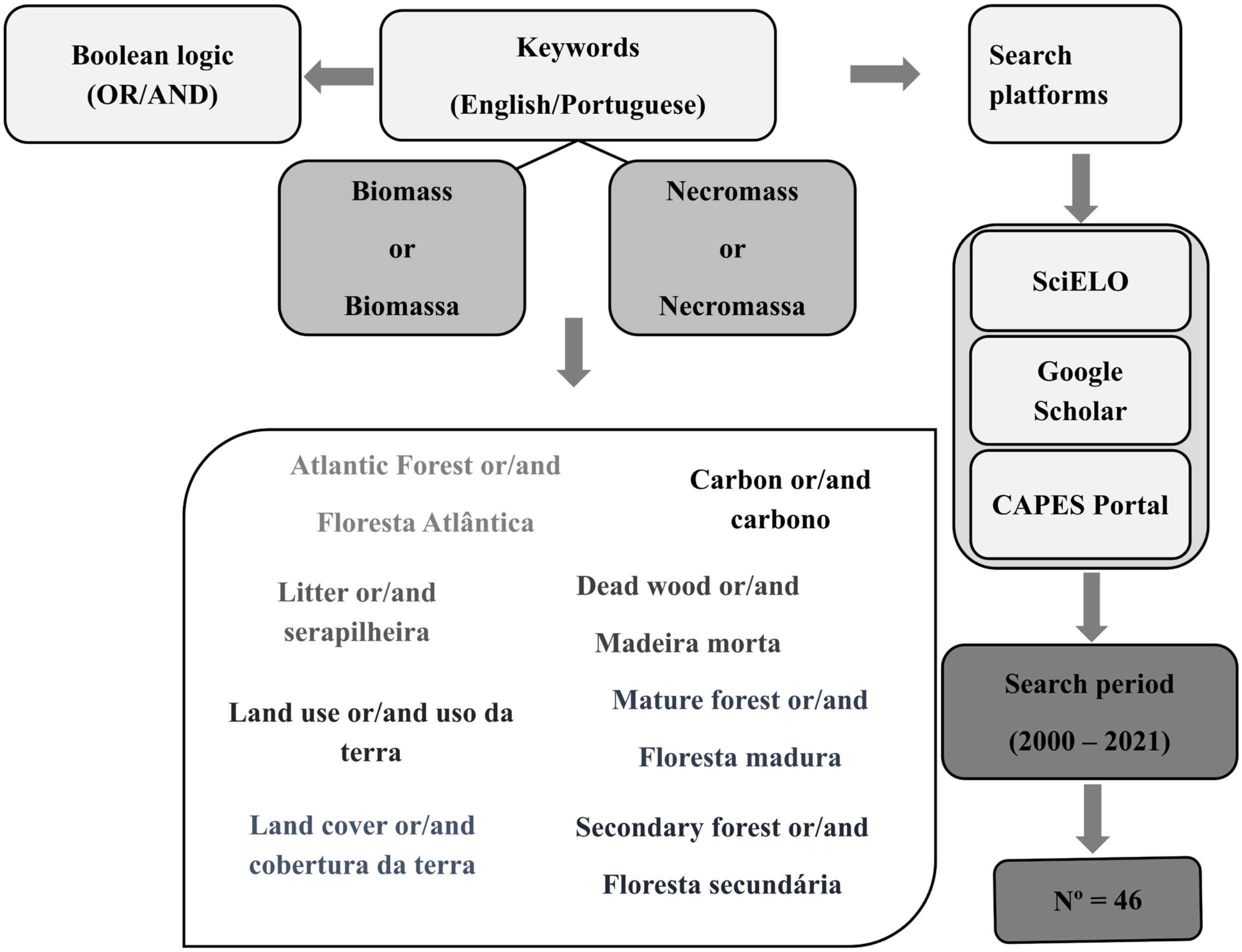

Figure 1. **Procedures and criteria established to perform the search for scientific articles carried out in the Brazilian Atlantic Forest between 2000 and 2021.**

included studies in the Brazilian Atlantic Forest, which informed data per sample area, allowing us to calculate stock per hectare. Articles covering different compartments (biomass and/or necromass) and/or different topographies in the same study area were included separately in the spreadsheets for analysis.

