MARCELA VENELLI PYLES

ECOLOGICAL DRIVERS AND STAND LEVEL EQUATIONS IN THE ESTIMATION OF ATLANTIC FOREST CARBON STOCKS

LAVRAS – MG
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ECOLOGICAL DRIVERS AND STAND LEVEL EQUATIONS IN THE ESTIMATION OF ATLANTIC FOREST CARBON STOCKS

IMPULSIONADORES ECOLÓGICOS E EQUAÇÕES EM NÍVEL DE POVOAMENTO NAS ESTIMATIVAS DE ESTOQUES DE CARBONO DA MATA ATLÂNTICA

Tese apresentada à Universidade Federal de Lavras, como parte das exigências do Programa de Pós-Graduação em Ecologia Aplicada, área de concentração em ecologia e conservação de recursos em paisagens fragmentadas e agrossistemas, para obtenção do título de Doutor.

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RESUMO

Compreender os mecanismos que controlam o armazenamento de carbono florestal é crucial para apoiar soluções "baseadas na natureza" para a mitigação das mudanças climáticas. No primeiro artigo, usamos um conjunto de dados de 892 inventários da Mata Atlântica para avaliar os efeitos diretos e indiretos das condições ambientais, impactos humanos, propriedades da comunidade arbórea e métodos de amostragem sobre os estoques de carbono de árvores acima do solo. Mostramos que os fatores amplamente aceitos de estoques de carbono, como clima, solo, topografia e fragmentação florestal, têm um papel muito menor do que o histórico de distúrbios florestais e as propriedades funcionais da Mata Atlântica. Especificamente, o nível de perturbação dentro da floresta foi o fator mais importante, com efeito pelo menos 30% maior do que qualquer uma das condições ambientais individualmente. Assim, nossos resultados sugerem que a conservação dos estoques de carbono tropical pode ser dependente, principalmente, de evitar a degradação florestal e que as políticas de conservação focadas apenas no carbono podem falhar na proteção da biodiversidade tropical. No segundo artigo, usando um grande conjunto de dados de 697 inventários da Mata Atlântica, avaliamos a aplicação de equações regionais e específicas do tipo de floresta para estimar os estoques de carbono com base em duas variáveis estruturais do povoamento: área basal do povoamento e densidade de árvores do povoamento. Comparamos a capacidade preditiva de equações de uma e duas variáveis e mostramos que estimar o estoque de carbono a partir da área basal e densidade do povoamento fornece resultados precisos para florestas úmidas e secas do domínio Mata Atlântica. As equações desenvolvidas com base apenas nas variáveis estruturais do povoamento explicaram 85,2%-96,2% das variações dos estoques de carbono com menos de 6,5% de erros de estimativa. Assim, os estoques de carbono das variáveis estruturais florestais do povoamento podem ser precisos e, portanto, podem representar uma alternativa quando medições e identificações de árvores individuais de onde não estão disponíveis inventários florestais completos.

Palavras-chave: Estoques de carbono, Distúrbios Humanos, Mudanças climáticas, Estimativas de carbono

ABSTRACT

Understanding the mechanisms controlling forest carbon storage is crucial to support "nature-based" solutions for climate change mitigation. In the first article, we used a dataset of 892 Atlantic Forest inventories to assess the direct and indirect effects of environmental conditions, human impacts, tree community proprieties and sampling methods on tree above-ground carbon stocks. We showed that the widely accepted drivers of carbon stocks, such as climate, soil, topography, and forest fragmentation have a much smaller role than the forest disturbance history and functional proprieties of the Atlantic Forest. Specifically, within-forest disturbance level was the most important driver, with effect at least 30% higher than any of the environmental conditions individually. Thus, our findings suggest that the conservation of tropical carbon stocks may be dependable on, principally, avoiding forest degradation and that conservation policies focusing only on carbon may fail to protect tropical biodiversity. In the second article, using a large dataset of 697 Atlantic Forest inventories, we evaluated the application of regional and forest type-specific equations to estimate carbon stocks based on two stand structural variables: stand basal area and stand density. We compared the predictive ability of one- and two-variable equations and showed that estimating carbon stock from the stand basal area and stand density provides accurate results for moist and dry forests of the Atlantic Forest domain. The developed equations based only on the stand structural variables explained 85.2%-96.2% of the carbon stocks variations having less than 6.5% of estimation errors. Thus, carbon stocks from the stand forestry structural variables can be accurate, and thus may represent an alternative when individual tree measurements and identifications from where complete forest inventories are not available.

Keywords: Carbon Stocks, Human Disturbances, Climate Change, Carbon Estimates

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INTRODUÇÃO GERAL

Com as nações fazendo pouco progresso na redução de suas emissões de carbono, as "soluções baseadas na natureza (NbS)" surgem como uma estratégia-chave para a mitigação das mudanças climáticas (POPKIN 2019). Essas soluções abrangem a conservação florestal, a restauração e a melhoria das práticas de manejo da terra, visando aumentar o armazenamento de carbono e/ou evitar a emissão de gases de efeito estufa (GRISCOM et al.,2017). Embora as soluções baseadas na natureza ofereçam oportunidades reais para a mitigação das mudanças climáticas, ainda são necessárias mais pesquisas (GIRARDIN et al., 2021). Por exemplo, umas das grandes barreiras para o êxito das NbS é a falta de abrangência na atual contabilidade de carbono que se concentrou em fluxos em vez de estoques de carbono e levou a resultados perversos (KEITH et al., 2021). Além disso, como os estoques de carbono acima do solo são amplamente inferidos a partir de equações alométricas genéricas, o desenvolvimento de métodos precisos e fáceis de aplicar para estimar os estoques de carbono tropical pode fornecer o tipo de informação necessária para que as estratégias de NbS atinjam efetivamente os resultados de mitigação.

Gradientes ambientais naturais (por exemplo, clima, solos, topografia) e impactos humanos podem impulsionar os estoques de carbono direta e indiretamente. Os efeitos diretos estão geralmente associados à mortalidade e ao crescimento das árvores. Por exemplo, condições ambientais que aumentam o risco de mortalidade de plantas, como eventos climáticos extremos (por exemplo, El Niño), tendem a resultar em menores quantidades de estoques de carbono (GRACE et al., 2006; STEGEN et al., 2009). Da mesma forma, os estoques de carbono são reduzidos pela fragmentação e distúrbios florestais (por exemplo, corte seletivo, fogo, pastagem e cultivo de gado no sub-bosque), com a mortalidade das árvores sendo impulsionada por mudanças na estrutura física das florestas (por exemplo, microclima, abertura do dossel (MAGNAGO et al.,2015). Efeitos indiretos são aqueles mediados por outras propriedades florestais, como propriedades de comunidades arbóreas (POORTER et al., 2017). As condições climáticas e os impactos humanos podem alterar a contribuição relativa de algumas características funcionais na comunidade, como densidade e estatura da madeira das árvores, que desempenham papéis importantes para o potencial de armazenamento de carbono florestal (SHEIL & BONGERS 2020; DURÁN et al.,2015). Da mesma forma, os distúrbios podem induzir uma sucessão regressiva em direção ao aumento da dominância por espécies de sucessão precoce, que por sua vez têm menor capacidade de armazenamento de carbono (por exemplo, baixa densidade de madeira, menor estatura) (TABARELLI et al., 2008).

Embora diferentes estudos tenham avaliado os efeitos dos fatores dos estoques de carbono, as evidências existentes sobre os fatores são inconsistentes. Por exemplo, alguns estudos mostraram as características das espécies como o principal condutor biológico dos estoques de carbono (ver FINERGAN et al., 2015, VAN DER SANDE, 2018), enquanto outros mostraram a diversidade funcional como o condutor mais importante (POORTER et al., 2015; ZHANG et al., 2012). Além disso, há algumas evidências contraditórias na literatura sobre a direção dos efeitos de alguns desses fatores. Por exemplo, em algumas florestas, a temperatura foi positivamente relacionada aos estoques de carbono (RAICH et al., 2006), enquanto em outras, o aumento da temperatura diminuiu os estoques de carbono (STEGEN et al., 2011). Da mesma forma, os estoques de carbono geralmente não aumentam com a fertilidade do solo (por exemplo, VAN DER SANDE, 2018). Nas florestas amazônicas, os maiores estoques de carbono foram encontrados em solos de baixa fertilidade (BAKER et al.,2004, MALHI et al.,2006, QUESADA et al.,2012). Tal inconsistência pode ser explicada por diferenças no papel desempenhado por esses drivers em contextos biogeográficos ou porque a maioria dos estudos avaliou um ou poucos drivers de estoques de carbono, o que impede a avaliação de efeitos interativos entre eles e a quantificação do papel relativo de cada driver (HOLDAWAY et al. 2016). Além disso, a diferença nos métodos utilizados entre os estudos (por exemplo, protocolos de campo, equações alométricas de carbono) também pode explicar essa inconsistência e ter consequências que vão além da identificação do mecanismo direcionador dos estoques (CHAVE et al., 2004).

Equações alométricas genéricas são amplamente utilizadas para inferir os estoques de carbono acima do solo em florestas tropicais (CHAVE et al., 2014). As mais utilizadas baseiam-se em diâmetro do caule a 1,3 m (peito) de altura (dbh) e altura da árvore (H) e oferecem estimativas confiáveis de carbono à nível da árvore. No entanto, a dependência de inventários florestais detalhados, árvore por árvore, faz com que a utilização dessas equações demande muito tempo e tenha maior custo associado (MCROBERTS et al., 2013). Como alternativa, o uso de equações alométricas baseadas em povoamento pode trazer grandes avanços nas estimativas de carbono, uma vez que as variáveis de povoamento são medidas rapidamente no campo e são comumente fornecidas em inventários florestais já publicados. Particularmente, equações alométricas usando a área basal do povoamento como preditor é uma opção promissora para estimar os estoques de carbono florestal. Por exemplo, a área basal provou ser um bom preditor da biomassa florestal ao integrar o efeito tanto do número quanto do diâmetro das árvores. Além disso, a densidade de árvores do povoamento também já provou ser uma opção para melhorar o desempenho das equações alométricas de carbono no nível do povoamento (ver KHAN et al., 2018).

Aqui, meu principal objetivo foi acessar os principais direcionadores dos estoques de carbono e desenvolver equações alométricas precisas capazes de expandir as estimativas de carbono da Mata Atlântica. Utilizei dados já coletados e compilados pertencentes ao banco de dados Neotropical Tree Communities -TreeCo e ao Inventário de Minas Gerais. 2000) e que devido a cinco séculos de intensa ocupação humana, mais de 80% de suas florestas são menores que 50 ha e cerca de 50% delas a menos de 100 m de uma borda (RIBEIRO et al. 2009), oferecem um dos exemplos mais dramáticos relacionados ao efeito dos humanos nos ecossistemas, refletindo assim o futuro de outras florestas onde os impactos estão avançando rapidamente (por exemplo, Amazônia).

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ARTIGO 1: HUMAN IMPACTS AS THE MAIN DRIVER OF TROPICAL FOREST CARBON

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ABSTRACT

Understanding the mechanisms controlling forest carbon storage is crucial to support "nature-based" solutions for climate change mitigation. We used a dataset of 892 Atlantic Forest inventories to assess the direct and indirect effects of environmental conditions, human impacts, tree community proprieties and sampling methods on tree above-ground carbon stocks. We showed that the widely accepted drivers of carbon stocks, such as climate, soil, topography, and forest fragmentation have a much smaller role than the forest disturbance history and functional proprieties of the Atlantic Forest. Specifically, within-forest disturbance level was the most important driver, with effect at least 30% higher than any of the environmental conditions individually. Thus, our findings suggest that the conservation of tropical carbon stocks may be dependable on, principally, avoiding forest degradation and that conservation policies focusing only on carbon may fail to protect tropical biodiversity.

Teaser

The human-induced disturbance is 2-6 fold more important than other drivers of tropical forest carbon stocks

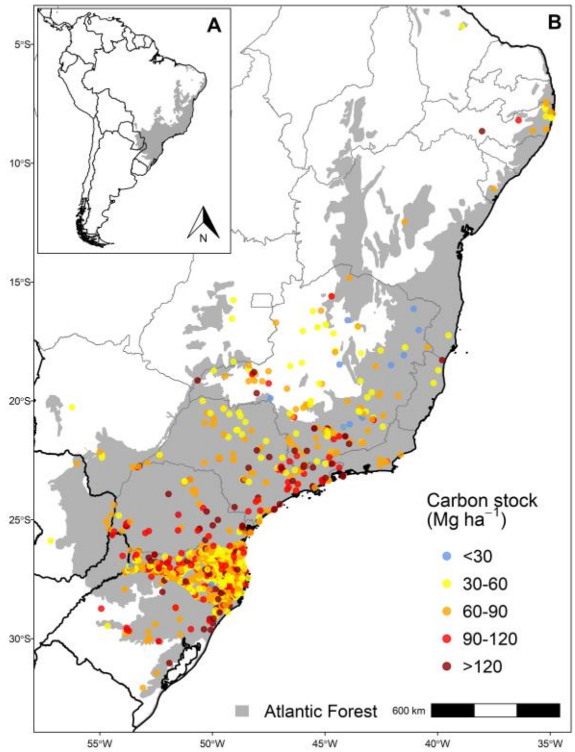
1 INTRODUCTION

Tropical forests play a central role in the carbon cycle on earth, not only regarding carbon flows but also in terrestrial carbon stocks (KEITH et al., 2021). We currently know that forest carbon stocks are determined by tree species proprieties, environmental conditions, and anthropic disturbances. Different tree community proprieties can increase carbon stocks through a more efficient use of the available resources (e.g., species niche complementarity) (ZHANG; CHEN; REICH, 2012) and through the carbon storage potential of the most dominant species (e.g. functional traits) (GRIME,2002). Climate and soil conditions (e.g., temperature, soil fertility) can directly affect forest carbon (STEGEN et al., 2011; QUESADA et al., 2012) but they can also control species composition, which in turn can affect the carbon storage potential of the forest (ENGELBRECHT et al., 2007; TOLEDO et al., 2012). Moreover, topography can influence carbon stocks through its influence on local soil conditions and sunlight incidence (LIN et al., 2016.). Finally, forest degradation and fragmentation not only cause the direct removal of biomass but also shifts in species' demography and functional tree composition (e.g., wood density, maximum height), which can translate into long-term losses of carbon storage potential (MAGNAGO et al., 2014; ANDRADE et al., 2017; AVILA et al., 2018).

Although different studies have evaluated the effects of tree community proprieties, environmental conditions, and human impacts on carbon stocks, the existing evidence is more concentrated in relatively undisturbed forests (e.g.(MALHI et al., 2006; PHILLIPS; LEWIS, 2014)) and it is inconsistent (e.g. (STEGEN et al. 2011; QUESADA et al., 2012; POORTER et al., 2017; MENSAH et al., 2016). Such inconsistency may be explained by differences in the role played by each driver across biogeographic contexts or in the methods used across studies, such as field protocols or carbon allometric equations (CHAVE et al., 2004). Furthermore, most studies have evaluated one or few drivers, which prevents more comprehensive assessments of their relative roles and of possible interactive effects among candidate drivers (HOLDAWAY et al., 2017). Regardless of the reason, a better understanding of what drives forest carbon storage, especially in highly altered tropical forests, may anticipate the outcomes of global changes in more intact forests (e.g. Amazon) (CHAVE et al., 2014), optimize the efficiency of carbon conservation and restoration projects (POPKIN, 2019) and to support nature-based solutions for climate change mitigation (POPKIN, 2019).

Here, we use a large dataset with 892 forest inventories to assess the relative role of tree community proprieties, environmental conditions, and human impacts as drivers of carbon stocks. We also assess the effect of field sampling methods on the estimation of above-ground carbon stocks. We focus on the highly-threatened Atlantic Forest (LIMA et al., 2015; LIMA et al., 2020) (Fig. 1), which comprises a wide spectrum of environmental conditions, biogeographic and human intervention histories (RIBEIRO et al., 2009) and represents the present or the future of other tropical forests, providing a good testing ground to answer our questions. We use a causal mediation analysis, which allows for the simultaneous quantification of many different drivers, and the separation into their direct and indirect effects (AUNG et al., 2020). Based on the present knowledge on forest carbon drives, we quantify the direct effects of tree community proprieties, environment, human impacts, and field methods and also the indirect effects of the environment and human impacts on carbon stocks through their effects on tree community proprieties. We address two questions: (i) what are the main drivers of the Atlantic Forest carbon stocks? and (ii) what are the direct and indirect effects of the different drivers? Finally, we explore the implications of our results for the future of carbon stocks, projecting carbon losses and gains in scenarios of climate and human impacts changes.

Figure 1 – The distribution of the Atlantic Forest inventories included in this study.



Subtitle: For each inventory (points) we present the estimated above-ground carbon stock, separated by classes (colors). The inventory data was obtained from the Neotropical Tree Communities database (Lima et al., 2020).

2 RESULTS

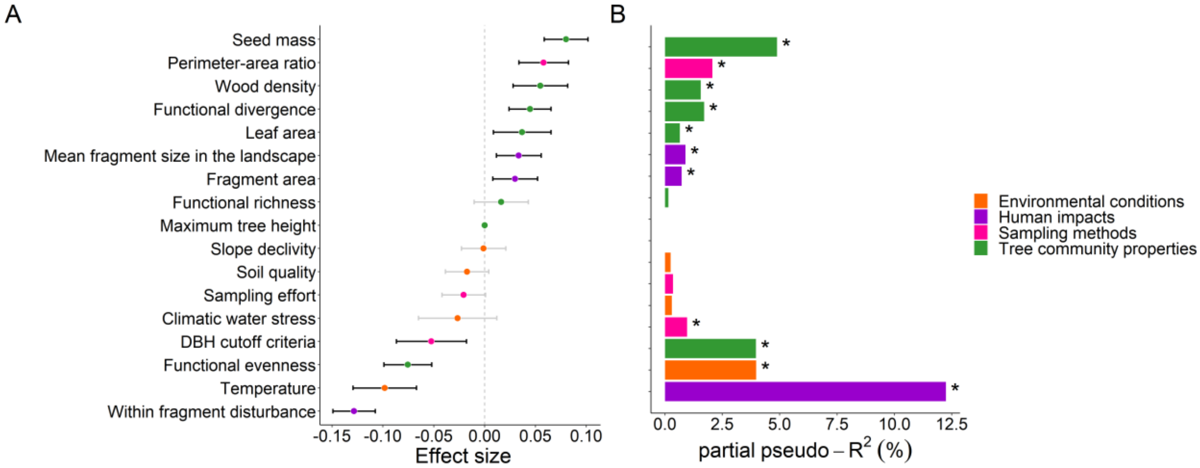
2.1 THE RELATIVE ROLES OF CARBON STOCK DIRECT DRIVERS

Human impacts, tree community proprieties, environmental conditions and field sampling methods (i.e. fixed effects) explained 34.76% of the total variance of the forest above-ground carbon stocks in the Atlantic Forest, with relative contributions of 39.95%,37.36%, 13.05% and 9.76%, respectively (Fig. 2 and Table S1). The within-forest disturbance level was the main driver of carbon stocks, with an effect that was at least 30% greater than the climatic driver with the greatest effect, namely temperature (Fig. 2 and Table S1). Forests with heavy, high and medium levels of human disturbance showed approximately

66%, 76% and 96% of the carbon stocks found in fragments with low levels of human disturbance (Fig. 3 and Table S2 and S3).

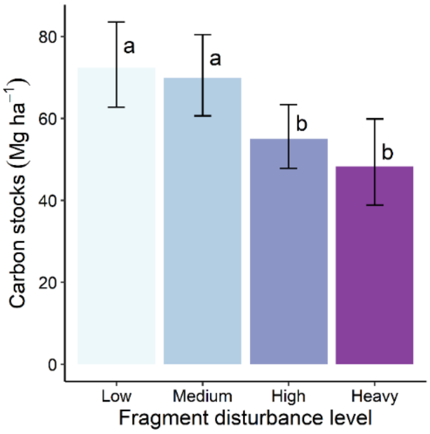
The CWM of seed mass was the second variable with the greatest effect size and partial pseudo-R^2 on carbon stocks (Fig. 2). Carbon stocks increased with the abundance of large-seeded, large-leaved, hardwood species (Fig. 2 and Table S1). Species functional evenness had a negative effect on carbon stocks, while the functional divergence had a positive one. Potential maximum tree height and functional richness had not displayed significant effects on the carbon stocks (Fig. 2 and Table S1). Carbon stocks decreased with temperature but were not affected by the climatic water stress (Fig. 2 and Table S1). Soil quality and slope declivity did not have a significant direct effect on Atlantic Forest carbon stocks. (Fig. 2 and Table S1). The reduction of fragment size (at the local scale) and mean fragment size (at landscape scale) both decreased the carbon stocks (Fig. 2 and Table S1). Finally, it is noteworthy that the effects of the dbh cutoff criteria and particularly of the perimeter-area ratio of the sampling units were equal or greater than some of the environmental, tree community and human-related variables (Fig. 2 and Table S1). The sampling effort did not have a significant effect on carbon stock estimates (Table Fig. 2 and Table S1).

Figure 2 – The main drivers of carbon stocks in the Atlantic Forest.



Subtitle: **(A)** Standardized estimates of the coefficients from averaged models containing the effects of environmental conditions, human impacts, tree community proprieties and sampling methods on carbon stocks. (**B**) Bars show the partial pseudo-R^2 values for each of the co-variables (Table S1) included in the averaged models (n = 892 inventories). Drivers with significant effects (p-value < 0.05) are shown with asterisks. The error bars show standard errors for 95% confidence intervals of the mean parameter estimates.

Figure 3 – Individual co-variable with the greatest effect on the Atlantic Forest carbon stocks.



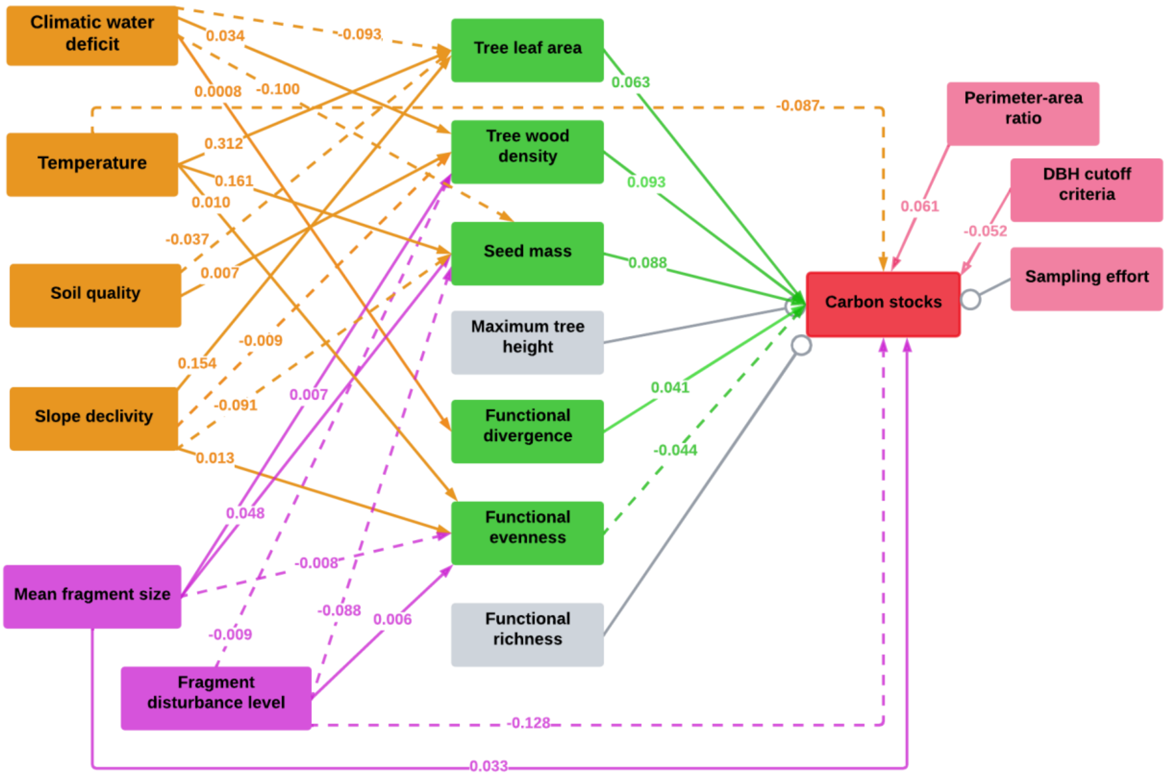
Subtitle: The effect of within fragment disturbance level on above-ground carbon stocks (Table S2 and S3), was fitted with the optimum model (Table S1). Within fragment disturbance level is shown as a categorical variable (i.e., without Ridit score transformation). Different letters are significantly different group means (*p*-value < 0.05). Error bars represent the 95% of confidence intervals (*n* = 892 inventories).

Source:

2.2 INDIRECT EFFECTS OF ENVIRONMENT AND HUMAN IMPACTS ON CARBON STOCKS

We found a considerable influence of the environmental conditions and human impacts on carbon stocks via effects on the tree community proprieties (Fig. 4 and Table 1). So, in addition to their direct effects, temperature, mean fragment size and within fragment disturbance level also presented indirect effects on carbon stocks. The stocks increased with mean fragment size, while they decreased with temperature and within fragment disturbance level (Fig.2). The indirect effects of within fragment disturbance level on carbon stocks were predominantly negative (via seed mass, wood density and FEve), whereas the indirect effects of temperature and mean fragment size in the landscape (via leaf area, wood density, FEve and FDiv) were predominantly positive (Fig. 4 and Table 1). Although climatic water stress, soil quality and slope declivity showed no significant direct effect on carbon stocks (Fig. 2), they affected the tree community proprieties, resulting in significant but indirect effects on carbon stocks (Fig. 4 and Table 1). Climatic water stress (via seed mass, wood density, leaf area and FDiv), soil quality (via wood density and leaf area) and slope declivity (via seed mass, wood density, leaf area, FEve and FDiv) indirectly decreased the Atlantic Forest carbon stocks (Fig. 4 and Table 1).

Figure 4 – Causal mediation analysis describing the direct and indirect effects of multiple drivers on the carbon stocks (n = 892).



Subtitle: Solid lines indicate positive significant effects (*p*-value < 0.05), whereas dotted lines indicate negative significant effects (*p*-value <0.05). Environmental conditions with significant effects are indicated in orange, human impacts in purple, tree community properties in green and field sampling methodology aspects in pink. Variables with non-significant effects on carbon stocks are indicated in grey. All model estimates are presented in Table S4.

Table 1 – Indirect effects of environmental conditions and human impacts on carbon stocks.

Driver	**via**	**Indirect effect**	**p-value**
Climatic water deficit	FDiv	0.00031	0.044
Climatic water deficit	FEve		
Climatic water deficit	WD	0.00222	<0.0001
Climatic water deficit	Seed mass	-0.00723	0.006
Climatic water deficit	Leaf area	-0.00358	0.01
Slope declivity	FDiv		
Slope declivity	FEve	-0.00099	<0.0001
Slope declivity	WD	-0.00058	<0.0001
Slope declivity	Seed mass	-0.00661	<0.0001
Slope declivity	Leaf area	0.00591	0.01
Within fragment disturbance level	FDiv		

Within fragment disturbance level	FEve	-0.00046	0.006
Within fragment disturbance level	WD	-0.00059	0.004
Within fragment disturbance level	Seed mass	-0.00637	<0.0001
Within fragment disturbance level	Leaf area		
Soil quality	FDiv		
Soil quality	FEve		
Soil quality	WD	0.00050	0.002
Soil quality	Seed mass		
Soil quality	Leaf area	-0.00144	0.048
Mean annual temperature	FDiv		
Mean annual temperature	FEve	-0.00076	0.002
Mean annual temperature	WD		
Mean annual temperature	Seed mass	0.01180	<0.0001
Mean annual temperature	Leaf area	0.01200	0.004
Mean fragment size	FDiv		
Mean fragment size	FEve	0.00067	<0.0001
Mean fragment size	WD	0.00047	0.008
Mean fragment size	Seed mass	0.00346	0.038
Mean fragment size	Leaf area		

Standardized coefficients with a significance level (significant; *p*-value <0 .05) are given for all relationships. Note: WD (CWM wood density), Seed mass (CWM Seed mass), Leaf area (CWM Leaf area), FEve (Functional evenness), FDiv (Functional divergence) (*n*= 892). Climatic water deficit was -1 transformed and WD, Seed mass and Leaf area were transformed in the natural logarithmic scale. All models were fitted with scaled drivers.

2.3 CARBON GAINS AND LOSSES TO CLIMATE AND FOREST HUMAN DISTURBANCES CHANGES

Projecting the carbon losses, we found that an increase of the within-forest disturbance level in 100%, 50% and 25% of the Atlantic Forest fragments with low to medium levels of disturbance to heavy and high levels would represent losses of 15.24%, 8.09% and 4.20% of Atlantic Forest carbon stocks (Table 2), respectively. If temperature increases 1.5°C without changes in precipitation, the regional carbon losses could be 5.12%, while an increase of 4°C in global temperatures may result in a decrease of 13.11% of carbon stocks across Atlantic Forest (Table 2). Projecting the carbon gains, if 100%, 50% and 25% of fragments with heavy and high levels of human disturbance advance in their successional trajectory to fragments with medium and low levels of human disturbance, the regional carbon gains would be 17.44%, 8.42% and 4.03%, respectively (Table 2).

Table 2 – Carbon gains and losses from forest human disturbance and climate changes.

Human impacts scenarios

	AGC stocks (ha^{-1})	**AGC stocks changes (%)**	**AGC stocks (Mg ha^{-1})**
Optimistic scenario			
100% of fragments with high and heavy levels of disturbances are recovered to medium and low levels of disturbances	80.92	17.44	12.02
50% of fragments with high and heavy levels of disturbances are recovered to medium and low levels of disturbances	74.70	8.42	5.80
25% of fragments with high and heavy levels of disturbances are recovered to medium and low levels of disturbances	71.79	4.20	2.896
Pessimistic scenario			
100% of fragments with low and medium levels of disturbances are degraded to high and heavy levels of disturbances	58.39	-15.24	-10.50
50% of fragments with low and medium of disturbances are degraded to high and heavy levels of disturbances	63.32	-8.09	-5.57
25% of fragments with low and medium of disturbances are degraded to high and heavy levels of disturbances	66.12	-4.03	-2.77

Climate impacts scenarios

	AGC stocks (ha^{-1})	**AGC stocks changes (%)**	**AGC stocks (Mg ha^{-1})**
MAT increases by 2°C	65.36	5.12	-3.53
MAT increase by 4°C	59.86	13.11	-9.03

Subtitle: The predictions were obtained from the direct and indirect effects provided by mediation causal analysis (Fig. 3 and Table 1).

Note: MAT= Mean annual temperature;

Carbon change estimates are shown according to the difference between the current carbon stock estimates and the projected carbon stock estimates. Current carbon stock: 68.9 (Mg ha^{-1}).

Source:

3 DISCUSSION

Given the global urgency to mitigate climate change, understanding the drivers of carbon stocks in tropical forests is increasingly important (HARRIS et al., 2021). Here, we found that widely accepted drivers of carbon stocks, such as climate, soil, topography, and forest fragmentation have a much smaller role than forest human disturbances and tree functional proprieties. In the Atlantic Forest, the greatest driver of the variation in carbon stocks was the level of human disturbances within fragments, with a role two- to six-fold greater than any other variable included in the analysis (Fig. 2 and Table 1). The greater accessibility to forest fragments increases their exposure to fire, selective logging and fuelwood extraction (LAURANCE; GOOSEM; LAURANCE, 2009). In addition, the opening of the fragment canopy and microclimatic changes created by disturbances can increase tree damage and mortality even after the disturbance has ceased (MAGNAGO et al., 2015; BALCH, 2011). Along with fragment disturbance, reductions in the fragment size and mean fragment size in the landscape also played an important role (Fig. 2 and Table 1). In small fragments, tree mortality is usually induced by stronger edge-effects which alter the fragment microclimate and increase wind turbulence (MAGNAGO et al., 2015). Furthermore, logging and forest ground fires can be aggravating sources of tree mortality in landscapes marked by high levels of forest fragmentation (BARLOW et al., 2003).

Tree community proprieties was also important, with larger carbon stocks found in forests dominated by heavy-seeded, large-leaved, hardwood trees (Fig. 2 and Table 1). Hardwood species can accumulate more carbon per unit of biomass but also more carbon over time due to the lower inherent mortality, turnover, and stem breakage (PRADO-JUNIOR et al., 2016). Seed mass does not directly affect species' carbons storage potential, but it correlates well with species longevity (MITTELMAN et al., 2021) and carbon storage potential (BELLO et al., 2015). In addition, if water availability is not a limiting factor, species with larger leaf areas can be more efficient to intercept light (WRIGHT et al., 2017), an essential resource for the growth and thus carbon assimilation. It has been well documented that carbon stocks are determined by these functional traits. However, our result contrasts with those of other studies conducted in Amazonia, where wood density was the main trait controlling the variation in carbon stocks (CAVANAUGH et al., 2014; FAUSET et al., 2015; SOUZA et al., 2019). In Atlantic Forest, the functional trait with the greatest effect on carbon stocks was seed mass, with an effect at the least 40% greater than wood density (Fig. 2 and Table S1).

We also found that how species concentrate and diverge in their functional niche spaces matters for carbon storage. In the Atlantic Forest, the negative effect of functional evenness was substantially greater than the positive effect of functional divergence on carbon stocks. Thus, we found more evidence supporting the mass ratio hypothesis, which proposes that carbon stocks are determined by the characteristics (traits) of the most dominant species in the community (GRIME, 2002), than the niche complementarity hypothesis, which predicts that the dominant species in the community have opposite functional trait values (i.e., different ecological strategies) allowing to accumulate more carbon due to a more efficient use of the available resources (ZHANG; CHEN; REICH, 2012). Therefore, we learned that not only the abundance of heavy-seeded, large-leaved, hardwood tree species is important for determining higher carbon stocks (CHAVE et al., 2009), but also the concentration of species exhibiting similar strategies of resource use (i.e. lower functional evenness) (KRAFT; GODOY; LEVINE, 2015).

We found smaller carbon stocks in sites with higher temperatures, where the rates of most of the ecophysiological processes that control primary productivity (i.e. photosynthesis and respiration) are higher (CLARK; CLARK, 2010). In boreal and temperate forests, increases in temperature allow plants to come close to the maximum photosynthetic threshold, increasing their carbon assimilation (KEITH; MACKEY; LINDENMAYER, 2009). However, in the warmer conditions of tropical and subtropical forests, the increase in temperature leads to higher maintenance costs for trees (e.g., higher respiration costs), and, thus, to a decrease in their carbon storage potential (STEGEN et al. 2011; CLARK; CLARK, 2010).

The effects of field sampling methodology on forest carbon estimates are poorly documented (CHAVE et al., 2003) and, as far as we know, this is the first time that their effects are weighted against well-known drivers of carbon storage. Here we found that field methods can be as important as some environmental and biological variables to explain the variation in carbon stock estimates. The effect of the dbh cutoff criteria was expected (due to the inclusion of more or fewer trees) and we reveal that the shape of the sampling units (i.e., plots) also plays an important role in carbon storage. Studies carried out using more elongated sampling units (i.e., higher perimeter-area ratio) tended to overestimate above-ground carbon stocks, which is probably related to the inclusion or exclusion of larger trees close to the plot limits (STOVALL; SHUGART; YANG, 2019). Therefore, we reinforce here that larger and less elongated sampling units (e.g. 20 x 20 m or higher) should be used to improve the accuracy of carbon stocks estimation (CHAVE et al., 2003; MAUYA et al., 2015). More generally, sampling aspects other than the total sampling area should be accounted for while modeling biomass stocks, particularly when using data from datasets using different sampling strategies. Our results suggest that the simple standardization of carbon estimates by the sampling effort alone (e.g. (POORTER et al., 2017; MENSAH et al., 2016; DURÁN et al., 2015) is not enough to guarantee unbiased interpretations of carbon stocks drivers.

3.1 INDIRECT EFFECTS OF ENVIRONMENT AND HUMAN IMPACTS ON CARBON STOCKS

While it has been documented that environmental conditions and human impacts affect forest carbon stocks, most studies have focused exclusively on direct effects, overlooking their indirect effects (DURÁN et al., 2015). Here we found that indirect effects of human impacts on carbon stocks via changes in species functional proprieties were predominantly negative (Table 1). The heterogeneity of disturbed fragments or landscapes may exclude competitively dominant species (i.e. high FEve) (CONNELL, 1978) and favor the proliferation of pioneer species, which have relatively low wood density and light seed mass, contributing to further reductions in carbon (MAGNAGO et al., 2014).

Temperature also presented both direct and indirect effects on carbon stocks. The abundance of heavy-seeded and large-leaved trees increased in warmer temperatures, resulting in a positive indirect effect on carbon stocks. The positive relationship between temperature and seed mass is considered an adaptation to improve germination rates in higher temperatures (ZHANG et al., 2019). On the other hand, warmer climates tend to present a greater dominance of small-leaved species due to the increase in transpiration rates (TOZER; RICE; WESTOBY, 2015). In the Atlantic Forest, there probably is enough water available for an effective transpiration cooling, allowing large-leaved species to assimilate carbon even in warmer climates (KIRSCHBAUM; MCMILLAN, 2019). Furthermore, the greater functional evenness among dominant species slightly decreased carbon stocks in warmer climates. But if we consider together all indirect effects, the overall effect of temperature on carbon stocks remained positive (Table 1 and S1).

Climatic water stress (i.e. CWD) decreased the abundance of heavy-seeded and large-leaved trees, while it increased the FDiv and the abundance of hardwood species (Fig. 4). Because the effect of the decrease in the abundance of heavy-seeded species was three times higher than any other indirect effects, the overall indirect effect of CWD on carbon stocks was negative (Table 1). Water stress conditions may favor the reduction of the functional similarity between co-occurring abundant species (increases in FDiv), probably due to the higher influence of resources competition (MAGNAGO et al., 2014). Moreover, due to the fibers and thick-walled vessels, higher wood density protects against vessel implosion and allows species survival during periods of water deficit (HACKE, 2001). However, these positive indirect effects on carbon stocks were compensated by the higher abundance of light-seeded and small-leaved trees in forests under drier climates.

Although soil quality and slope declivity showed no significant direct effect on carbon stocks (Fig. 2), they affected the tree community properties variables (Fig. 4), which resulted in significant indirect effects on carbon stocks (Table 1). Soil quality increased the abundance of hard-wood trees and decreased the abundance of large-leaved ones, resulting in an overall negative indirect effect on carbon stocks (Table 1). Interestingly, although we showed that low fertility soils have higher carbon stocks, as many findings of several other studies conducted in Amazonia (QUESADA et al., 2012), unlike many others, this negative effect is due to the greater dominance of species with greater leaf area in low fertility soils. Steeper slopes had smaller carbon stocks (Table 1), mainly driven by the decrease in the abundance of species wood density, leaf area and seed mass and by the increase in functional evenness (Fig. 4). On steep slopes, soil leaching, water runoff, higher light incidence and wind exposure, filter out some plant strategies that are not already adapted to these conditions (WERNER; HOMEIER, 2015) and favor the proliferation and survival of individuals with a short lifespan (i.e., lighter wood density and seed mass) (HOFHANSL et al., 2020).