We registered the following information from each study whenever possible: geographical coordinates (latitude and longitude), altitude (m), vegetation type (Dense Ombrophilous, Mixed Forests, Seasonal Semideciduous and Deciduous), succession stage (mature - MF or secondary forest - SF), forest size (ha), historical climate (mean precipitation and temperature), sampling method (direct and indirect), and carbon stock (MgC.ha^{-1}) in biomass (tree in DBH > 5 cm) and necromass. This latter compartment includes fine litter (plant pieces with a diameter ≤10 cm) and coarse woody debris (diameter ≥ 10 cm). It is worth mentioning that most studies did not provide a carbon estimation and when they did, the estimates were based on different sampling methodologies (plots and line transects) and different conversions of biomass to carbon (factors: 0.46, 0.47 or 0.5). Therefore, to avoid bias in the analyses, we applied the factor of 0.47 to all studies, to convert biomass into carbon and 0.37 to convert necromass into carbon (IPCC 2006).

An additional search of published articles in the same study area was carried out to gather complementary information for articles that did not contain altitude, forest size, precipitation or temperature. The geographic coordinates and the Google Earth Pro software (google.com.br/intl/pt-BR/earth/) were used to obtain fragment altitude and size variables. In the absence of information on temperature and precipitation, data on climate was collected from the database of the Instituto Nacional de Meteorologia (INMET- portal.inmet.gov.br/).

Statistical analysis

After organising a databank with carbon data for each Atlantic Forest compartment (biomass and necromass), we tested the data for homogeneity (Fligner test) and normality (Shapiro-Wilk test), according to Zuur et al. (2010). Subsequently, we used analyses of variance (ANOVAs) and the Tukey test at 5% probability to identify differences between carbon stock at the different stages of succession (MF and SF), for biomass and necromass separately and for the carbon stock in different compartments in the necromass (fine and coarse litter).

We applied the generalised linear mixed model (GLMM) to test the relationship between the independent variables (altitude, successional stage, forest size, mean precipitation and average temperature) on the carbon stock in different compartments of forest ecosystems. Predictor variables were standardised to mean 0 and 1 standard deviation, using the method Standardize in the decostand function (R package Vegan, Oksanen et al. 2020). Sampling methods (direct and indirect) were considered random factors to reduce bias in the analyses. We adopted the protocol by Zuur et al. (2010) for data exploration. This protocol comprises six steps intended to identify possible problems and facilitate the choice of the best analysis. We used a Gaussian distribution in the response model. The models were selected using the Akaike Criterion (AIC). This procedure removes non-significative variables ($p > 0.05$) to enhance model fit and reduce the correlation structure between predictor variables (Zuur et al. 2010). Additionally, we calculated the explained variance of the fixed effects (R^2 GLMM(m)) and fixed + random effects (R^2 GLMM(c)) (Nakagawa & Schielzeth 2013). We used R version 3.3.1 (R Development Core Team 2020) and the appropriate analysis packages. For the ANOVA analysis, we used the aov function from the car package (Fox & Weisberg 2019); for the GLMM, the following packages were used: nlme (Pinheiro & Bates 2022); lme4 (Bates et al. 2015) and MuMIn (Bartoń 2022). Ggplot2 was used to prepare the plot (Wickham 2016).

RESULTS

Biomass and necromass in the Atlantic Forest: geographical extent of the available data

A total of 46 scientific articles were published between 2000 and 2021 for the Brazilian Atlantic Forest, of which four carried out estimates of biomass and/or carbon at different successional stages (MF and SF) and different altitudes during the same study. Only one study (Cunha et al. 2009) estimated stocks for both compartments (biomass and necromass) in the same area. Of these 46 studies, 65% were related to the aboveground biomass compartment, whereas 35% were related to necromass. Most studies were conducted in the Southeast and Southern regions (92%), while there were fewer studies for the Northeast (Figure 2).

Over the decades, an average of three articles were published annually, two related to tree biomass and one to the necromass compartment. The sizes of the studied forests ranged from 1 hectare (ha) to 185,265.50 ha,

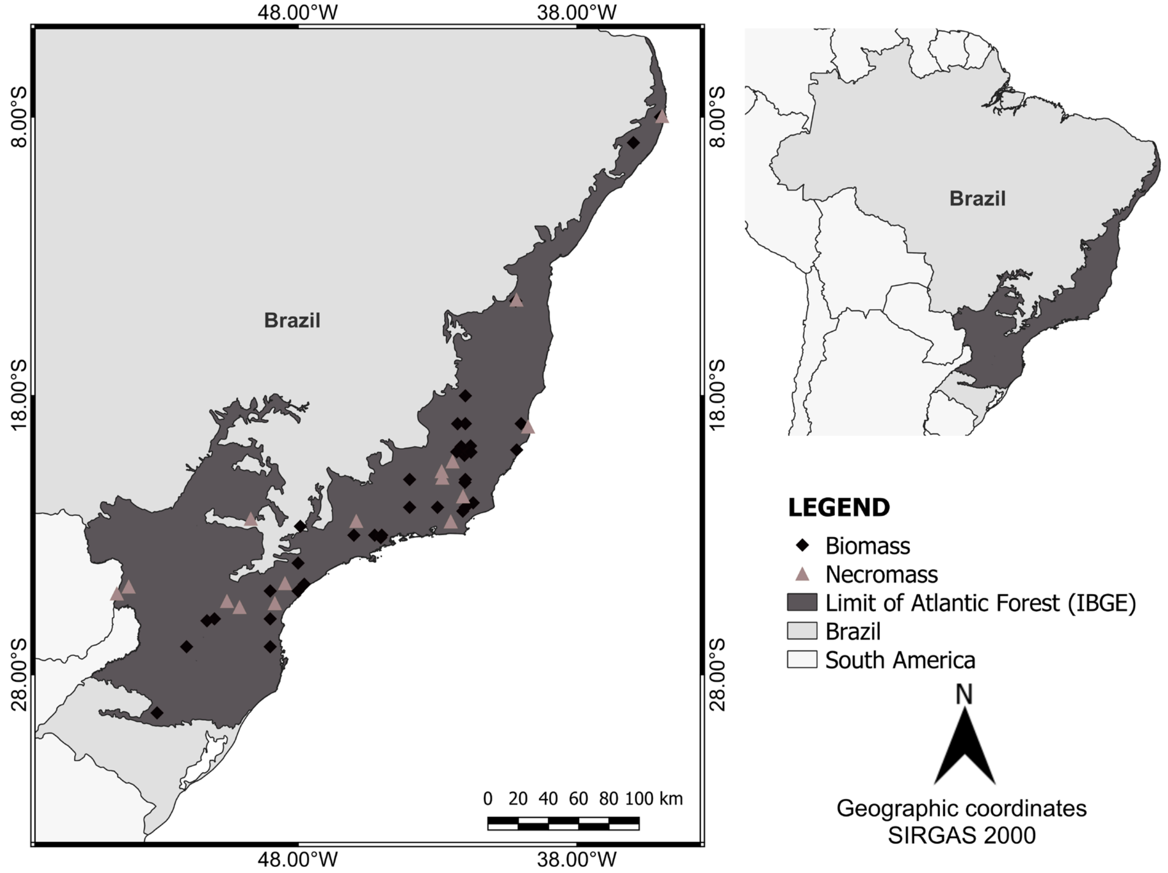

Figure 2. Location of the forest areas with inventories of aboveground biomass and necromass in the Brazilian Atlantic Forest, based on published studies from 2000 to 2021.

with altitudes varying from 50 m to 1,200 m (Supplementary Material - Table SI). Regarding the climate, average annual temperatures in the studied areas ranged from 16° C to 25.8° C, with a mean and standard deviation of 21±2.33 °C. The mean annual rainfall of the studied areas varied between 850 and 2,821 mm, with an average of 1,652 ± 619 mm.