3.2 IMPLICATIONS FOR CARBON PROTECTION POLICIES

Under the current global change scenario, the conservation and restoration of forest carbon have attracted unprecedented attention. Here, we provided a comprehensive assessment of the main drivers of carbon stocks for the Atlantic Forest with important implications for nature-based solutions to mitigate climate changes. First, the conservation of the Atlantic Forest carbon stocks is highly dependent on avoiding forest degradation, which can generate carbon losses at least two times higher than any future climate change. Moreover, emissions from forest degradation can jeopardize efforts of conservation planning and climate change mitigation agreements (e.g. REDD+, AICHI targets). For instance, the intensification of within fragment disturbances could lead to carbon losses of up to 10.50 Mg ha^{-1} (-15.24%), while the carbon protection and enhancement could achieve carbon gains by 12.02 Mg ha-1 (+17.44%) (Table 2). Second, the Atlantic Forest carbon stocks are also threatened by climate changes, specifically increases in temperature and water stress. If global warming were constrained to 1.5° C above pre-industrial levels, as suggested by Intergovernmental Panel on Climate Change (IPCC, (54)), 3.53 Mg ha^{-1} (-5.12% carbon loss) of carbon would be released only from the Atlantic Forest. If global warming continues at its current rate, carbon emissions can exceed 9.03 Mg ha-1 (-13.11% carbon loss) (Table 2). Third, initiatives aimed at mitigating climate change through the restoration of forest ecosystems could benefit from including species with greater wood density, heavier seeds masses and larger leaves. Fourth, the relationship between the taxonomic and functional diversity and carbon stocks was weak in Atlantic Forest, revealing that conservation policies focusing only on carbon may fail to protect biodiversity and highlighting the importance of separate add-on incentive mechanisms to achieve biodiversity conservation as well (PHELPS; WEBB; ADAMS, 2012). Finally, policies of carbon conservation should take into account the sampling methodology aspects across inventories, which can lead to biases in carbon estimation and, consequently, the misinterpretation of the efficiency of climate mitigation actions. Thus, the use of “good measurement practices to carbon stocks estimation” across forests (MCROBERTS et al., 2010) should be accounted for in carbon stock reporting.

4 MATERIALS AND METHODS

4.1 FOREST INVENTORIES

We used forest inventory data stored in the Neotropical Tree Communities database (TreeCo (LIMA et al., 2015; LIMA et al., 2020)) continuous effort to compile and organize plant community data in eastern South America (http://labtrop.ib.usp.br/doku.php?id=projetos:treeco:start). Here, we selected data from forest inventories with any type of stand biomass estimate (i.e., basal area or above ground biomass) conducted in any Atlantic Forest types. Aiming to reduce the noise in the dataset, we applied four filters to the inventory data: (i) a total sampling area equal or larger than 0.25 ha; (ii) a cutoff criterion of stem diameter at breast height (dbh) above 4.8 cm (e.g., dbh≥5.0 cm, dbh ≥10.0 cm); (iii) data on species names, abundance and biomass fully available and extractable; (iv) inventories with species trait data (see details below) that together made up at least 80% of the total community abundance. The first filter was applied to reduce common overestimation biases of above-ground carbon related to small sample sizes (CHAVE et al., 2004). The second filter was applied to avoid including tree regeneration and shrubs data. The third and fourth were necessary to calculate biotic metrics and ensure that they were representative of the community (PAKEMAN; QUESTED, 2009). In the end, we performed data analysis using a subset of 892 forest inventories (Fig. 1).

4.2 ABOVE-GROUND CARBON STOCKS

Among the 892 inventories considered here, 365 contained only estimates of the stand basal area (BA, $m^2\ ha^{-1}$) and 527 contained estimates of both BA and above-ground biomass (AGB, $Mg\ ha^{-1}$). To make the most out of the available data, we built an equation based on the inventories that had both BA and AGB to obtain AGB from BA estimates (eq 1). To do this, we first calculated the above-ground carbon stocks (i.e. AGC or carbon stocks) by multiplying AGB by the conversion of 0.456 g carbon per gram of AGB (MARTIN; DORAISAMI; THOMAS, 2018). Then, because inventories used 20 different allometric equations to estimate biomass (Table S5), we converted the AGC values obtained using each of the equations to the value expected using a single and common allometric equation, which here was the one proposed by ref. (CHAVE et al., 2014). To perform this correction, we used individual tree dbh and height measurements available from 109 Atlantic Forest inventories available from the Minas Gerais Forest Inventory (SCOLFORO, 2008) to estimate the relationships between each of the 20 allometric equations and the one equation proposed by (CHAVE et al., 2014). A simple linear regression model was used to describe the relationship between each pair of allometric equations and for all pairs of equations, the variance explained by the model was above 93% (Fig. S1). After obtaining AGC values using a common allometric equation for the 527 inventories with both BA and AGC (or AGB), we compared the performance of two linear and 12 non-linear candidate equations to select the one that best described the relationship between BA and AGC. The selection was based on the visual assessment of the residues and the lowest value of Akaike Information Criterion (Table S6 and Fig. S2). The Gompertz equation had the best performance (Fig. S3) and it was used to obtain AGC from BA for the all 892 of inventories:

Eq. 1: $\ln(AGC)=5.067*\exp(-0.807*\exp(-0.058*BA))$,

where AGC is given in Mg ha^{-1} using the allometric equation of ref. (CHAVE et al., 2014) and BA is given in m^2 ha^{-1}.

4.3 PRE-SELECTION OF CO-VARIABLES

A wide range of co-variables associated with each inventory could be combined to explain the variation of above-ground carbon stocks, generating thousands of possible models. To limit the number of possible models, we performed model construction and selection in two steps. First, we separated the available co-variables in groups based on our a priori hypotheses (i.e. climatic, topographic, soil, biological, human-related and methodological co-variables, Fig. S4 and Supplementary Data 1). We then performed a pre-selection of the candidate co-variables within each of these groups, based on their individual contribution to model performance (i.e. Akaike Information Criteria, AIC and R-squared of the models) and based on their biological meaning and ease-of-interpretation in the context of global changes. We constructed 54 candidate models including several possible combinations of the pre-selected candidate co-variables related to environmental conditions (17 co-variables), human-related impacts (7 co-variables), tree community diversity (8 co-variables) and field sampling methodology (3 co-variables) (Supplementary Data 1). To select the best candidate co-variables, each co-variable was included individually in the model, and its additional contribution to improving the model performance was evaluated by the decrease in the model AIC value (AIC) and, in case of minimal change in AIC value, we evaluated the increase in the full model explained variance, R^2. At this point, the collinearity was not evaluated because our intention was only to select candidate co-variables and not to estimate the regression coefficients. The final candidate co-variables selected for modeling carbon stocks included four environmental (i.e., Mean annual temperature, climatic water deficit, slope declivity and soil quality), three human-related (i.e. Within fragment disturbance level, Mean fragment size in the landscape and fragment size), seven related to tree community proprieties and diversity (i.e., CWM of tree maximum height, wood density, leaf area and seed mass and functional richness, evenness and divergence) and three related to the field sampling methodology used in the inventories (i.e., dbh cutoff criteria, perimeter area-ratio and sampling effort).

4.4 SITE DESCRIPTORS

To describe local climate conditions, we extracted the mean annual temperature (MAT, °C) and climatic water deficit (CWD, mm) from the geographical coordinates of each inventory. MAT was obtained from the maps provided by refs. (ALVARES et al., 2013; ALVARES et al., 2013b) at 100 m resolution and ranged in our dataset from 11.5° to 25.6° C. For inventories from Paraguay and Argentina, not covered by refs. (ALVARES et al., 2013; ALVARES et al., 2013b) MAT was obtained from WorldClim 2 at 1 km resolution (FICK; HIJMANS, 2017). The long-term climatic water deficit (CWD) was obtained from maps provided by ref. (CHAVE et al., 2014) at ~4.5 km resolution, available at https://chave.ups-tlse.fr/pantropical_allometry.htm. This variable is calculated as the total rainfall minus evapotranspiration during the dry months, when evapotranspiration is equal or exceeds precipitation and is commonly used to reflect seasonal water stress. As CWD is by definition negative, we decided to multiply it by -1 to facilitate its interpretation. Thus, sites with higher CWD values are more seasonally water-stressed.

Slope declivity (º) was the selected co-variable to describe site topography (range in the dataset: 0º to 44º), and it was calculated from the SRTM elevation data (~30 m resolution) (FARR et al., 2007). To represent the soil conditions, we used the soil quality index, which takes into account the soil depth, fertility, drainage and aluminum toxicity for plant growth (LIMA et al., 2020). Each soil attribute (depth, fertility, drainage and toxicity of aluminum) was classified with a value of 0 (worst quality for plant growth) to 4 (better quality for plant growth). Thus, this index ranged from 0 (worst quality) to 16 (best quality). The soil type information necessary for the construction of this index was extracted from the original publication or, when absent, from local, state and / or national soil maps. We used the database of soil profiles provided by (BENEDETTI et al., 2011) to obtain mean soil physical properties.

To describe human impacts related co-variables, three were selected because they explained better the variation of carbon stocks in our dataset (see Supplementary Data 1): within fragment disturbance level, fragment size and mean fragment size in the landscape.

The within disturbance level of fragment was classified based on the information about the type, intensity and timing of human disturbances (i.e. selective logging, fire, hunting, thinning) or/and forest successional stage (e.g., initial, early and late secondary or advanced and old-growth) provided by the authors of the inventories. Although we recognize that natural disturbance events can alter the carbon stocks of forest fragments, these events are rare, so we assumed that the major drivers of forest succession are related to human disturbances (e.g., clear-cutting, logging, and fire). Then, we considered four levels of within fragment disturbance: heavy (N=11), high (N=423), medium (N=285) and low (N=173 inventories). Heavy levels are represented by early secondary forest regrowing after clear cut 10–20 years before the inventory, locally known as 'capoeiras'. The high level represents chronically disturbed fragments, typically disturbed less than 50 years before the inventory. The medium level represents lightly or sporadically disturbed fragments, and/or forests disturbed 50–80 years before the inventory. Finally, the low level represents fragments without records of disturbances or those undisturbed for at least 80 years. We recognize that this is a rather coarse classification, with substantial variation in forest conditions within levels; however, we were unable to refine this classification any further due to a lack of more objective and detailed information in the original publications. Still, this classification has support in the legal classification of the Atlantic Forest (FUNDAÇÃO S.O.S MATA ATLÂNTICA, 2017) and is the best information available to take into account within-fragment disturbances across the entire Atlantic Forest (LIMA et al., 2020).

The size of the inventoried fragment was extracted from the original publications and double-checked by comparing it with other sources of information (FUNDAÇÃO S.O.S MATA ATLÂNTICA, 2017). The mean fragment size is the mean area of all fragments present in 4 × 4 km landscape subset centered on the coordinate of each inventory. Landscapes were obtained from vegetation cover maps (30 m resolution (HANSEN et al., 1979)) and a 70% canopy closure threshold was used to classify landscapes into fragment or non-fragment pixels. Classified landscapes were then used to calculate mean fragment size and other landscape metrics not used for analyses (LIMA et al., 2020). Smaller mean fragment sizes are indicative of higher forest loss and lower habitat amount. Landscape metrics were extracted in R version 4.2.0 (2022) using the contributed packages 'raster' and SDMTools (VANDERWAL, 2013).

To assess effects of tree community properties on above-ground carbon stocks, we used three types of metrics: (1) community-weighted means (CWM) of species trait values;

(2) functional trait diversity indices; and (3) a taxonomic diversity index, namely the Shannon-Wiener index. The CWM represents the central tendency of the species traits in the community and was calculated as the mean of each trait weighted by the abundance of the species in each community. The abundance was chosen as a weighting factor because basal area is strongly related to community biomass/carbon. We computed the CWM of four species-level traits considered important for carbon accumulation: maximum height (Hmax, m), wood density (WD, g.cm^{-3}), seed mass (SM, g) and leaf area (LA, cm^2). The species maximum height was calculated as the 90th-percentile height of all trees of the species and species WD was obtained from the Global Wood Density database (filtered by Tropical South America (CHAVE et al., 2009)). Seed mass and leaf area values were obtained in the literature (LIMA et al., 2020). For the species with no available WD, seed mass and leaf area, we used the genera or family mean values. In the end, 100% of the species had values of maximum height and wood density, 76% of seed mass and 42% has values of leaf area. For wood density, CWM was obtained after removing palms, palmoids, cacti, and tree ferns. For maximum height, we removed shrubs prior to the calculation of CWM. For seed mass, we removed tree ferns prior to the calculation of CWM.

We used three measures of functional diversity: functional richness (FRic), functional evenness (FEve) and divergence (FDiv). Functional indices were calculated for each inventory based on Hmax, WD, seed mass, leaf area and other species traits (i.e., leaf type and dispersion syndrome) available from the TreeCo database (see ref (LIMA et al., 2020)) for the full list of trait sources stored in TreeCo).

We included as many traits as available for computing indices so we could better describe the functional composition of the community, and not regarding those traits that are related to species carbon storage potential. FRic represents the amount of niche space filled by species in the community. FEve represents the regularity in the distribution of species dominance and reflects how thoroughly the resources available are being exploited by the plant community and is higher when the functional strategies of co-occurring species are evenly distributed in relation to resource use (KRAFT; GODOY; LEVINE, 2015). FDiv represents the functional distance among the most dominant species and is higher when the dominant species have high functional trait differentiation (KRAFT; GODOY; LEVINE, 2015). For FEve and FDiv, species abundances were used as weights to generate species multivariate-trait spaces. The CWMs, functional and diversity indices were calculated in R version 4.2.2 (2022) using packages “FD” and “vegan” (OKSANEN et al., 2017).

Finally, we obtained for each inventory the sampling methods used to estimate carbon stocks. The dbh cutoff criteria was obtained from the original publications and it ranged in our dataset from 4.8 cm to 20 cm. The perimeter-area ratio of the sampling units was obtained from the dimensions of sampling units (range: 0.025 to 0.92) and it provides a simple quantitative description of the shape of the sampling unit: the greater the ratio, the more elongated the plots sample units are. Sampling effort was obtained from the original publications, and it ranged from 0.25 to 26 ha.

4.5 STATISTICAL ANALYSIS

The statistical analysis was divided into two parts. First, we assessed the relative role and direct effects of environmental conditions, human impacts, tree community proprieties and sampling methods on carbon stocks using an approach based on model selection and multi-model inference. In the second part, we assessed the indirect effects of environmental conditions and human impacts on carbon stocks mediated by tree community proprieties using causal mediation analysis. Although both analyses were based on regression models and, causal mediation analysis may also provide the direct effects, the separation was necessary because it would not be possible to achieve the variation in carbon stocks explained by each co-variable, neither to compare the effect of important but high correlated co-variables (Spearman's Rho coefficient <0.6), as fragment size and mean fragment size (Fig. S5), avoiding multicollinearity issues.

Model selection and multi-model inference was performed with all the candidate co-variables selected in pre-selection (Supplementary Data 1). We constructed candidate models using all possible combinations of the co-variables and ranked them based on the model AIC and performed a model selection based on the lowest Akaike Information Criterion values (ΔAICc ≤ 4) followed by model averaging to infer about the relative effects of individual variables. The selected models were constrained to have co-variables with spearman coefficients lower than 0.6 (Fig. S5) and low variance inflation values (VIF ≤ 4) (LAFOURCADE et al., 2013). As no individual model had support from the data to be considered as the single best model (AIC weights <0.10), the first forty equally-plausible candidate models (i.e. delta AIC≤ 4 and AIC weights sum >0.77) were averaged to address the uncertainty in the selection of the best candidate co-variables (BURNHAM; ANDERSON; HUYVAERT, 2011). Finally, to describe the relative variable importance of each co-variable we calculated the partial pseudo-R^2 (Table S1), which represents the variance explained by each co-variable taking into account the effects of other co-variables present in the model.

Causal mediation analysis was performed because it allows the simultaneous computation of multiple paths (e.g. AUNG et al., 2020; HAUGHIAN; FREGO, 2017). Linear mixed-effects models were created as the basis of the mediation analysis: firstly, models expressing variation in tree community properties variables (i.e. mediator) in relation to environmental conditions and human impacts (the ‘mediator model’, Table S4 a,b,c,d,e) and then, a model expressing variation in carbon stocks in relation to the mediators, environmental conditions and human impacts , considering the effects of all co-variables (the ‘outcome model’, Table S4 f). Finally, we constructed mediation models (effects of X via M on Y, Fig. S5), to identify how much of the effect of environmental conditions and human impacts were direct and how much were indirect, mediated by tree community properties variables. Indirect effects represent the expected difference in the potential outcome when the mediator took the value that would realize under the treatment condition as opposed to the control condition, while the treatment status itself is held constant (IMAI; TINGLEY; YAMAMOTO, 2012; IMAI; KEELE; TINGLEY, 2010). Given the impossibility to constrain high correlated co-variables (>0.6) in causal mediation analysis, mean fragment size in the landscape was included in this analysis rather than fragment size (Fig. S5).

For the mixed-effects models and causal mediation analysis, the biogeographical sub-regions of the Atlantic Forest (OLSON; DINERSTEIN, 2002) were defined as random effects (to account a possible lack of independence between sites within the same biogeographical region). The carbon stocks of each inventory were ln-transformed to: (i) achieve the residual normality and homoscedasticity assumptions, (ii) reduce the effect of outliers and (iii) account for possible nonlinear relationships between variables. We also ln-transformed the CWM of functional traits prior to analyses. The within fragment disturbance level, the only ordinal variable, we transformed into a continuous variable using “ridit scores", by assigning values of 0 (bottom of hierarchy, heavy level of within fragment disturbance) to 1 (top of hierarchy, low level of within fragment disturbance), reflecting the relative ranking of each level (CHEN; WANG, 2014). All co-variables were standardized to a mean of zero and a standard deviation of one to allow comparisons of the strength of the effects among variables of the model.

Residual diagnostics plots were used to examine the all model residuals normality and homoscedasticity assumptions (Fig. S7). We also used correlograms of Moran's I to assess the spatial autocorrelation of model residuals. When the presence of spatial autocorrelation was significant, we added spatial filters to the models (MEMs, Moran’s eigenvector maps (DRAY; LEGENDRE; PERES-NETO, 2006)). The "mediation" package does not provide a validation function to assess the goodness of fit of mixed regression models. In this way, the validation of the causal mediation analyzes were achieved by ensuring the fit of all models included in the analyzes (Table S4 and Fig. S7). Analyses and graphs were performed using R version 4.2.0 (2022) and the following packages: mediation (DUSTIN et al., 2019), lme4 (BATES et al., 2015), MuMIn (BARTON, 2022) and ggplot2 (GGPLOT2, s.d.). The Moran's I tests and correlograms were performed using the spDep (BIVAND, 2022) and ncf (BJORNSTAD; CAI, 2018) packages.

4.6 PREDICTING CARBON GAINS AND LOSSES TO CLIMATE AND FOREST HUMAN DISTURBANCES CHANGES

We used the direct and indirect effects provided by mediation causal analysis (Figure 4 and Table 1) to predict the impact of changes in climate and fragment disturbance on the future carbon stocks across Atlantic Forest. Predictions of fragment human disturbances were made for two different scenarios: an optimistic and a pessimistic scenario. In the optimistic scenario, we assumed a widespread decrease in fragment disturbance and projected carbon gains related to the advance of fragments with heavy and high levels of disturbance to medium and low levels of disturbance, respectively. In the pessimist scenario we assumed an increase of fragment disturbances, so that fragments with low and medium levels of disturbance are disturbed to heavy and high levels, respectively. Future climate changes were simulated based on the IPCC Special Report (MASSON-DELMOTTE, 2019) and as above we simulated different scenarios: a stringent mitigation scenario (RCP2.6 (MASSON-DELMOTTE, 2019)) and scenarios without additional efforts to constrain emissions (’baseline scenarios’) (RCP6.0 and RCP8.5 (MASSON-DELMOTTE, 2019)). The first scenario (RCP2.6) aims to keep global warming below 2°C of pre-industrial temperatures (1850-1900) and in the second we assume an increase in mean temperature by 4°C of pre-industrial levels (MASSON-DELMOTTE, 2019).

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Competing interests: We declare no conflicts of interest.

Data Availability: All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials.

SUPPLEMENTARY MATERIALS

Human impacts as the main driver of tropical forest carbon

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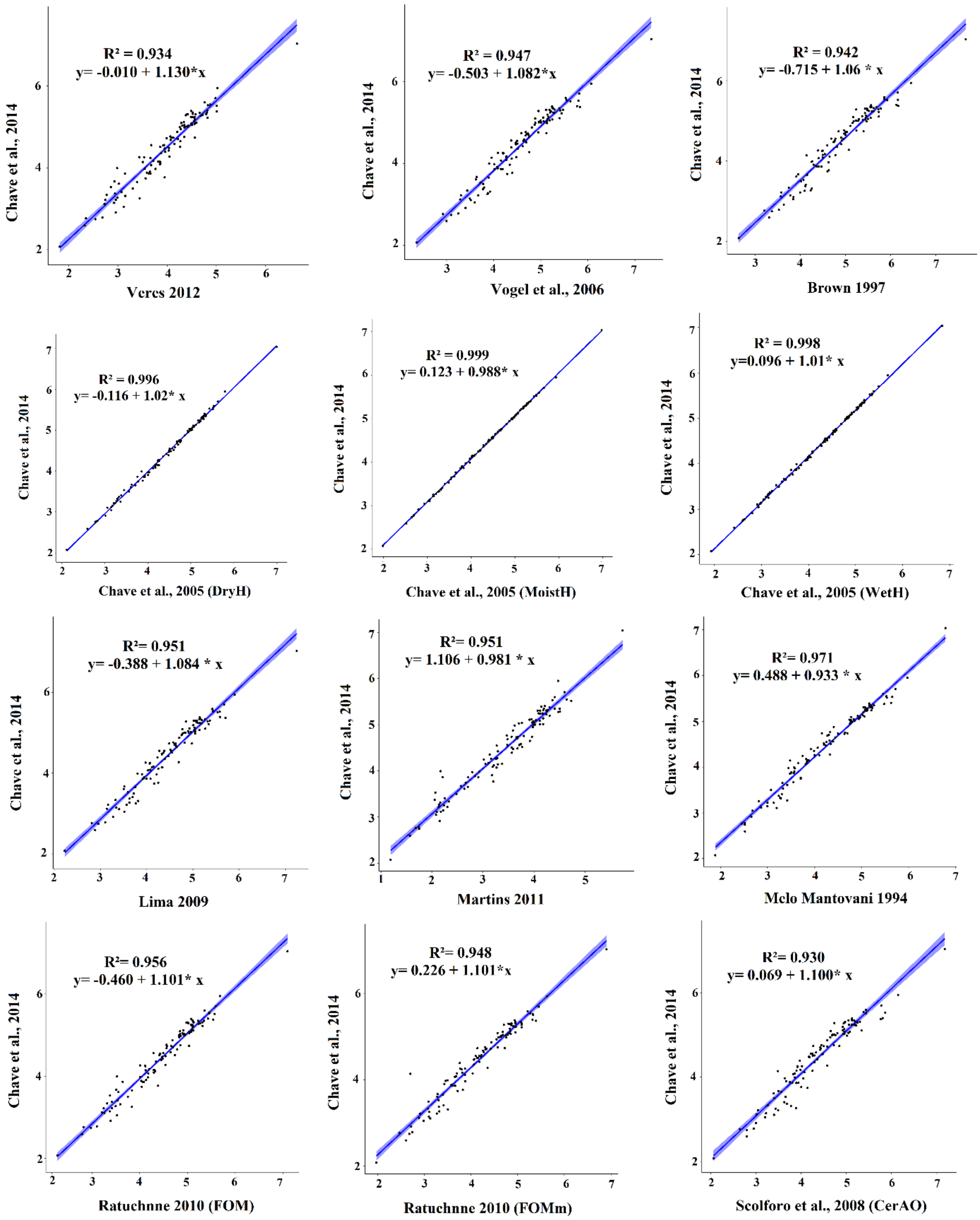
Figs. S1 to S7

Tables S1 to S6

References (1 to 13)

Fig S1: The relationship between the 20 allometric equations found to estimate AGC (Table S1) and the one provided by ref. (1). The *y*-axis is the natural logarithmic of the estimate provided by ref. (1) formula and the *x*-axis is the natural logarithmic of the aboveground carbon of each allometric equation. We present the mean prediction of the linear regression model (in blue) and the associated R^2 of the model.



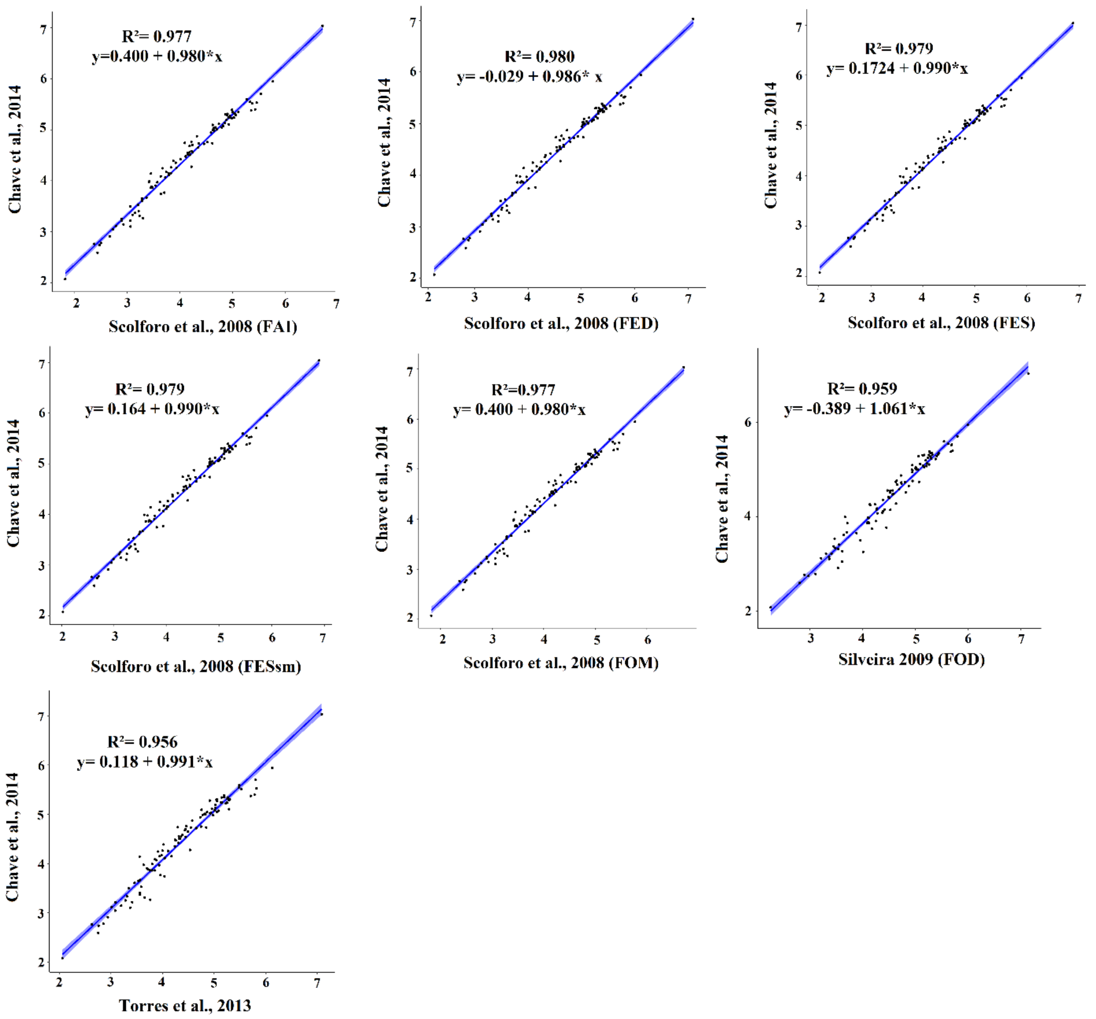

R²= 0.977
y=0.400 + 0.980*x
Chave et al., 2014
Scolforo et al., 2008 (FA1)
R²= 0.980
y= -0.029 + 0.986* x
Chave et al., 2014
Scolforo et al., 2008 (FED)
R²= 0.979
y= 0.1724 + 0.990*x
Chave et al., 2014
Scolforo et al., 2008 (FES)
R²= 0.979
y= 0.164 + 0.990*x
Chave et al., 2014
Scolforo et al., 2008 (FESsm)
R²=0.977
y= 0.400 + 0.980*x
Chave et al., 2014
Scolforo et al., 2008 (FOM)
R²= 0.959
y= -0.389 + 1.061*x
Chave et al., 2014
Silveira 2009 (FOD)
R²= 0.956
y= 0.118 + 0.991*x
Chave et al., 2014
Torres et al., 2013

Fig S2: Carbon equations residual plots. Smoothers between residuals and fitted values from different models tested to find the best description of the relationship between above-ground carbon (AGC; estimated by ref. (1)) and basal area (BA) based on from 527 inventories reporting both AGC and BA estimates.

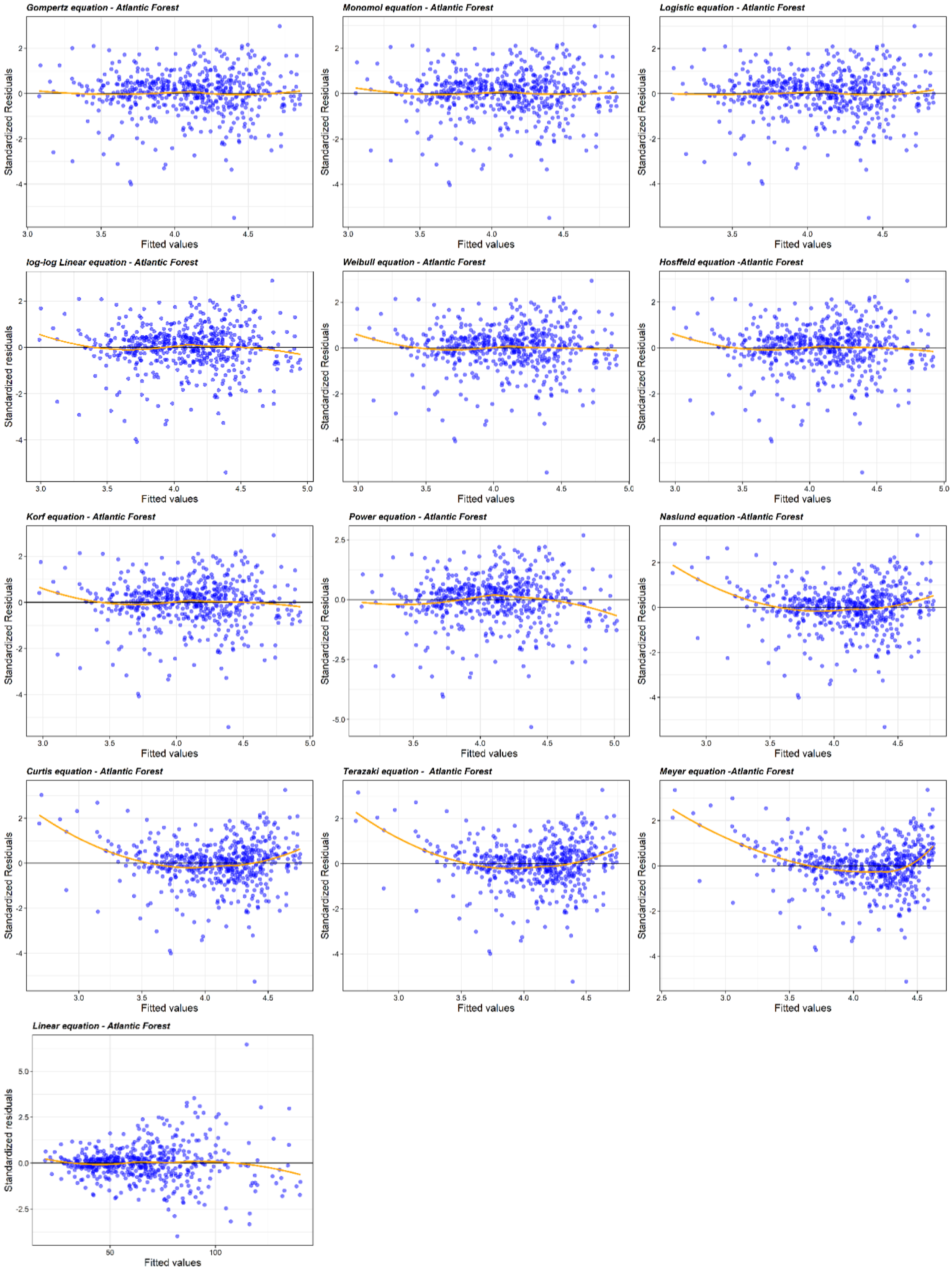


Fig. S3.:The relationship between above-ground carbon and basal area for 527 forest inventories. Values of above-ground carbon were obtained from values of above-ground biomass estimated using the allometric equation provided by ref.(1)). The green line is the fit of the Gompertz equation, whose parameter estimates, explanatory power (R^2) and standard residual error (%) are provided. Points represents the values for each inventory.

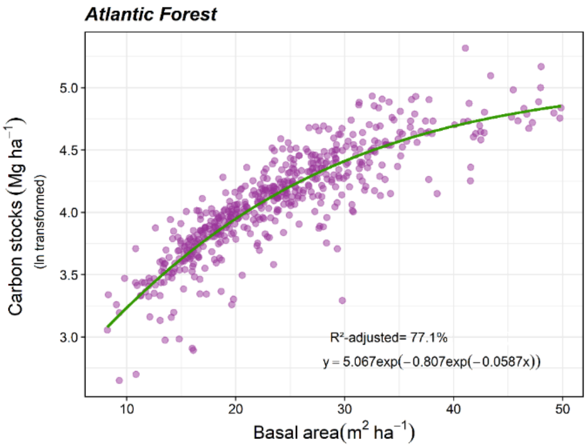


Figure S4: An a priori model of the causal relationships among climate, soil properties, topography, human impacts, tree community properties, and aboveground carbon storage (AGC) in Atlantic Forest. We hypothesize that effect of human impacts is negative, the soil properties is positive and the climate, slope declivity and field sampling methods can be positive or negative depending on the evaluated variable. Taller and hard wood species and taxonomic and functional diversity increases the carbon stocks.

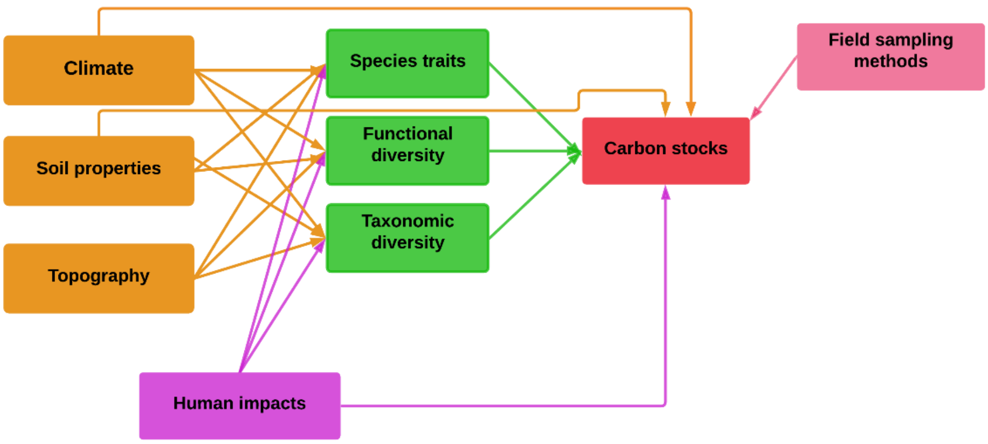


Figure S5:
Correlation matrix between potential carbon stocks drivers. Wg_gcm3_log (CWM wood density log transformed), MaxHeight_m_log (CWM Maximum height log transformed),

FEve.n (Functional evenness), FDiv.n (Functional divergence), FRic.n (Functional richness), PAR (perimeter area ratio), DBH_inclusion_c (Dbh cutoff criterion), Ridit_DL (Within fragment disturbance level), MAT (Mean annual temperature), ppt (Mean annual precipitation), CWD_T (Climatic water deficit -1 transformed), frag_area (Fragment size), mean.patch_area (Mean fragment size), DECLIV (Slope declivity), Soil.Quality_T (soil quality), LeafArea_log (CWM Leaf area log transformed) and SeedMass_g_log (CWD seed mass log transformed).

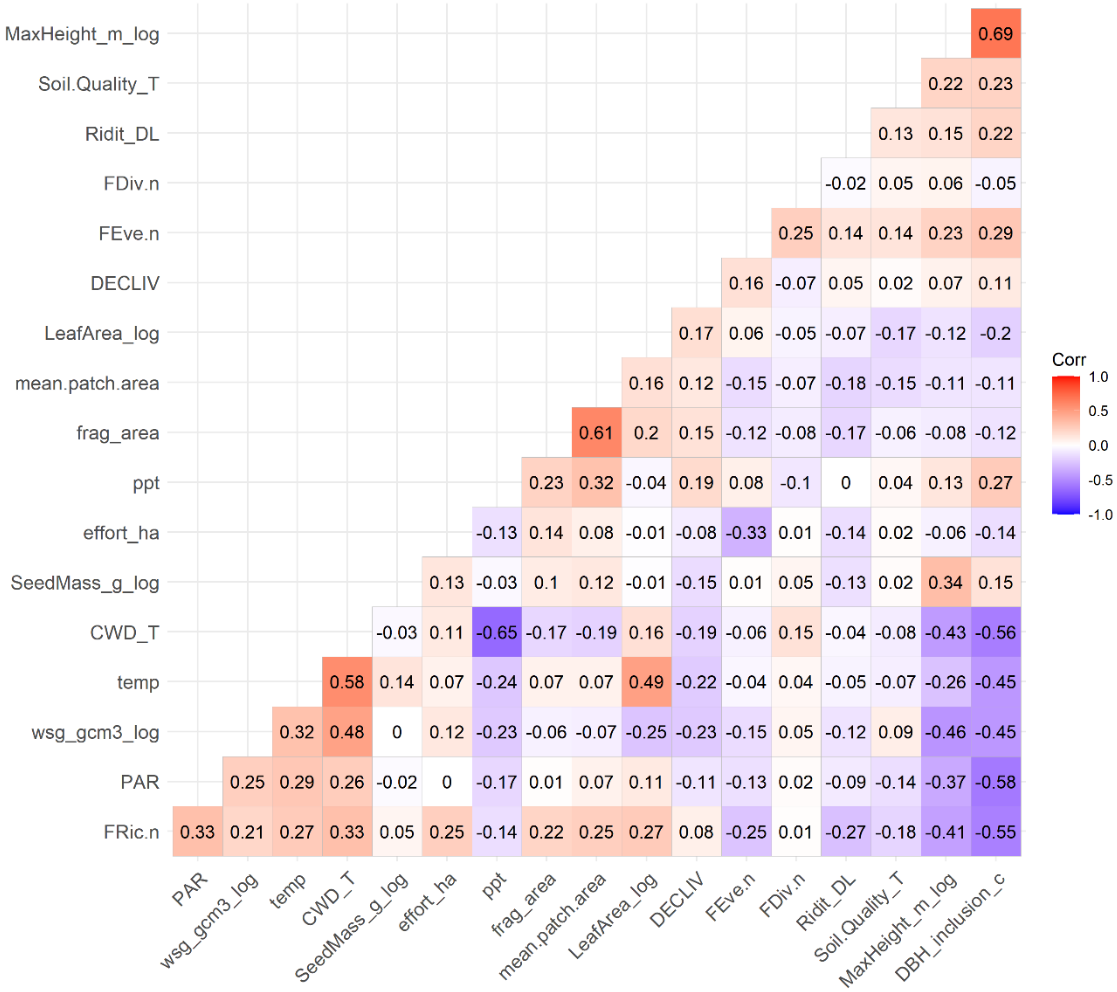


Figure S6:

Causal mediation analysis in its simplest form. a’ = effect of X on Y; b’ = effect of X on M, b’c’= effect of X on Y mediated by M.