Among the articles assessing the biomass compartment, 57% were carried out in secondary forests (SF), i.e., forests that have been disturbed at some point, followed by a recovery in the following years, and have yet to reach the expected maximum development. The remaining 43% of studies were carried out in areas classified by the authors as mature forests (MF) or advanced succession. The most used sampling method for biomass estimation was the indirect method (94%), which consists of using allometric equations without cutting trees (direct method). In the indirect method, biomass is estimated based on other variables measured in the field, such as the diameter at breast height, total height, and basic wood density (Somogyi et al. 2006, Ferraz et al. 2014). We observed that many biomass estimations in the Atlantic Forest were based on specific equations for the target forests. Seven equations were registered: three for Dense Rainforest (Tiepolo et al. 2002, Burger & Delitti (2008) and Fonsêca et al. 2020), one for Subtropical Evergreen Forest (Uller et al. 2019), two for Seasonal Semi-Deciduous Forest (Scolforo et al. 2008, Ferez et al. 2015); and one for Mixed Rain Forest (Ratuchne 2010). In the absence of these equations, the pantropical equations developed by Chave et al. (2005, 2014), Brown et al. (1989, 1999) and Brown (1997) were used.

Regarding necromass, there is a notoriously low number of scientific studies in the Brazilian Atlantic Forest (Figure 2). Of the analysed studies, 59% were performed in SF and 41% in MF. Of these, 58% focused on the fine litter compartment (diameter ≤10 cm), 24% on the coarse litter compartment (diameter ≥ 10 cm), and 18% quantified both compartments (Table SI). A total of 87% used the fixed area method (plots), and only two studies used the Line Intercept Sampling (LIS method, by Warren & Olsen 1964, Palace et al. 2012). The LIS method counts and measures the number of wood pieces intercepted along a pre-established line; a minimum circumference is defined as an inclusion criterion.

Carbon stock in the aboveground biomass and necromass of the Brazilian Atlantic Forest

The aboveground tree biomass in the Atlantic Forest ranged from 38.9 to 431.4 $Mg.ha^{-1}$, with a mean and a standard deviation of 218 ± 94.2 $Mg.ha^{-1}$, without considering the distinct forest successional stages (Table I and SI). However, stocks were highly variable along the biome and dependent on successional stage. In mature forests (MF), biomass ranged from 90 to 431.4 $Mg.ha^{-1}$ (mean = 267 ± 85.8 $Mg.ha^{-1}$), much larger than the stock in secondary forests (SF) (*p-value* = 0.0016**), where biomass ranged from 38.9

Table I. Aboveground biomass and necromass values (in megagrams per hectare, $Mg.ha^{-1}$) obtained from studies along the Brazilian Atlantic Forest for the total sample and different forest successional stages (mature forests, MF and Secondary Forests, SF). Necromass stocks are also presented by fractions (fine and coarse litter). Calculated numbers of carbon stocks are given for each compartment. Numbers in bold show statistical differences between successional stages (p<0.01); SD: standard deviation.

ABOVEGROUND BIOMASS						
Successional stage	**Biomass ($Mg.ha^{-1}$)**			**Carbon ($MgC.ha^{-1}$)**		
	Mean ± SD	**Min**	**Max**	**Mean ± SD**	**Min**	**Max**
MF	**267 ± 85.8**	90.0	431.4	**125.3 ± 40.3**	42.5	202.28
SF	**175.6 ± 81.3**	38.9	428.9	**82.7 ± 38.2**	34.2	201.5
Total	218 ± 94.2	38.9	431.4	102.3 ± 44.2	18.28	202.8

ABOVEGROUND NECROMASS						
Successional stage	**Necromass ($Mg.ha^{-1}$)**			**Carbon ($MgC.ha^{-1}$)**		
	Mean ± SD	Min	Max	Mean ± SD	Min	Max
MF	11.6 ± 7.3	4.4	25.2	4.3±2.8	1.63	9.33
SF	10.5 ± 7.39	5.1	31.0	3.9 ± 2.73	1.90	11.47
Total	11 ± 7.3	4.4	31.0	4.08±2.71	1.63	11.47