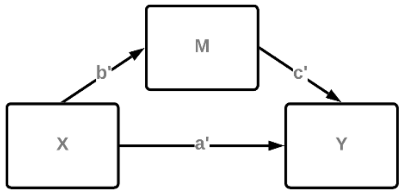


Figure S7: Residual plots. (A) AGC main drivers model (Table S1 and Fig 1). (B-F) Causal mediation models (Table S4).

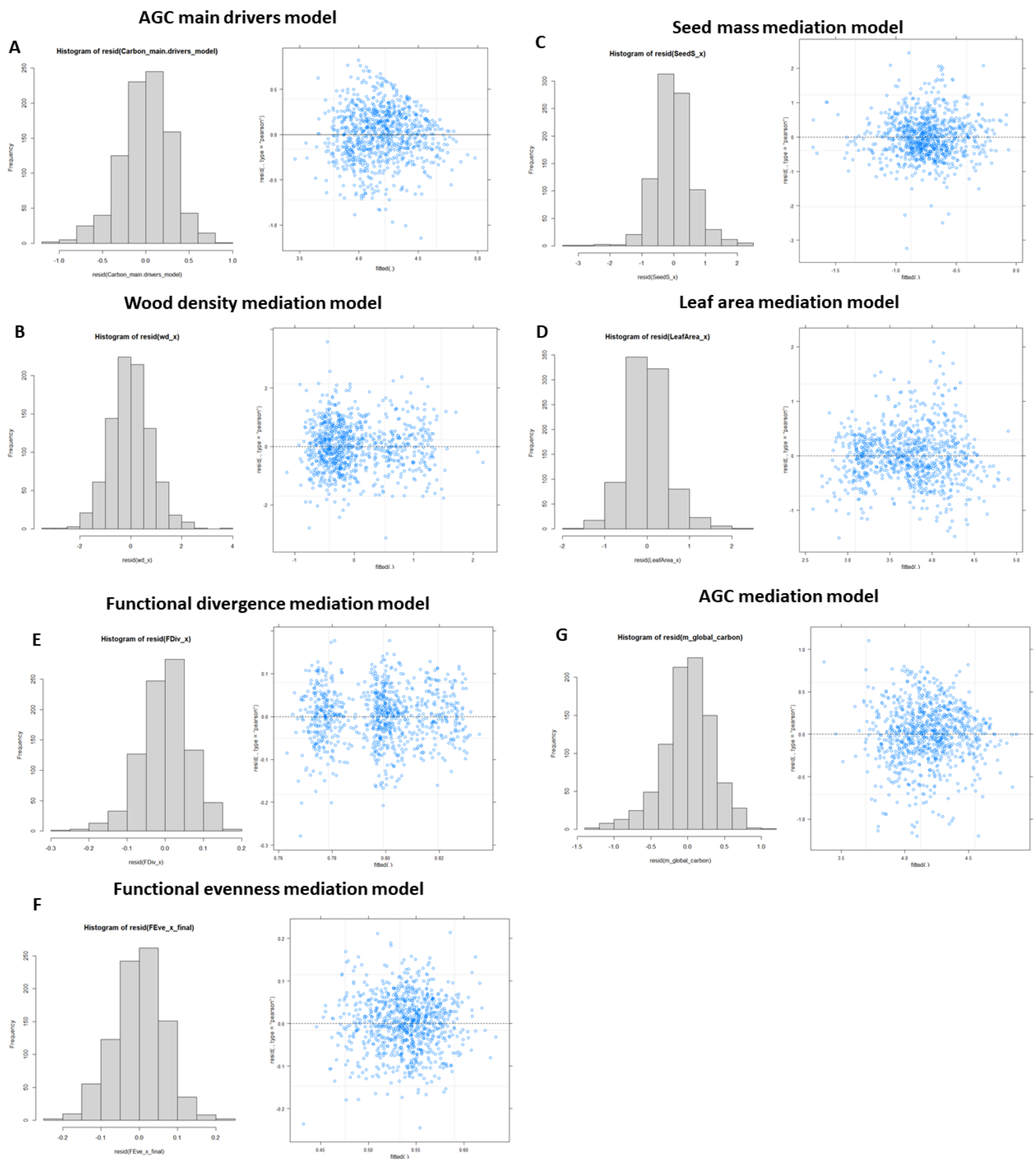


Table S1: Standardized coefficients and partial pseudo-R² of model-averaged of AGC main drivers model of Atlantic Forest. Model averaging was developed with all candidate models that presented ΔAICc ≤ 4. Note: AGC (Above-ground carbon stocks); SE (standard error).

Log(AGC)~scale(FRic.n)+scale(effort_ha)+scale(DBH_inclusion_c)+scale(PAR)+scale(log(LeafArea))+scale(FDiv.n)+scale(FEve.n)+scale(log(SeedMass_g))+scale(log(wsg_gcm3))+scale(log(MaxHeight_m))+scale(mean.patch.area)+scale(frag_area)+scale(Frag_Dist_L)+scale(CWD_T)+scale(temp)+scale(Soil.Quality_T)+scale(Slope)+(1|ecoreg)

Variable Code	Drivers	Estimate	SE	*p-value*	partial pseudo-R² (%)
	Intercept	4.132	0.054	<0.0001	
Frag_Dist_L	Within fragment disturbance level	-0.128	0.010	<0.0001	12.24
FEve.n	Functional evenness	-0.075	0.011	<0.0001	3.97
CWD_T	Climatic water deficit (-1 transformed)	-0.026	0.019	0.174	0.30
temp	Mean annual temperature	-0.098	0.015	<0.0001	3.97
DBH_inclusion_c	Dbh cuttoff criteria	-0.052	0.017	0.002	0.97
Soil.Quality_T	Soil quality	-0.017	0.010	0.110	0.25
Slope	Slope declivity	-0.001	0.011	0.921	0.00
FRic.n	Functional richness	0.016	0.013	0.234	0.15
SeedMass_g	CWM Seed mass	0.079	0.010	<0.0001	4.88
frag_area	Fragment size	0.029	0.011	0.007	0.73
FDiv.n	Functional divergence	0.044	0.010	<0.0001	1.71
mean.patch.area	Mean fragment size	0.033	0.011	0.002	0.90
LeafArea	CWM Leaf area	0.036	0.014	0.011	0.64
wsg_gcm3	CWM Wood density	0.054	0.013	<0.0001	1.56
PAR	Perimeter-area ratio	0.057	0.012	<0.0001	2.06
MaxHeight_m	Maximum tree height	0	0	0	0.00
effort_ha	Sampling effort	-0.020	0.010	0.059	0.35

Table S2: The carbon estimate ± standard error (SE) from optimum linear mixed model (Fig.2 and Table S1). Note: Within fragment disturbance level is shown here as a categorical variable (i.e., without Ridit score transformation).

Within Disturbance levels	Estimate	SE	df
Low	72.399	4.574	8.939
Medium	69.838	4.231	7.613
High	55.056	3.326	7.455
Heavy	48.241	5.225	75.295

Table S3: Tukey test results from generalized linear mixed models testing effects of within fragment disturbances on carbon stocks (AGC).

Within disturbances levels	*p- value*
Low - Medium	0.595
Low - High	<.0001*

Low - Heavy	<.0001*
Medium - High	<.0001*
Medium - Heavy	<.0001*
High - Heavy	0.445

"*" p-value > 0.05, significant values

Table S4: Causal mediation analysis models. The estimated coefficients ± standard error (SE) from multiple linear mixed models, testing the effects of human impacts (mean fragment size and forest degradation level) and environmental conditions (climate, slope declivity and soil quality) on functional traits (wood density -WD, Seed mass and Leaf area) and functional diversity (functional richness – FRic, functional evenness -FEve and functional divergence -FDiv). Note: MAT (Mean annual temperature), CWD (climatic water deficit), MEMs: Moran's eigenvector maps, spatial filters. Climatic water deficit was -1 transformed and AGC, WD, seed mass and leaf area were transformed in the natural logarithmic scale. All models were fitted with scaled drivers.

a) Wood density mediation model

	Estimate	SE	*p-value*
Intercept	-0.4869	0.0166	<0.0001
Within fragment disturbance level	-0.0091	0.0024	0.0002
Mean fragment size	0.0073	0.0026	0.0054
Slope declivity	-0.0092	0.0025	0.0002
Soil quality	0.0079	0.0025	0.0017
MAT	0.0061	0.0034	0.0750
CWD	0.0345	0.0046	<0.0001

b) Seed Mass mediation model

	Estimate	SE	*p-value*
Intercept	-0.7511	0.1159	0.0004
Within fragment disturbance level	-0.0885	0.0211	<0.0001
Mean fragment size	0.0487	0.0225	0.0308
Slope declivity	-0.0912	0.0215	<0.0001
Soil quality	0.0343	0.0217	0.1138
MAT	0.1611	0.0294	<0.0001
CWD	-0.1002	0.0387	0.0103

c) Leaf area mediation model

	Estimate	SE	*p-value*
Intercept	3.6961	0.1019	<0.0001
Within fragment disturbance level	-0.0120	0.0171	0.4833
Mean fragment size	-0.0246	0.0182	0.1771
Slope declivity	0.1545	0.0174	<0.0001
Soil quality	-0.0377	0.0175	0.0319
MAT	0.3129	0.0238	<0.0001
CWD	-0.0938	0.0317	0.0033

d) Functional divergence mediation model

	Estimate	SE	*p-value*
Intercept	0.7895	0.0072	<0.0001
Within fragment disturbance level	-0.0024	0.0021	0.2696
Mean fragment size	0.0001	0.0023	0.9634
Slope declivity	-0.0013	0.0022	0.5586
Soil quality	0.0012	0.0022	0.5864
MAT	0.0008	0.0030	0.7666
CWD	0.0073	0.0036	0.0468

e) Functional evenness mediation model

	Estimate	SE	*p-value*
Intercept	0.5245	0.0102	<0.0001
Within fragment disturbance level	0.0061	0.0022	0.0074
Mean fragment size	-0.0089	0.0024	0.0002
Slope declivity	0.0132	0.0023	<0.0001
Soil quality	0.0040	0.0023	0.0866
MAT	0.0102	0.0032	0.0015
CWD	-0.0069	0.0040	0.0870
MEM10	-0.0104	0.0022	<0.0001
MEM15	0.0071	0.0022	0.0017
MEM86	0.0072	0.0022	0.0010
MEM3	-0.0133	0.0030	<0.0001
MEM14	0.0075	0.0022	0.0008

f) AGC stocks mediation model

	Estimate	SE	*p-value*
Intercept	4.1420	0.0526	<0.0001
Within fragment disturbance level	-0.1272	0.0106	<0.0001
Mean fragment size	0.0329	0.0114	0.0040
Slope declivity	-0.0036	0.0111	0.7464
Soil quality	-0.0191	0.0108	0.0789
MAT	-0.0975	0.0164	<0.0001
CWD	-0.0253	0.0197	0.2008
Wood density	0.0642	0.0142	<0.0001
Tree Maximum Height	0.0265	0.0154	0.0863
Leaf area	0.0383	0.0147	0.0093
Seed mass	0.0721	0.0116	<0.0001
PAR	0.0552	0.0123	<0.0001
DBH cutoff	-0.0614	0.0189	0.0012
Sampling effort	-0.0211	0.0108	0.0516

Table S5. List of the all allometric equations reported in the forest inventories used for data analysis. AGB= Above-ground biomass, H= Height of the tree, DBH= diameter at breast height, WD= wood density and DW= Dry weight.

Allometric equations	Authors
AGB=0.0673*(WD*(DBH^2)*H)^(0.976)	Ref. 1
AGB=0.033430*(DBH^2.397902)*(H^0.426536)	Ref. 2
AGB=exp(-2.289+2.649*ln(DBH)-0.021*(ln(DBH))^2)	Ref. 3
AGB=exp(-2.187+0.916*ln(WD*(DBH^2)*H))	Ref. 4
AGB=exp(-2.977+ln(WD*(DBH^2)*H))	Ref. 4
AGB=exp(-2.557+0.940*ln(WD*(DBH^2)*H))	Ref. 4
DW=(59.321357)+(-12.28289)*DBH+(0.8396136)*(DBH^2)	Ref. 5
AGB=0.04821*(DAP^1.34374)*(H^1.26829)	Ref. 6
ln(AGB)=-4.15190+1.06068*ln((DBH^2)*H)	Ref. 7
AGB=0.317*(DBH^2)+0.009*((DBH^2)*H)	Ref. 8
AGB=-3.025*DBH+0.425*(DBH^2)+0.006*((DBH^2)*H)	Ref. 8
AGB=exp(-10.8771683824+2.6359736325*ln(DBH)+0.0878059946*ln(H))/(0.4802)	Ref. 9
AGB= exp(-11.319842099+2.1415723631*ln(DBH)+0.8134282561*ln(H))/(0.4833)	Ref. 9
AGB=exp(-10.7501678493+2.0580637328*ln(DBH)+0.8604515609*ln(H))/(0.4860)	Ref. 9
AGB=exp(-10.9520199234+2.0898526615*ln(DBH)+0.8096162241*ln(H))/(0.4839)	Ref. 9
AGB=exp(-10.9520199234+2.0898526615*ln(DBH)+0.8096162241*ln(H))/(0.4802)	Ref. 9
AGB=exp(-11.319842099+2.1415723631*ln(DBH)+0.8134282561*ln(H))/(0.4833)	Ref. 9
AGB=25.87071+0.02909*(DBH^2)-0.21382*(H^2)+0.03189*(DBH^2)*H	Ref. 10
AGB = 0.024530*(DAP^2.443356)*(H^0.423602) + 0.2596*(0.024530*(DAP^2.443356)*(H^0.423602)) + 0.0445*(0.024530*(DAP^2.443356)*(H^0.423602))	Ref. 11
AGB=(-4.8639)+0.3981*DBH+0.2625*(DBH^2)	Ref. 12
$\log_{10}$(AGB)=-0.88239023+2.40959057* $\log_{10}$ (DBH)	Ref. 13

Table S6. Performance of carbon equations based on basal area. Comparison of the equations used to find the best description for the relationship between above-ground carbon (AGC; estimated by ref.1) and basal area (BA) based on from 527 inventories reporting both estimates. Best equation (i.e Gompertz equation) was selected based on the lowest AIC value and are shown in blue.

		Akaike value
Gompertz equation	**$\log_{10}$ (AGC) ~ A*exp(-c*exp(-k*BA))**	**-184.821**
Monomol equation	$\log_{10}$ (AGC) ~ A*(1-c*exp(-k*BA))	-184.783
Log-Log linear equation	$\log_{10}$(AGC)~$\log_{10}$(BA)	-183.039
Weibull equation	$\log_{10}$ (AGC) ~ A*(1- exp(-k*BA^c))	-182.772
Hosffeld equation	$\log_{10}$ (AGC) ~ A/ (1+c*exp(-k*ln(BA))	-182.287
Korf equation	$\log_{10}$ (AGC) ~ A*exp(-k/BA^c)	-181.787
Power equation	$\log_{10}$(AGC) ~ A* (BA^k)	-174.293
Naslund equation	$\log_{10}$ (AGC) ~ BA/ (A*BA+k)^2	-160.107
Curtis equation	$\log_{10}$ (AGC) ~ A*(BA/(1+BA))	-150.323

Terazaki equation	$\log_{10}$ (AGC) ~ A*exp(-k/BA)	-144.777
Meyer equation	$\log_{10}$ (AGC) ~ A*(1-exp(-k*BA))	-102.209
Linear equation	AGC ~ BA	4268.906

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ARTIGO 2: ESTIMATING STAND CARBON STOCKS FROM STRUCTURAL VARIABLES IN TROPICAL FORESTS

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ABSTRACT

Estimating of carbon stocks from tropical forests is a key part of the unfolding climate crisis. Using a large dataset of 697 Atlantic Forest inventories, we evaluated the application of regional and forest type-specific equations to estimate carbon stocks based on two stand structural variables: stand basal area and stand density. We compared the predictive ability of one- and two-variable equations and showed that estimating carbon stock from the stand basal area and stand density provides accurate results for moist and dry forests of the Atlantic Forest domain. The developed equations based only on the stand structural variables explained 85.2%-96.2% of the carbon stocks variations having less than 6.5% of estimation errors. Thus, carbon stocks from the stand forestry structural variables can be accurate, and thus may represent an alternative when individual tree measurements and identifications from where complete forest inventories are not available.

1 INTRODUCTION

Tropical forests play a key part in the unfolding climate change crisis. Globally, they are responsible for great removals of carbon dioxide from the atmosphere, store almost half of the terrestrial aboveground carbon (Lewis et al., 2015) and account for 78% of GHG gross emissions (Harris et al., 2021). Given such importance, these forests have attracted unprecedented attention and several investments for carbon protection and enhancement (Ardila et al., 2021), which led governments and forest landowners to track forest carbon cycling closely (Vorster et al., 2020). However, measuring forest carbon stocks remains a challenge and the development of easy-to-apply methods to expand the estimation of carbon stocks could, therefore, make a significant contribution to improving the performance of mitigation strategies.

Forest carbon stocks can be estimated by direct or indirect methods. Direct method involves the destructive sampling and weighting of all trees in the forest, which is the most accurate method but is seldom feasible (Tashi et al., 2017). Indirect method mostly involves the use of tree allometric equations that are based on tree specific measures or characteristics, such as diameter at breast height, tree height and species wood density (see Chave et al., 2014). This method is the most widely used and offers reliable carbon estimates of individual trees, forest types and stands (Petersson et al., 2012). However, it depends on detailed, tree-by-tree forest inventories, which are time-consuming and costly (McRoberts et al., 2013). In addition, carbon stocks can be indirectly estimated using remote sensors based on the spectral reflectance of the vegetation (Lu, 2006) and/or high-resolution maps of forest structure (e.g Light Detection and Ranging (LiDAR), Silva et al., 2017). These methods are the best ones for estimating carbon over large areas (Vicharnakorn et al., 2014), but they still depend on direct and indirect methods of carbon stocks estimation for calibration (Baccini et al., 2012; Clark & Kellner, 2012).