NECROMASS COMPARTMENTS												
Successional stage	**Fine litter**						**Coarse litter**					
	Necromass ($Mg.ha^{-1}$)			**Carbon ($MgC.ha^{-1}$)**			**Necromass ($Mg.ha^{-1}$)**			**Carbon ($MgC.ha^{-1}$)**		
	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max	Mean ± SD	Min	Max
MF	8.0±2.7	4.4	11.6	2.9±1.0	1.6	4.2	16.2±9.7	6.7	25.2	6.0± 3.6	2.48	9.33
SF	11.5±7.8	5.1	31.0	4.3±2.8	1.9	11.4	6.1± 0.7	5.6	6.6	2.2± 0.3	2.0	2.4
Total	10.3±6.5	4.4	31.0	3.8±2.4	1.63	11.4	12.7 ± 9.3	5.6	25.22	4.6 ± 3.4	2.0	9.3

to 428.9 Mg ha^{-1} (mean = 175.6 ± 81.3 $Mg.ha^{-1}$). Carbon stored in the biomass ranged from 18.28 to 202.8 $MgC.ha^{-1}$ (mean = 102.3 ± 44.2 $MgC.ha^{-1}$), much lower (*p-value* = 0.001**, see Figure 3) in SF (82.7 ± 38.2 $MgC.ha^{-1}$) than in MF (125.3 ± 40.3 $MgC.ha^{-1}$).

Regarding necromass (Table I), stocks ranged from 4.4 to 31 $Mg.ha^{-1}$ (mean of 11 ± 7.3 $Mg.ha^{-1}$), equivalent to 5% of the aboveground biomass compared to the overall average (218 $Mg.ha^{-1}$). There was no difference between necromass (F = 0.108, p-value = 0.746) and carbon stocks (F = 0.106, p-value = 0.749) between the different forest successional stages (MF and SF) (F = 0.108, p-value = 0.746). MF exhibited an average necromass stock of 11.66 ± 7.3 $Mg.ha^{-1}$ and carbon of 4.3±2.8 $MgC.ha^{-1}$, whereas, in SF, the necromass was 10.55 ± 7.39 $Mg.ha^{-1}$ and 3.9 ± 2.73 $MgC.ha^{-1}$ of stored carbon. In the necromass, the compartment of the fine litter (diameter ≤ 10 cm) stores an average of 10.3 ± 6.5 $Mg.ha^{-1}$ (3.8±2.4 $MgC.ha^{-1}$). The coarse litter compartment (diameter ≥ 10 cm) throughout the Atlantic Forest, despite the lower number of studies (six in total), provided an outstanding contribution to necromass, with an average of 12.7 ± 9.3 $Mg.ha^{-1}$ and carbon of 4.6 ± 3.4 $Mg.ha^{-1}$. The necromass compartments (fine and coarse litter) did not differ in carbon stock (*p-value* = 0.526).

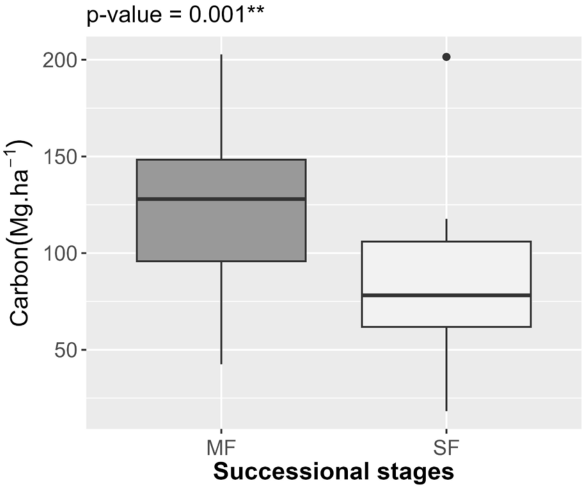

Figure 3. Comparative analysis of the carbon stock ($MgC.ha^{-1}$) in the aboveground biomass at different successional stages (mature forests, MF and secondary forests, SF) in the Brazilian Atlantic Forest, based on published studies from 2000 to 2021. p-value: 0.001*.

Drivers of variations in carbon stock throughout the Brazilian Atlantic Forest

Spatial (altitude, forest size) and environmental (annual mean precipitation, temperature and successional stage) variables were tested as drivers of change in the carbon stocks along the Atlantic Forest through the GLMM. For the aboveground biomass compartment, only the mean annual precipitation (*p-value* = 0.0033*) and the successional stage (*p-value* = 0.000***) explained the stored carbon remaining in the selected model 4, according to the AIC (-12.42) and explained the variance of the fixed effects (R^2 GLMM(m) = 0.287) and fixed + random effects (R^2 GLMM(c) = 0.569) (Table II, for adjustments of other models, see Table SII). For the fine and coarse (Deadwood) litter, which did not differ in their respective carbon stocks (*p-value* = 0.526), none of the spatial and environmental variables explained the carbon stored throughout the Brazilian Atlantic Forest.

DISCUSSION

Aboveground carbon stock in the Atlantic Forest

Aboveground biomass and necromass play a crucial role in the global carbon cycle, accounting for a significant fraction of forest ecosystems' total stock (Silva et al. 2018, FAO 2020). Through the data analysed in this research, it was possible to verify that 96% of the aboveground carbon across the Atlantic Forest is stored in the biomass. As previously acknowledged, biomass carbon stocks vary according to succession stage, increasing along succession gradients (Diniz et al. 2015, Poorter et al. 2016, Azevedo et al. 2018).

Table II. **Results of the Generalised Linear Mixed Models (GLMM) to assess the contribution of the explanatory variables (altitude, successional stage, forest size, precipitation and temperature) to the aboveground carbon stock in the Brazilian Atlantic Forest, based on published studies from 2000 to 2021.**

<table>
<tr><th>Model</th><th colspan="4">Carbon <i>versus</i> explanatory variables</th><th>AIC</th><th>Variance explained</th></tr>
<tr><td>Mod.4</td><td colspan="4">Mod4 <- lmer (Carbon ~ Stage_succession + Precipitation + (1 | Sampling_method), REML = TRUE, data = carb_bio, family = “gaussian”)
R^2_{GLMM} (c) = 0.569</td><td>-12.42</td><td>R^2_{GLMM} (m) = 0.287</td></tr>
<tr><td></td><td>Estimate</td><td>Std. Error</td><td>df</td><td>t value</td><td colspan="2">Pr(>|t|)</td></tr>
<tr><td>(Intercept)</td><td>0.5104</td><td>0.1351</td><td>1.1736</td><td>3.778</td><td colspan="2">0.1353^{ns}</td></tr>
<tr><td>Stage_successionSF</td><td>-0.2218</td><td>0.0588</td><td>35.0024</td><td>-3.773</td><td colspan="2">0.0005***</td></tr>
<tr><td>Precipitation</td><td>0.3261</td><td>0.1038</td><td>35.5090</td><td>3.141</td><td colspan="2">0.0033**</td></tr>
</table>

Significance codes: ‘*’ 0,001 ‘**’ 0,01. ns: non significant.**

We confirmed this pattern by analysing all the Atlantic Forest data, where the most extensive stocks are recorded in mature forests. Thus, our findings reinforce the need for conserving mature forest patches throughout the biome since one hectare of mature forest can store almost twice as much carbon as one hectare of secondary young patches.

In addition to age, it is widely documented that the amounts of carbon stored in different vegetation types are influenced by climatic conditions (precipitation and temperature), biotic variables such as species richness and diversity, and topographic conditions that may alter the entire carbon cycle (Alves et al. 2010, Becknell et al. 2012, Poorter et al. 2016, Arasa-Gisbert et al. 2018, Rodríguez-Alarcón et al. 2018). When considering large spatial scales, as in our analysis, climatic factors are often acknowledged as the main drivers influencing carbon stocks, as reported for other biomes (Malhi et al. 1999, Keeling & Phillips 2007, Vayreda et al. 2012). Along a climatic gradient of vegetation in Mexico (dry, semi-arid, evergreen, semi-deciduous, broadleaf, mixed and coniferous forests), carbon stock was strongly correlated with precipitation in almost all forest types (Arasa-Gisbert et al. 2018). At the local level, topographic and soil variables and forest disturbances also become essential predictors of carbon stocks (McEwan et al. 2011, Xu et al. 2015, De Lima et al. 2020).