The use of allometric equations based on the stand variables (i.e "stand allometric equations") could be an important alternative when measurements of tree diameter, height, and wood density are not available. These variables can rapidly be measured in the field and are commonly provided in published forest inventories. Particularly, allometric equations using stand basal area as a predictor is a promising option to estimate forest carbon stocks. The basal area has proven to be a good predictor of forest biomass by integrating the effect of both the number and diameter of trees. Stand density can also be an option to improve the performance of carbon allometric equations at stand level (see Khan et al., 2018). Reductions in the carbon stocks of individual trees are commonly related to the increase in the stand density (Yoda et al., 1963; Weller, 1987). Some studies have already developed stand-level equations to estimate carbon stocks from the basal area (de Lima et al., 2020; Torres & Lovett, 2013) and basal area with others stand variables, such as stand density (Khan et al., 2018). But, most were developed single species and/or planted species (e.g. Khan et al., 2018, 2020; Rahman et al., 2015) and the errors were rarely reported.

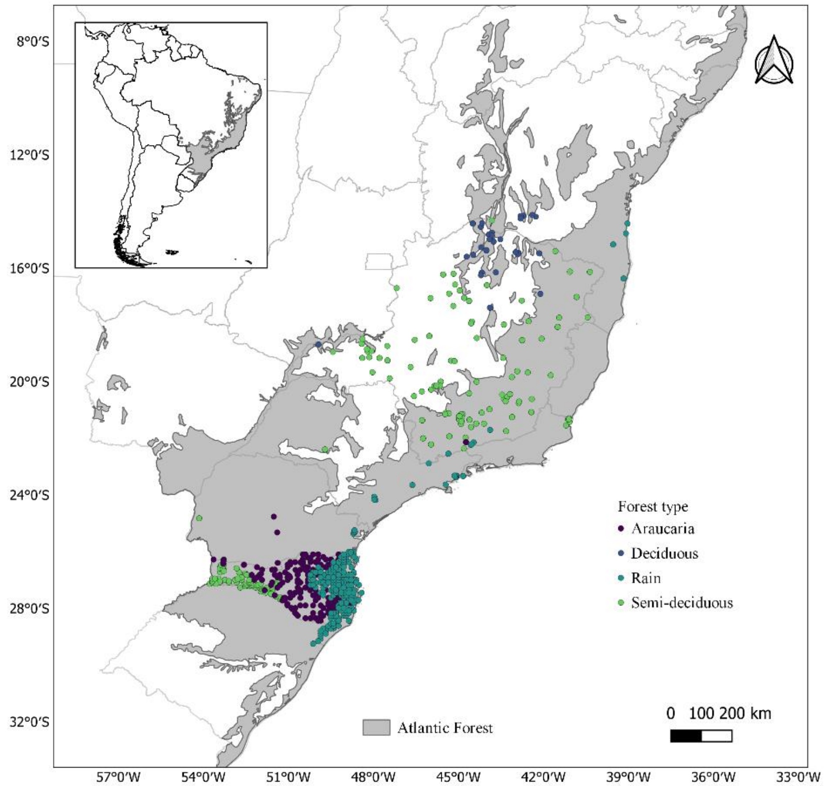
In this study, we use a large database to propose allometric equations for estimating carbon stocks from forest structural variables. With the substantial amount of published forest inventory data with the only basal area and tree density, these equations can be useful for expanding carbon estimates in the Atlantic Forest. We assess the potential of using stand basal area (BA) and stand density (SD) to predict above-ground carbon stocks (AGC) in natural mixed-species forests. This assessment is performed individually for four different tropical/subtropical forest types of the Atlantic Forest domain and also for this tropical forest as a whole. For this, we use a dataset of 697 inventories (Scolforo et al.2008; Lima et al., 2015, 2020), in which the community basal area, stand density and above-ground biomass estimates are reported. We asked the following question: Are stand basal area and stand density capable of generating accurate estimates of carbon stocks?

2 MATERIALS AND METHODS

2.1 FOREST INVENTORIES

We used forest inventory data stored in the Neotropical Tree Communities database (TreeCo, version 4.0, Lima et al., 2015, 2020), in the Santa Catarina Forest Inventory (Vibrans et a. 2020), and in the Minas Gerais Forest Inventory database (Scolforo et al., 2008), which contain more than 4000 forest inventories from eastern South America in the Brazilian Cerrado, Caatinga and Atlantic Forest domains. Here, we restricted our analyses only to forest inventories of Atlantic Forest due to the lower representation and spatial concentration of forest inventories in the Brazilian Cerrado and Caatinga. In addition, we selected only inventories with (i) a total sampling area equal to or larger than 0.25 ha (ii) a cut-off criterion of stem diameter at breast height (dbh) above 4.8 cm (e.g., dbh≥5.0 cm, dbh ≥10.0 cm) and (iii) basal area estimates higher than 8 m^2 per hectare. The first filter was applied to reduce common overestimation biases of above-ground carbon related to small sample sizes (Chave et al., 2004). The second filter was applied to avoid the noise related to the inclusion of trees from different forest strata. The third was applied to exclude the initial secondary (*capoeiras*). In the end, we performed data analysis using 697 forest inventories of Atlantic Forest (Fig. 1), composed of 234 rain forests, 158 *Araucaria* forests, 63 deciduous forests and 233 semi-deciduous forests. Other forest types present in the databases (e.g. Altitude Forest and Restinga) were not included in the analyses due to their small representativeness (n<10).

Figure 1 – Sites in Atlantic Forest included in the study. The data from the Neotropical Tree Communities and Minas Gerais Forest Inventory database.



Source:

2.2 BASAL AREA, STAND DENSITY AND ABOVE-GROUND CARBON ESTIMATES

Basal area, stand density and aboveground carbon (AGC) estimates were compiled from the original inventories. Most inventories reported above-ground biomass (AGB) instead of the AGC. So, we first obtained the AGC stocks (i.e. carbon stocks) by multiplying AGB by the standard conversion of 0.456 g carbon per gram of biomass (Martin et al., 2018). Because the 697 inventories used here used 20 different allometric equations to estimate biomass/carbon stocks (Table S1), we converted all carbon estimates to those using the allometric equation AGB_{est} = 0.0673 x (WD x DAP² x H) 0.976 proposed by Chave et al. (2014), where AGBest is the AGB estimated, WD is the species wood density, DAP is the diameter at 1.3m and H is the tree height. To do so, we used the linear regression equations available in Pyles et al., 2022 (Table S1 and Figure S1).

2.3 EQUATION'S DEVELOPMENT

We compared the performance of one- and two-stand variable equations to estimate log values of aboveground carbon stocks for the four different forest types in our dataset and for the Atlantic Forest as a whole. The AGC was log10 transformed before equations fitted to address the normality and homoscedasticity assumptions and reduce the effect of outliers. Eighteen commonly used linear and non-linear equations forms (Table 1) were compared for their predictive ability to identify the best fit. The first variable was stand basal area (BA) and the second was stand density (SD) (e.g. Khan et al., 2018). The equation parameters were estimated using maximum likelihood fit from "nlme" and "nls2" packages (Grothendieck, 2015; Pinheiro et al., 2021) in the R software version 4.0 (R Core Team, 2021).

Table 1. The candidate equations used to estimate log values of carbon (AGC, Mg ha-1) from stand basal area (BA, m^2 ha^{-1}) and stand density (SD, ha^{-1}). Values of AGC correspond to the estimates obtained using the equation proposed by Chave et al. 2004. β0, β1, β2, β3, β4 are the model coefficients to be estimated.

Equation	Type	Reference name
$\log_{10}$ (AGC)~ β0 + β1* $\log_{10}$(BA)	Linear	Log-log
$\log_{10}$ (AGC)~ β0*(BA/(1+BA))	Non-linear	Curtis
$\log_{10}$ (AGC)~ β0*exp(-β1*exp(-β2*BA))	Non-linear	Gompertz
$\log_{10}$ (AGC) ~ β0/ (1+ β1*exp (-β2* $\log_{10}$ (BA))	Non-linear	Hosffeld
$\log_{10}$ (AGC) ~ β0*exp(-β1/$BA^{\beta 2}$)	Non-linear	Korf
$\log_{10}$ (AGC) ~ β0*(1-exp(-β1*BA))	Non-linear	Meyer
$\log_{10}$ (AGC) ~ β0*(1- β1*exp(-β2*BA))	Non-linear	Monomol
$\log_{10}$ (AGC)~ BA/ (β0*BA+ β1)^2	Non-linear	Naslund
$\log_{10}$ (AGC) ~ β0* ($BA^{\beta 1}$)	Non-linear	Power
$\log_{10}$ (AGC) ~ β0*exp(-β1/BA)	Non-linear	Terazaki
$\log_{10}$ (AGC) ~ β0*(1- exp(-β1*$BA^{\beta 2}$))	Non-linear	Weibull
$\log_{10}$ (AGC) ~ β0+ β1* $\log_{10}$ (BA)+β2 $\log_{10}$ (SD)	Linear	Schumacher and

		Hall (logarithmic)
$\log_{10}$ (AGC) ~ β0+ ($BA^{\beta 1}$)*(SD $^{\beta 2}$)	Non-linear	Schumacher and Hall
$\log_{10}$ (AGC) ~ β0+ β1* $\log_{10}$ (BA^2*SD)	Linear	Spurr (logarithimic)
$\log_{10}$ (AGC) ~ β0+ (BA^2*SD)$^{\beta 1}$	Non-linear	Spurr
$\log_{10}$ (AGC) ~ β0+ β1*BA^2+ β2*(BA^2*SD)+ β3*(BA*SD^2)+ β4*SD	Non-linear	Naslund
$\log_{10}$ (AGC) ~ β0+ β1*BA^2+ β2*(BA^2*SD) + β3*SD	Non-linear	Stoate

2.4 EQUATION'S SELECTION AND VALIDATION

The selection of the equation that best describes the AGC-BA-SD relationship was based on the lowest value of the Akaike Information Criterion (AIC) and on the visual assessment of the residual standard error (RSE). The AIC is a measure of the relative performance of statistical models for describing a given dataset, while the RSE is a goodness-of-fit measure that can be used to analyze how well a set of data points fit with the proposed equation. We also reported the coefficient of determination (R^2), which indicates the explanatory power of each regression equation and the mean relative estimation error (Sxy %), which measures the relative error that should be expected in the estimate of a single stand (Li et al., 2013) .The systematic biases introduced by the natural logarithmic transformation of AGC were corrected using the correction factor (CF) calculated for each equation (Sprugel 1983). The Sxy and CF were computed using the formulas below:

$$Sxy = \sqrt{\frac{\sqrt{\frac{(P_i - O_i)^2}{n}}}{\overline{Oi}}}\ x100$$

$$CF = exp\ (\frac{RSE^2}{2})$$

,where Pi are the predicted carbon values, Oi are the observed carbon values, $\overline{Oi}$ the mean value of observed carbon, n is the sample size and RSE is the residual standard error. The predictive performance of the selected equations was evaluated using an independent dataset and a 10-fold cross-validation approach. The dataset of each forest type and with all datasets together was randomly split into 10 subsamples of approximately the same size (i.e., 10 parts). A small part of the data (i.e., 1/10 of total samples) was used as validating data (independent), while the remaining 9 parts were used as training data. This process was repeated 10 times. The coefficient of determination and the mean relative estimation error were calculated for each dataset and were averaged to obtain the final R^2 and Sxy values for each model. Good equations have R^2 and Sxy of testing dataset quite similar to R^2 and Sxy of the training dataset. We also evaluate the predictive performance of the selected equations by graphical analysis of the AGC predicted vs. observed values, which consisted of comparing the trend of predicted vs. observed values to the linear 1:1 trend.

3 RESULTS

For the rain, *Araucaria* and semi-deciduous forests, the log-transformed values of AGC were best predicted by equations with stand basal and stand density values (see below equation (1), (2) and (4)), whereas for the deciduous, the equation-based only on stand basal area (i.e. one-variable (equation (3)), was found suitable for predicting stand-level carbon stocks. For the Atlantic Forest as a whole, equations with stand basal area and stand density showed the best performance for predicting carbon stocks. The coefficient of determination of developed equations ranged from 85.28% to 94.14% and the relative estimation error from 2.48% to 6.50% (Table 2). The goodness of fit statistics for the carbon equations was shown in table 2 and estimated parameters for each selected equation were shown in table 3

Table 2: Model selection parameters. ΔAIC: Delta Akaike information; RSE: residual standard error; Sxy: relative estimation error; R^2: coefficient of determination; CF: correction factor.

Rain forest (n=234)

Allometric equations	Equations goodness of fit					Cross-validation		
	ΔAIC	**RSE**	**Sxy (%)**	**R^2**	**CF**	**RSE**	**Sxy (%)**	**R^2**
$\log_{10}(AGC) \sim \beta0+ \beta1* \log_{10}(BA)+\beta2 \log_{10}(SD)$	*0*	*0.124*	*2.966*	*91.09*	*1.0151*	*0.124*	*2.973*	*89.87*
$\log_{10}(AGC) \sim \beta0+ (BA^{\beta1})*(SD^{\beta2})$	-278.452	0.13	3.114	90.17	1.0174			
$\log_{10}(AGC) \sim \beta0 + \beta1* \log_{10}(BA)$	-201.673	0.153	3.681	86.04	1.0118			
$\log_{10}(AGC) \sim \beta0*(1- \exp(-\beta1*BA^{\beta2}))$	-201.611	0.161	3.855	85.18	1.0131			
$\log_{10}(AGC) \sim \beta0*(1- \beta1*\exp(-\beta2*BA))$	-201.561	0.161	3.855	85.18	1.0131			
$\log_{10}(AGC) \sim \beta0/ (1+ \beta1*\exp (-\beta2* \log_{10}(BA))$	-201.484	0.161	3.856	85.17	1.0131			
$\log_{10}(AGC) \sim \beta0*\exp(-\beta1/BA^{\beta2})$	-201.336	0.161	3.857	85.16	1.0131			
$\log_{10}(AGC) \sim \beta0*\exp(-\beta1*\exp(-\beta2*BA))$	-201.153	0.161	3.857	85.16	1.0131			
$\log_{10}(AGC) \sim BA/ (\beta0*BA+ \beta1)^2$	-195.496	0.164	3.918	84.62	1.0135			
$\log_{10}(AGC) \sim \beta0* (BA^{\beta1})$	-192.509	0.164	3.925	84.56	1.0136			
$\log_{10}(AGC) \sim \beta0*(BA/(1+BA))$	-191.030	0.165	3.956	84.32	1.0138			
$\log_{10}(AGC) \sim \beta0*\exp(-\beta1/BA)$	-189.042	0.166	3.973	84.19	1.0139			
$\log_{10}(AGC) \sim \beta0*(1-\exp(-\beta1*BA))$	-164.946	0.174	4.172	82.56	1.0153			
$\log_{10}(AGC) \sim \beta0+ \beta1*BA^2+ \beta2*(BA^2*SD)+ \beta3*(BA*SD^2)+ \beta4*SD$	-99.133	0.19	4.544	79.09	1.0377			
$\log_{10}(AGC) \sim \beta0+ \beta1*BA^2+ \beta2*(BA^2*SD) + \beta3*SD$	-89.161	0.195	4.663	77.98	1.0396			
$\log_{10}(AGC) \sim \beta0+ \beta1* \log_{10}(BA^2*SD)$	38.549	0.259	6.193	61.16	1.0703			
$\log_{10}(AGC) \sim \beta0+ (BA^2*SD)^{\beta1}$	48.584	0.265	6.329	59.44	1.0730			

***Araucaria* (n= 158)**

Allometric equations	Equation's goodness of fit					Cross-validation		
	ΔAIC	**RSE**	**Sxy (%)**	**R^2**	**CF**	**RSE**	**Sxy (%)**	**R^2**
$\log_{10}(AGC) \sim \beta0+ \beta1* \log_{10}(BA)+\beta2 \log_{10}(SD)$	*0*	*0.103*	*2.483*	*94.14*	*1.005*	*0.098*	*2.376*	*91.70*
$\log_{10}(AGC) \sim \beta0+ (BA^{\beta1})*(SD^{\beta2})$	29.036	0.113	2.722	92.96	1.006			

$\log_{10}(AGC) \sim \beta0 + \beta1 * \log_{10}(BA)$	59.068	0.125	3.012	91.33	1.007
$\log_{10}(AGC) \sim \beta0 * \exp(-\beta1/BA^{\beta2})$	59.297	0.125	3.024	91.48	1.007
$\log_{10}(AGC) \sim \beta0/(1+\beta1 * \exp(-\beta2 * \log_{10}(BA))$	59.545	0.125	3.026	91.47	1.007
$\log_{10}(AGC) \sim \beta0 * (1-\exp(-\beta1 * BA^{\beta2}))$	59.923	0.125	3.03	91.44	1.007
$\log_{10}(AGC) \sim \beta0 * (1-\beta1 * \exp(-\beta2 * BA))$	66.184	0.128	3.091	91.10	1.008
$\log_{10}(AGC) \sim \beta0 * \exp(-\beta1 * \exp(-\beta2 * BA))$	69.276	0.129	3.121	90.92	1.008
$\log_{10}(AGC) \sim \beta0 * (BA^{\beta1})$	72.938	0.131	3.167	90.59	1.008
$\log_{10}(AGC) \sim BA/(\beta0 * BA+\beta1)^2$	88.354	0.138	3.326	89.63	1.009
$\log_{10}(AGC) \sim \beta0 * (BA/(1+BA))$	96.323	0.141	3.411	89.09	1.010
$\log_{10}(AGC) \sim \beta0 * \exp(-\beta1/BA)$	100.763	0.143	3.459	88.78	1.010
$\log_{10}(AGC) \sim \beta0+\beta1 * BA^2+\beta2 * (BA^2 * SD) + \beta3 * SD$	154.282	0.167	4.020	84.65	1.014
$\log_{10}(AGC) \sim \beta0+\beta1 * BA^2+\beta2 * (BA^2 * SD)+\beta3 * (BA * SD^2)+\beta4 * SD$	155.012	0.166	4.004	84.78	1.014
$\log_{10}(AGC) \sim \beta0 * (1-\exp(-\beta1 * BA))$	170.850	0.179	4.318	82.52	1.016
$\log_{10}(AGC) \sim \beta0+\beta1 * \log_{10}(BA^2 * SD)$	234.439	0.217	5.247	73.86	1.024
$\log_{10}(AGC) \sim \beta0+(BA^2 * SD)^{\beta1}$	366.636	0.331	7.973	39.66	1.057

Seasonally Dry Tropical Forest deciduous (n=63)

Allometric equations	**Equation's goodness of fit**					**Cross-validation**		
	ΔAIC	**RSE**	**Sxy (%)**	**R^2**	**CF**	**RSE**	**Sxy (%)**	**R^2**
$\log_{10}(AGC) \sim \beta0 * \exp(-\beta1 * \exp(-\beta2 * BA))$	*0*	*0.234*	*6.500*	*85.28*	*1.0292*	*0.234*	*6.331*	*79.64*
$\log_{10}(AGC) \sim \beta0 * (1-\exp(-\beta1 * BA^{\beta2}))$	0.108	0.234	6.506	85.25	1.0293			
$\log_{10}(AGC) \sim \beta0 * (1-\beta1 * \exp(-\beta2 * BA))$	0.349	0.235	6.518	85.19	1.0294			
$\log_{10}(AGC) \sim \beta0 * (1-\exp(-\beta1 * BA))$	0.751	0.239	6.589	84.62	1.0301			
$\log_{10}(AGC) \sim \beta0/(1+\beta1 * \exp(-\beta2 * \log_{10}(BA))$	0.811	0.236	6.542	85.08	1.0296			
$\log_{10}(AGC) \sim \beta0 * \exp(-\beta1/BA^{\beta2})$	1.486	0.237	6.577	84.92	1.0299			
$\log_{10}(AGC) \sim \beta0 * \exp(-\beta1/BA)$	3.061	0.244	6.711	84.04	1.0312			
$\log_{10}(AGC) \sim \beta0 * (BA/(1+BA))$	3.774	0.245	6.749	83.86	1.0316			
$\log_{10}(AGC) \sim BA/(\beta0 * BA+\beta1)^2$	5.658	0.249	6.851	83.37	1.0325			
$\log_{10}(AGC) \sim \beta0 + \beta1 * \log_{10}(BA)$	15.918	0.270	7.432	80.43	1.0384			
$\log_{10}(AGC) \sim \beta0+\beta1 * \log_{10}(BA)+\beta2 \log_{10}(SD)$	17.537	0.269	7.291	80.50	1.0360			
$\log_{10}(AGC) \sim \beta0 * (BA^{\beta1})$	25.267	0.291	8.004	77.30	1.0430			

$\log_{10}$ (AGC) ~ β0+ ($BA^{β1}$)*($SD^{β2}$)	27.941	0.292	7.919	77.00	1.0435			
$\log_{10}$ (AGC) ~ β0+ β1*BA^2+ β2*(BA^2*SD)+ β3*(BA*SD^2)+ β4*SD	55.930	0.354	9.579	66.43	1.0646			
$\log_{10}$ (AGC) ~ β0+ β1* $\log_{10}$ (BA^2*SD)	65.341	0.400	10.826	57.13	1.0832			
$\log_{10}$ (AGC) ~ β0+ β1*BA^2+ β2*(BA^2*SD) + β3*SD	74.775	0.417	11.303	53.27	1.0908			
$\log_{10}$ (AGC) ~ β0+ (BA^2*SD)^{β1}	86.227	0.472	12.778	40.28	1.1178			

Seasonally Dry Tropical Forest semideciduous (n= 233)

Allometric equations	**Equation's goodness of fit**					**Cross-validation**		
	ΔAIC	**RSE**	**Sxy (%)**	**R^2**	**CF**	**RSE**	**Sxy (%)**	**R^2**
$\log_{10}$ (AGC) ~ β0+ β1 $\log_{10}$ (BA)+β2 $\log_{10}$ (SD)*	*0*	*0.186*	*4.561*	*88.63*	*1.0174*	*0.186*	*4.556*	*86.58*
$\log_{10}$ (AGC) ~ β0+ ($BA^{β1}$)*($SD^{β2}$)	45.466	0.205	5.028	86.18	1.0212			
$\log_{10}$ (AGC) ~ β0*(1- exp(-β1*$BA^{β2}$))	194.389	0.290	6.967	72.41	1.0429			
$\log_{10}$ (AGC) ~ β0/ (1+ β1*exp (-β2* $\log_{10}$ (BA))	194.395	0.283	6.967	73.81	1.0408			
$\log_{10}$ (AGC)~ β0 + β1* $\log_{10}$(BA)	194.525	0.284	6.983	73.580	1.0411			
$\log_{10}$ (AGC) ~ β0*exp(-β1/$BA^{β2}$)	194.596	0.283	6.970	73.79	1.0408			
$\log_{10}$ (AGC) ~ β0*(1- β1*exp(-β2*BA))	195.888	0.284	6.989	73.65	1.0411			
$\log_{10}$ (AGC)~ β0*exp(-β1*exp(-β2*BA))	197.349	0.285	7.011	73.48	1.0414			
$\log_{10}$ (AGC)~ BA/ (β0*BA+ β1)^2	204.545	0.290	7.135	72.41	1.0429			
$\log_{10}$ (AGC) ~ β0* ($BA^{β1}$)	204.598	0.290	7.136	72.41	1.0429			
$\log_{10}$ (AGC) ~ β0+ β1*BA^2+ β2*(BA^2*SD)+ β3*(BA*SD^2)+ β4*SD	205.838	0.287	7.033	72.96	1.0420			
$\log_{10}$ (AGC)~ β0*(BA/(1+BA))	210.044	0.294	7.220	71.75	1.0441			
$\log_{10}$ (AGC) ~ β0*exp(-β1/BA)	212.973	0.296	7.266	71.40	1.0447			
$\log_{10}$ (AGC) ~ β0*(1-exp(-β1*BA))	241.052	0.314	7.717	67.73	1.0505			
$\log_{10}$ (AGC) ~ β0+ β1*BA^2+ β2*(BA^2*SD) + β3*SD	282.399	0.340	8.325	62.13	1.0595			
$\log_{10}$ (AGC) ~ β0+ (BA^2*SD)^{β1}	383.793	0.427	10.438	40.47	1.0959			
$\log_{10}$ (AGC) ~ β0+ β1* $\log_{10}$ (BA^2*SD)	384.870	0.428	10.462	40.19	1.0959			

Atlantic Forest (n= 696)

Allometric equations	**Equation's goodness of fit**					**Cross validation**		
	ΔAIC	**RSE**	**Sxy (%)**	**R^2**	**CF**	**RSE**	**Sxy (%)**	**R^2**
$\log_{10}$ (AGC) ~ β0+ β1 $\log_{10}$ (BA)+β2 $\log_{10}$ (SD)*	*0*	*0.190*	*4.648*	*85.9*	*1.0180*	*0.191*	*4.542*	*85.55*

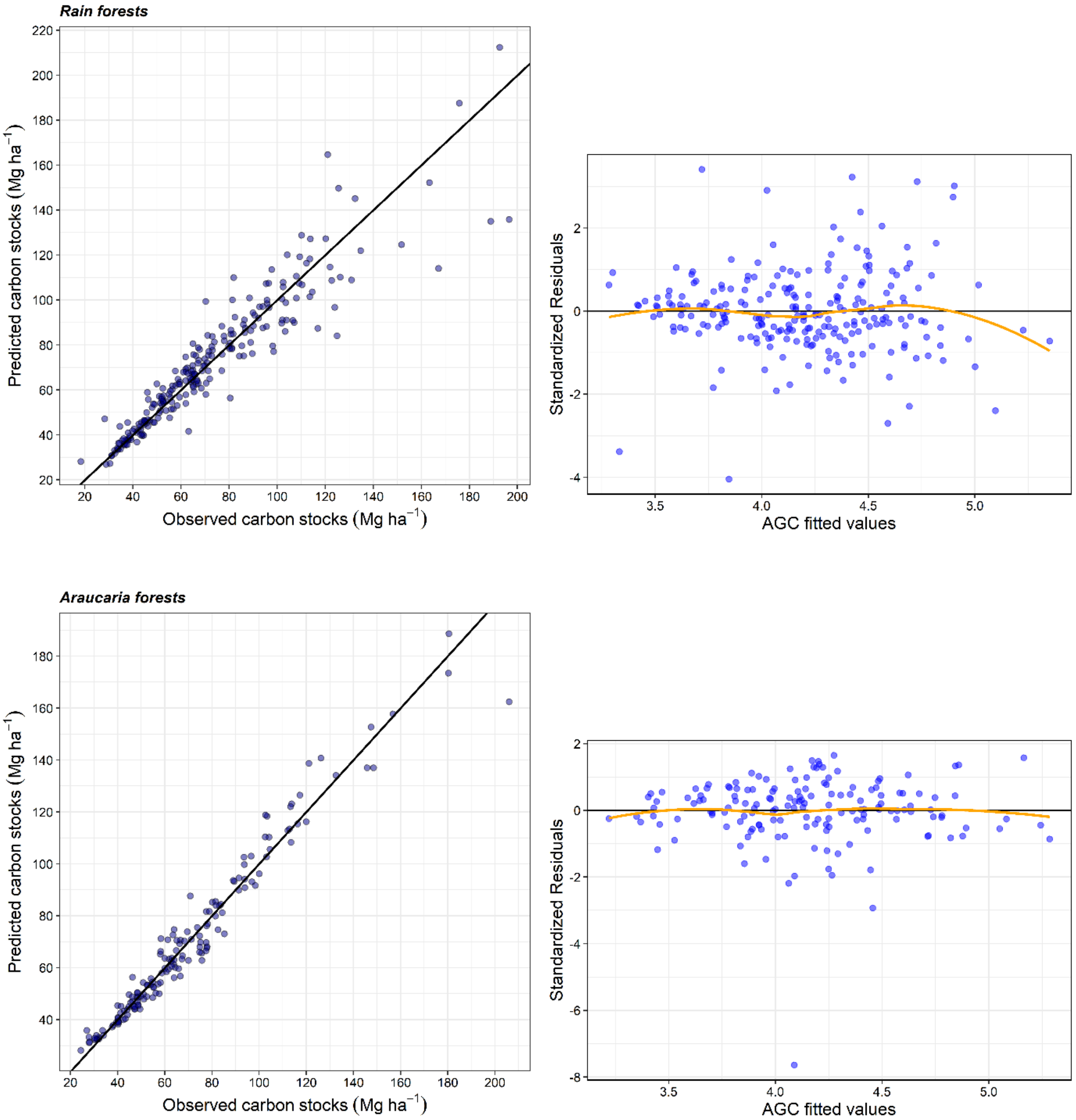
$\log_{10}$ (AGC) ~ β0+ ($BA^{\beta1}$)*($SD^{\beta2}$)	100.966	0.205	4.998	83.7	1.0213
$\log_{10}$ (AGC) ~ β0*exp(-β1/$BA^{\beta2}$)	196.658	0.220	5.380	81.91	1.0246
$\log_{10}$ (AGC) ~ β0/ (1+ β1*exp (-β2* $\log_{10}$ (BA))	197.596	0.220	5.384	81.89	1.0246
$\log_{10}$ (AGC) ~ β0*(1- exp(-β1*$BA^{\beta2}$))	200.565	0.220	5.395	81.81	1.0247
$\log_{10}$ (AGC)~ BA/ (β0*BA+ β1)^2	211.809	0.222	5.442	81.47	1.0251
$\log_{10}$ (AGC) ~ β0*(1- β1*exp(-β2*BA))	213.513	0.222	5.445	81.48	1.0252
$\log_{10}$ (AGC)~ β0 + β1* $\log_{10}$(BA)	220.149	0.224	5.475	81.25	1.0254
$\log_{10}$ (AGC)~ β0*exp(-β1*exp(-β2*BA))	223.141	0.224	5.483	81.22	1.0255
$\log_{10}$ (AGC)~ β0*(BA/(1+BA))	225.195	0.224	5.494	81.11	1.0256
$\log_{10}$ (AGC) ~ β0*exp(-β1/BA)	232.669	0.226	5.524	80.91	1.0259
$\log_{10}$ (AGC) ~ β0* ($BA^{\beta1}$)	281.07	0.233	5.717	79.56	1.0278
$\log_{10}$ (AGC) ~ β0*(1-exp(-β1*BA))	326.032	0.241	5.902	78.21	1.0296
$\log_{10}$ (AGC) ~ β0+ β1*BA^2+ β2*(BA^2*SD)+ β3*(BA*SD^2)+ β4*SD	718.269	0.318	7.765	60.66	1.0525
$\log_{10}$ (AGC) ~ β0+ β1*BA^2+ β2*(BA^2*SD) + β3*SD	776.581	0.332	8.109	57.1	1.0572
$\log_{10}$ (AGC) ~ β0+ β1* $\log_{10}$ (BA^2*SD)	936.231	0.374	9.121	45.73	1.0728
$\log_{10}$ (AGC) ~ β0+ (BA^2*SD)$^{\beta1}$	944.338	0.376	9.174	45.1	1.0736

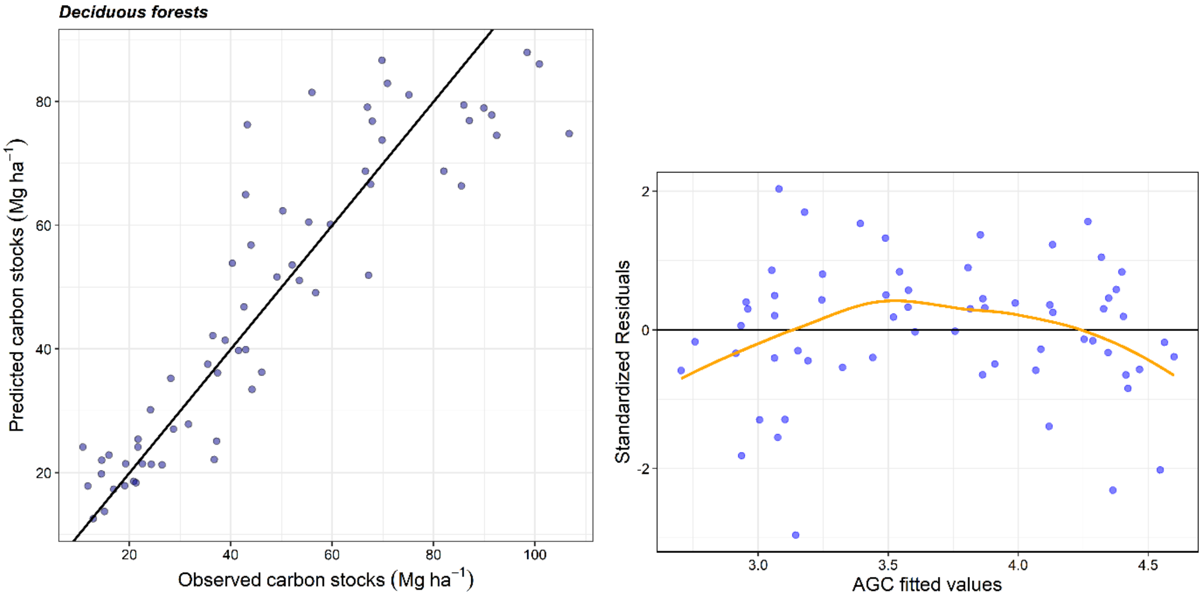
Table 3: Estimated parameters for the AGC equations based on stand structural variables. AGC: Above-ground carbon stocks; BA: Stand basal area; SD: Stand density; SE = standard error at 95%. CIL= confidence interval limits.

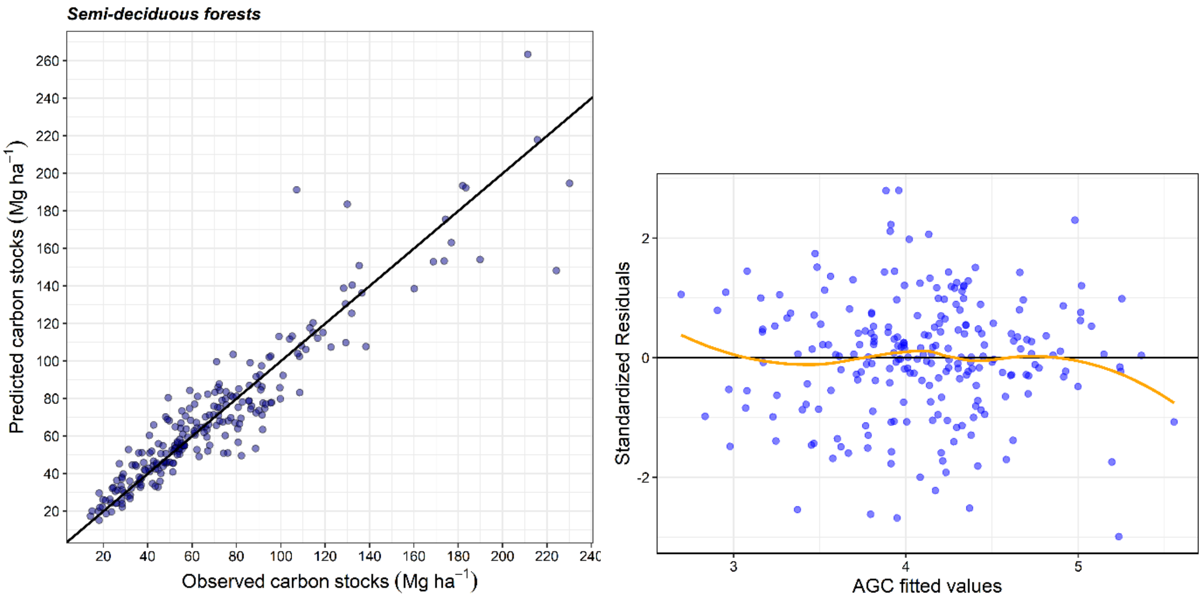
Forest types						
Rain						
	$AGC = e^{1.570+1.390\ \ln(BA)-0.274\ln(SD)} * \mathbf{1.007}$					
	Estimate	**SE**	**2.5% CIL**	**97.5% CIL**	**t-value**	**p-value**
β0	1.570	0.125	1.322	1.818	12.47	<0.001
β1	1.390	0.031	1.329	1.451	44.7	<0.001
β2	-0.274	0.023	-0.32	-0.228	-11.74	<0.001
Araucaria						
$AGC = e^{1.918+1.092\ \ln(BA)-0.196\ln(SD)} * \mathbf{1.005}$						
	Estimate	**SE**	**2.5% CIL**	**97.5% CIL**	**t-value**	**p-value**
β0	1.918	0.116	1.689	2.148	16.503	<0.001
β1	1.092	0.024	1.043	1.141	44.261	<0.001
β2	-0.196	0.023	-0.242	-0.151	-8.552	<0.001
Deciduous						
$AGC = e^{4.456\exp(-2.098\exp(-0.156\,\mathrm{BA}))} * \mathbf{1.029}$						
	Estimate	**SE**	**2.5% CIL**	**97.5% CIL**	**t-value**	**p-value**
β0	4.456	0.093	4.292	4.678	47.891	<0.001
β1	0.156	0.023	0.112	0.207	6.621	<0.001
β2	2.098	0.474	1.400	3.471	4.42	<0.001
Semi-deciduous						
$AGC = e^{1.978+1.467\ \ln(BA)-0.361\ln(SD)} * \mathbf{1.017}$						
	Estimate	**SE**	**2.5% CIL**	**97.5% CIL**	**t-value**	**p-value**
β0	1.978	0.113	1.755	2.202	17.45	<0.001
β1	1.467	0.035	1.396	1.538	40.88	<0.001
β2	-0.361	0.020	-0.402	-0.320	-17.45	<0.001
Atlantic Forest						
$AGC = e^{4.456\exp(-2.098\exp(-0.156\,\mathrm{BA}))} * \mathbf{1.029}$						
	Estimate	**SE**	**2.5% CIL**	**97.5% CIL**	**t-value**	**p-value**
β0	1.526	0.080	1.367	1.685	18.88	<0.001
β1	1.228	0.019	1.190	1.265	64.23	<0.001
β2	-0.190	0.012	-0.214	-0.166	-15.73	<0.001

*Correction factor (CF) is shown in bold in AGC equation.