In our analysis of the entire Brazilian Atlantic Forest, previous findings led us to expect that climatic variables would explain a relevant amount of forest carbon stocks. We also expected that the biome’s intense anthropogenic pressures, represented by forest size, a striking feature pointed out by Ribeiro et al. (2009a), would also play an important role. Overall, the findings in this research corroborate our initial predictions, where we saw that carbon storage potential in Atlantic Forest ecosystems responds positively with the advancement of the successional stage and increasing precipitation. Additionally, the increase in the amount of carbon stored is independent of forest size.

In particular, forests in a mature or advanced stage of succession and located in regions with high precipitation deserve focused attention in terms of conservation. In such environments, climate positively influences species composition and growth and favours a more significant carbon accumulation in biomass (Dorner et al. 2002, Soethe et al. 2008, Alves et al. 2010, Dybala et al. 2018). These areas are vital for avoiding and mitigating the effects of expected climate changes (Capon et al. 2013, Rieger et al. 2015, 2016 Dybala et al. 2018).

Necromass, another assessed compartment, stores up to 20% of the aboveground carbon in forest ecosystems, configuring itself as a critical component to understanding forest ecosystem functioning and productivity (Houghton et al. 2001, Keller et al. 2004, Fonsêca et al. 2019). Due to the low number of studies compiled on carbon stock in necromass, it was not possible to trace a pattern of the effect of climatic and spatial variables on the carbon stock for the Brazilian Atlantic Forest. Although it contributes a considerable amount of carbon to ecosystems, necromass is probably less studied due to difficulties in standardising the methodological protocols that capture the variation in space and time of its fractions (Deus et al. 2018, Fonsêca et al. 2019). Its quantification, characterisation and understanding of deposition patterns widely vary according to the spatial configuration (succession stage, size, shape, and isolation of the patches), matrix type and chronic disturbances (i.e., selective and continuous extraction of small amounts of timber and non-timber resources) and acute disturbances (i.e., loss of vegetation cover).

Necromass compartments are studied when there is a demand for understanding their ecosystemic role related to carbon stock, restoration actions, management, and the successional diagnosis of ecosystems (Fonsêca et al. 2019, Maas et al. 2020). Studies performed in Brazil have mainly been carried out in the Amazon Forest (Keller et al. 2004, Chao et al. 2009, Strassburg et al. 2016) and are still incipient in Brazilian Atlantic Forest regions. This revision reinforces the need to include this compartment in project designs, seeking to understand the pattern that explains carbon stock in trees, bringing more clarity to the functioning and productivity of the Brazilian Atlantic Forest. Along with necromass, carbon in the soil, not considered in this study, must be investigated more. It constitutes the most significant carbon reservoir in forests, storing twice the amount of C in the atmosphere (Scharleman et al. 2014) and interacting directly with the other compartments aboveground, especially with the necromass. Therefore, understanding the carbon stored in distinct compartments and the fluxes between them is crucial for the Atlantic Forest, a biome highly threatened by conversion for other uses. Such conversions imply modifications in the carbon reserve and alteration of the carbon fluxes (Paul Obade & Lal 2013).

As caveats and limitations of our study, we can list a few that might have influenced our analysis and interpretation. Firstly, we assumed that all data were accurate, although coming from different studies. However, there is no standard protocol guiding them, and data on biomass and carbon were collected and estimated by applying a wide range of methods. Secondly, some empirical studies did not provide information about climate, forest size, or altitude, and we gathered complementary data from other sources. As a final limitation, most authors did not describe successional stages in detail, which led to grouping them under secondary forests (SF). However, we know the implications of such an assumption since successional stages vary greatly depending on age, surrounding matrix, and type of disturbances.

Changes in forest coverage and carbon stocks in the Atlantic Forest

Under the new circumstances of size, isolation and edge effect, changes in the physical environment led to increased tree mortality, reduced plant density, and loss of large and old trees (Laurance 2008, Haddad et al. 2015). Changing forest configuration and composition is undoubtedly detrimental to the structural pattern of forests and the provision and maintenance of ecosystem services (Ribeiro et al. 2009a, Haddad et al. 2015, Alroy 2017). Carbon sequestration may be hindered in forests due to these changes, compromising and affecting the global climate system (IPCC 2015). Taubert et al. (2018) point out that forest loss for alternative land uses is one of the main causes of forest degradation and carbon loss over the last decades.

The Brazilian Atlantic Forest is an ideal scenario for understanding the process of modifying the carbon cycle for two reasons: the forest stores a significant amount of carbon and is one of the world's most fragmented and threatened forests (Rezende et al. 2018). The Atlantic Forest has been converted into heterogeneous landscapes, with a dynamic combination of fragments of various sizes and succession stages. Old forest remnants and early and late secondary patches occupy the same landscapes, surrounded by pastures and agricultural land (Rezende et al. 2018). According to our analysis of the Atlantic Forest, mature forests possess the most extensive carbon stocks (average = 125.3 ± 40.3 MgC.ha^{-1}), while areas of pasture and agriculture store 46 and 41 MgC.ha^{-1}, according to Jesus et al. (2019).

Based on the above data, the carbon loss resulting from the conversion of forests into pastures and agricultural lands is around 65%. On the other hand, secondary forests hold 34% less carbon per hectare compared to mature patches. Furthermore, they are not expected to reach carbon stocks like those found in mature forests. According to Liebsch et al. (2008), a secondary forest would take approximately 150 years to reach a mature forest's structural standard. A recent study by De Lima et al. (2020), using data from a field survey of the entire Atlantic Forest, revealed that the deforestation of about 25% of the biome between 1985 and 2017 significantly reduced forest biomass, with losses of 451-525 Tg of carbon - equivalent to 55-70 thousand km^2. The research emphasises that protected areas are fundamental for maintaining biomass and carbon, decreasing losses with increased protected areas.

In this context, more incentives and the implementation of practices aimed at restoring Atlantic Forest ecosystems are needed. Restoring these remnants to reduce edge effects, control invasive species, and plantation enrichment is an effective measure to reverse forest degradation (FAO 2015). In Brazil, the goal is to restore 12 million hectares of forests, mainly in Permanent Preservation Areas (PPAs) and Legal Reserves (LRs), but also in degraded areas with low productivity (BRASIL 2017). Additionally, there is an incentive to reduce greenhouse gas emissions from deforestation and forest degradation (REDD +). However, the initiative is concentrated in the Amazon (De Lima et al. 2020). Despite this goal and other promises to reduce GHG emissions (Atlantic Forest pact, Bonn challenge, Paris Agreement), there are currently no actions to modify forest degradation in the Atlantic Forest, such as the reintroduction of species with high storage potential for carbon (FAO 2020, De Lima et al. 2020).

CONCLUSIONS

This research provides the first comprehensive analysis of carbon drivers and stocks in different aboveground compartments in the Atlantic Forest. We reinforce the need to conserve forest remnants, specially mature forest ones, that still resist anthropic disturbances, given their high importance for carbon storage. Initiatives to reduce and reverse degradation processes are decisive for the future of this hotspot. Such initiatives must promote the conservation, sustainable use, and recovery of forest ecosystems and guarantee the storage and fixation of carbon stocks in the intermediate and long term. A positive carbon balance must be created in each system, contributing to the mitigation of Greenhouse Gases (GHG) and, consequently, to the climate changes predicted for the coming decades. Finally, we suggest that more research is needed to gather the information that will allow for more consistent estimates and robust applications in decision-making.

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SUPPLEMENTARY MATERIAL

Tables SI-SII.

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This study is part of the PhD thesis in Forest Sciences of the researcher Nathan C. Fonsêca, under Dr Ana C. B. Lins e Silva's supervision. NCF: contributed to the design and implementation of the research, collected the data; carried out the analysis and interpretation of the results and wrote the manuscript with input from all authors. JSAC and ERGMA: contributed to the analysis and aided in interpreting the results. ACBLS: contributed to research design and implementation, the analysis and interpretation of the results, and the writing and translation of the manuscript.