In general, the plots of the observed versus predicted values of AGC showed good correspondence to the 1:1 linear trend, suggesting that it is possible to obtain accurate AGC stocks estimates from stand basal and density (Fig 2), Cross validation approach also showed a good match, that is, the values of R^2 and Sxy, provided by selected equations were similar using testing and training dataset, which indicates that AGC can be confidently inferred from stand basal area and density. However, some deviations from straight lines were found in stands with high and/or low basal areas in rain, deciduous, semi-deciduous and in Atlantic Forest as a whole (Fig. 2)




Deciduous forests
Predicted carbon stocks (Mg ha^{-1})
Observed carbon stocks (Mg ha^{-1})
20
40
60
80
100
Standardized Residuals
AGC fitted values
3.0
3.5
4.0
4.5
2
0
-2


Semi-deciduous forests
Predicted carbon stocks (Mg ha^{-1})
Observed carbon stocks (Mg ha^{-1})
20
40
60
80
100
120
140
160
180
200
220
240
260
Standardized Residuals
AGC fitted values
3
4
5
2
0
-2

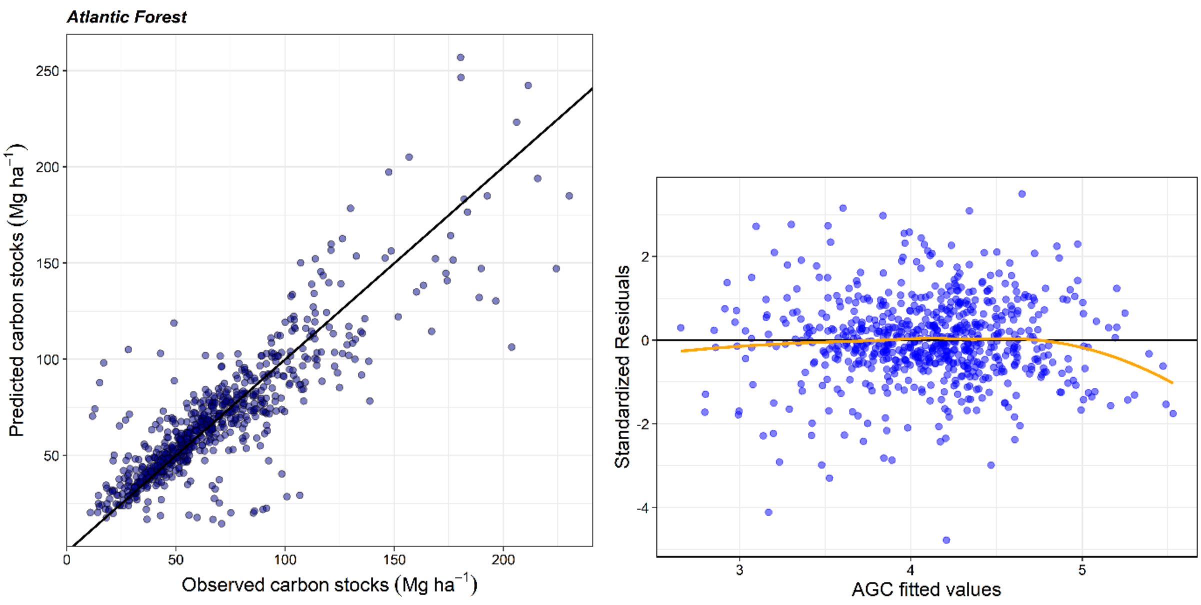


Figure 2: Relationship between predicted carbon stocks with developed equations (Table 3) and observed carbon stocks in four forest types and in Atlantic Forest as whole with residuals graph.

4 DISCUSSION

4.1 CARBON ALLOMETRIC EQUATIONS BASED ON STAND STRUCTURAL VARIABLES

We showed that estimating carbon stocks from the stand forestry structural variables can be accurate (Fig. 2), and thus may represent an alternative when individual tree measurements and identifications from where complete forest inventories are not available (Chave et al., 2009, 2014). With the developed equations (Table 3), stand basal area and density explained more than 85% of the Atlantic Forest carbon stocks (Table 2). Perhaps more importantly than to this good explanatory power (i.e. high R^2 values), the equations to estimate AGC based on stand basal area and density had low levels of uncertainties associated with their use (Sxy <7%), which is a prerequisite for their use in climate change mitigation strategies, as REDD+ projects (Sheng 2017). However, despite the low errors, there were some variations between observed and predicted carbon stocks in stands with low and high values of basal area (Fig. 2). Therefore, for conservative estimates, we suggest that the carbon stocks estimates made from our equations are accompanied by maximum and minimum values (Table 3).

Previous studies have already shown high accuracy of carbon estimates from stand structural variables equations. Lima et al., (2020), also provide carbon stocks equations based on stand basal area to some forest types and for Atlantic Forest as a whole (see Lima et al., 2020, Supplementary Information). In general, our equations had slightly less predictive powers (R^2 value = 85.9%- 94.1% against R^2= 88.2% - 97.3%). However, its use may be preferable since we used a larger number of samples, especially in deciduous and semi-deciduous forests, we developed forest type-specific equation for these forests, including rain forests in the southeast of the Atlantic Forest and, finally, we reported the error associated with the carbon stocks estimation. Nevertheless, as our dataset did not cover all existing sites nor was evenly distributed among forest types, we suggest the use of the equation proposed here for Atlantic Forest as a whole in absence of forest type-specific allometric equations.

For the rain, Araucaria and semi-deciduous forests, the inclusion of stand density substantially improved the explanatory power of carbon equations. In these forest types, the stand basal area had a positive effect on AGC, while the stand density showed a negative effect. This phenomenon is known as “self-thinning” and usually occurs when, under conditions of limited resource availability, the growth of larger trees increases competitiveness and induces the mortality of weaker trees (Brunet-Navarro et al., 2016). Thus, forests dominated by fewer larger trees tend to accumulate more carbon. However, for deciduous forests, the best carbon estimates were reached from the stand basal area only equations (Table 2), suggesting that stand density apparently does not influence carbon stocks in all forest types of Atlantic Forest. Indeed, some studies have shown that the impact of tree density (e.g. competition for resources) on forest growth is greater in humid forests than in permanently dry forests (see Gleason et al, 2017).

Predicting AGC from stand-level equations could facilitate the carbon stock estimation in several ways. First, it can considerably reduce field measurement requirements in comparison with complete inventory methods (Torres and Lovett, 2012). Second, the stand basal area and stand density may be easily and quickly measured by instruments, which do not require individual tree measurements, such as Criterion RD 1000, Spiegel Relaskop and wedge prison (Torres and Lovett, 2012 and Khan et al.,2020). Third, there is a huge number of forest inventories published only with the basal area and stand density information (e.g. Lima et al., 2015 and 2020), which could provide historical carbon estimates, enabling projections and supporting decisions for reductions and/or increases of carbon stocks (Torres and Lovett, 2012). Furthermore, future studies with stand allometric equations could be used together with new remote sensing technologies, such as Radar and Light Detection and Ranging (LiDAR), which can map the stand basal area and density in extensive forest areas.

5 CONCLUSION

This study presents the first mixed-species allometric equations for estimating stand carbon stocks from structural variables in different types of tropical forests. The high explanatory power and low associated estimation error confirm that the equations developed with stand basal area and stem density are robust and reliably estimate the carbon stocks of the Atlantic Forest, allowing the expansion of estimates and greater knowledge about the distribution of stocks in this domain.

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SUPPLEMENTARY MATERIAL

Estimating stand carbon stocks from structural variables in tropical forests

Authors

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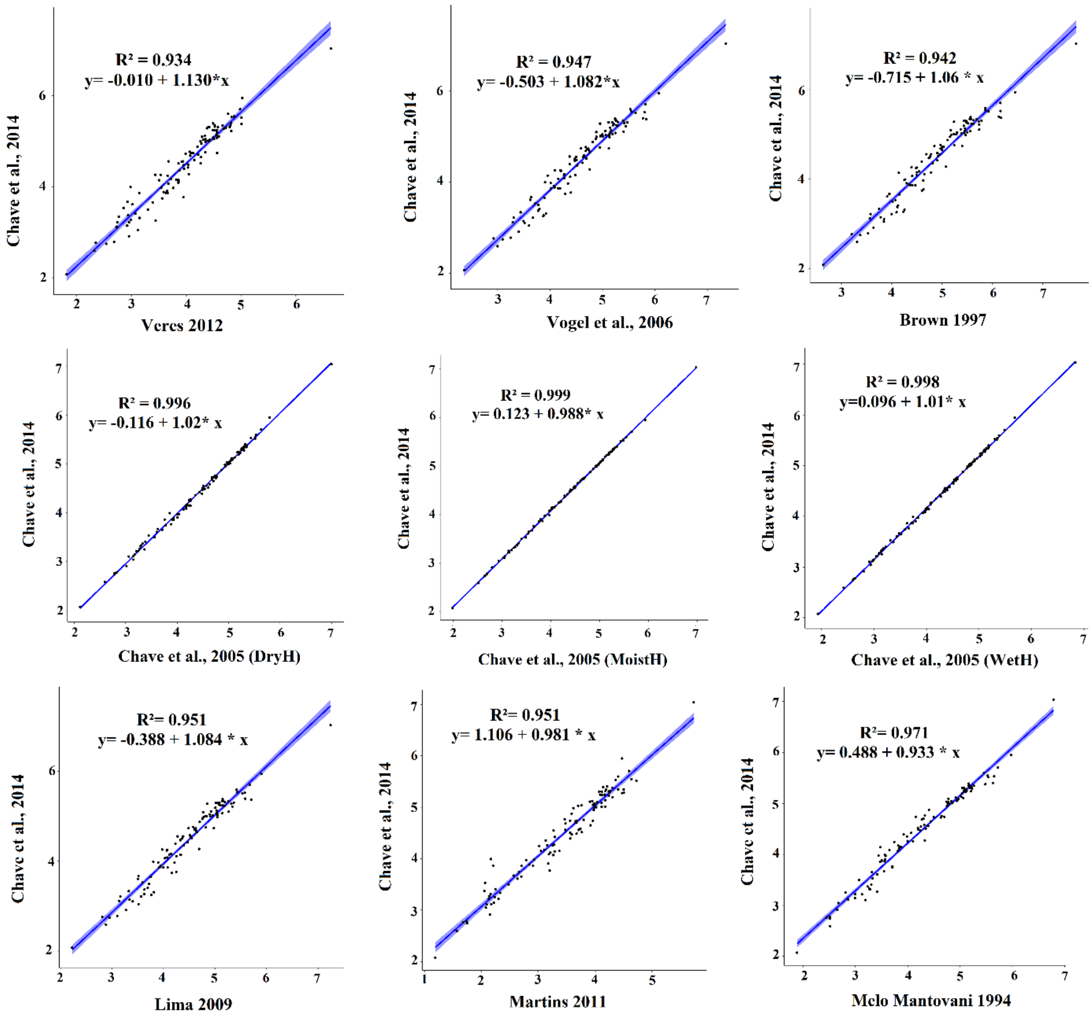
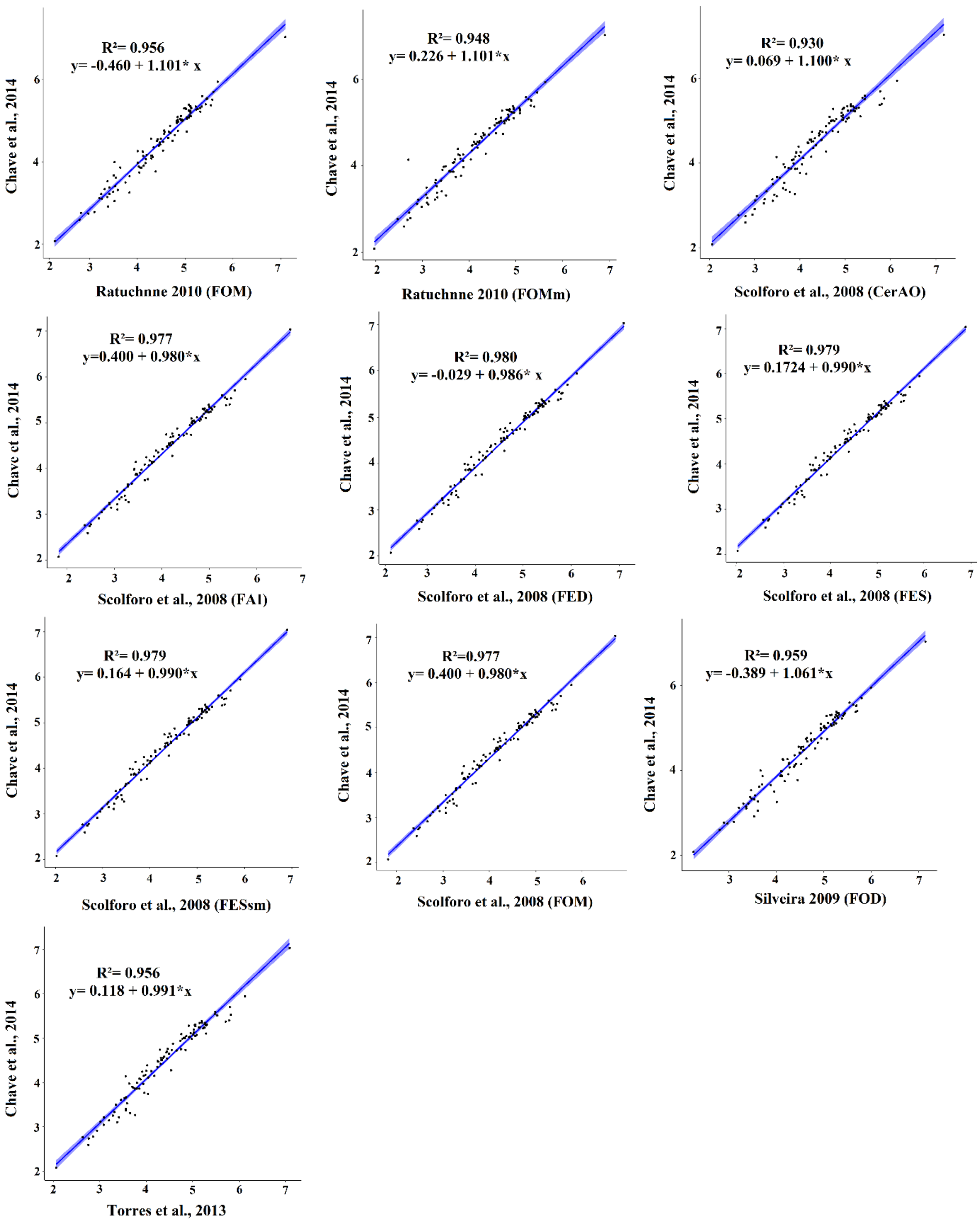
Table S1: List of the all allometric equations reported in the forest inventories used for data analysis. AGB= Above-ground biomass, H= Height of the tree, DBH= diameter at breast height, WD= wood density and DW= Dry weight.

Allometric equations	**Authors**
AGB=0.0673*(WD*(DBH^2)*H)^(0.976)	Chave et al., 2014
AGB=0.033430*(DBH^2.397902)*(H^0.426536)	Amaro 2010
AGB=exp(-2.289+2.649*ln(DBH)-0.021*(ln(DBH))^2)	Brown 1997
AGB=exp(-2.187+0.916*ln(WD*(DBH^2)*H))	Chave et al., 2005(DryH)
AGB=exp(-2.977+ln(WD*(DBH^2)*H))	Chave et al., 2005(MoistH)
AGB=exp(-2.557+0.940*ln(WD*(DBH^2)*H))	Chave et al., 2005(WetH)
DW=(59.321357)+(-12.28289)*DBH+(0.8396136)*(DBH^2)	Lima 2009
AGB=0.04821*(DAP^1.34374)*(H^1.26829)	Martins 2011
ln(AGB)=-4.15190+1.06068*ln((DBH^2)*H)	Melo & Mantovani 1994
AGB=0.317*(DBH^2)+0.009*((DBH^2)*H)	Ratuchne 2010 FOM
AGB=-3.025*DBH+0.425*(DBH^2)+0.006*((DBH^2)*H)	Ratuchne 2010 FOMm
AGB=exp(-10.8771683824+2.6359736325*ln(DBH)+0.0878059946*ln(H))/(0.4802)	Scolforo et al., 2008(CerAO)
AGB= exp(-11.319842099+2.1415723631*ln(DBH)+0.8134282561*ln(H))/(0.4833)	Scolforo et al., 2008(FAl)
AGB=exp(-10.7501678493+2.0580637328*ln(DBH)+0.8604515609*ln(H))/(0.4860)	Scolforo et al., 2008(FED)
AGB=exp(-10.9520199234+2.0898526615*ln(DBH)+0.8096162241*ln(H))/(0.4839)	Scolforo et al., 2008(FES)
AGB=exp(-10.9520199234+2.0898526615*ln(DBH)+0.8096162241*ln(H))/(0.4802)	Scolforo et al., 2008(FESsm)
AGB=exp(-11.319842099+2.1415723631*ln(DBH)+0.8134282561*ln(H))/(0.4833)	Scolforo et al., 2008(FOM)
AGB=25.87071+0.02909*(DBH^2)-0.21382*(H^2)+0.03189*(DBH^2)*H	Silveira 2009 (FOD)
AGB = 0.024530*(DAP^2.443356)*(H^0.423602) + 0.2596*(0.024530*(DAP^2.443356)*(H^0.423602)) + 0.0445*(0.024530*(DAP^2.443356)*(H^0.423602))	Torres et al., 2013
AGB=(-4.8639)+0.3981*DBH+0.2625*(DBH^2)	Veres 2012
$\log_{10}$(AGB)=-0.88239023+2.40959057* $\log_{10}$ (DBH)	Vogel et al., 2006

Figure S1: The relationship between the 20 allometric equations found to estimate AGC (Table S1) and the one provided by Chave et al. (2014). The *y*-axis is the natural logarithmic of the estimate provided by Chave's formula and the *x*-axis is the natural logarithmic of the aboveground carbon of each allometric equation. We present the mean prediction of the linear regression model (in blue) and the associated R^2 of the model. Here, we obtained AGB estimates for each equation using individual tree data (species, diameter and height) from 109 plots of the Atlantic Forest available from the Minas Gerais Forestry Inventory (Scolforo et al.,2008). Species wood density used in some of the allometric equations was obtained from the Global Wood Density database (filtered for Tropical South America, Zanne et al. 2009).




R²= 0.956
y= -0.460 + 1.101* x
Chave et al., 2014
Ratuchnne 2010 (FOM)
R²= 0.948
y= 0.226 + 1.101*x
Chave et al., 2014
Ratuchnne 2010 (FOMm)
R²= 0.930
y= 0.069 + 1.100* x
Chave et al., 2014
Scolforo et al., 2008 (CerAO)
R²= 0.977
y=0.400 + 0.980*x
Chave et al., 2014
Scolforo et al., 2008 (FA1)
R²= 0.980
y= -0.029 + 0.986* x
Chave et al., 2014
Scolforo et al., 2008 (FED)
R²= 0.979
y= 0.1724 + 0.990*x
Chave et al., 2014
Scolforo et al., 2008 (FES)
R²= 0.979
y= 0.164 + 0.990*x
Chave et al., 2014
Scolforo et al., 2008 (FESsm)
R²=0.977
y= 0.400 + 0.980*x
Chave et al., 2014
Scolforo et al., 2008 (FOM)
R²= 0.959
y= -0.389 + 1.061*x
Chave et al., 2014
Silveira 2009 (FOD)
R²= 0.956
y= 0.118 + 0.991*x
Chave et al., 2014
Torres et al., 2013

CONCLUSÃO GERAL

No atual cenário de mudanças globais, a conservação e restauração do carbono florestal atraíram atenção sem precedentes. Aqui, fornecemos uma avaliação abrangente dos principais impulsionadores dos estoques de carbono para a Mata Atlântica e desenvolvemos equações alométricas que podem expandir as atuais estimativas de estoques de carbono do bioma. Nossas conclusões foram: Primeiro, a conservação dos estoques de carbono da Mata Atlântica é altamente dependente da degradação florestal, a qual pode gerar carbono perdas pelo menos 30% maiores do que qualquer mudança climática futura. Além disso, emissões da degradação florestal podem comprometer os esforços de conservação acordos de planejamento e mitigação das mudanças climáticas (por exemplo, metas de REDD+ e AICHI). Por exemplo, a intensificação da distúrbios dentro do fragmento pode levar a perdas de carbono de até 10,50 Mg ha^{-1} (-15,24%), enquanto a proteção de carbono e seu aumento poderia alcançar ganhos de carbono em 12,02 Mg ha^{-1} (+17,44%). Em segundo lugar, os estoques de carbono da Mata Atlântica também são ameaçados pelas mudanças climáticas, especificamente pelo aumento de temperatura e estresse hídrico. Se o aquecimento global fosse restringido a 1,5°C acima níveis pré-industriais, como sugerido pelo Painel Intergovernamental sobre Mudanças Climáticas, 3,53 Mg ha^{-1} (-5,12% de perda de carbono) de carbono seria liberado apenas da Mata Atlântica. Se o aquecimento global continuar em sua taxa atual, as emissões de carbono podem exceder 9,03 Mg ha^{-1} (-13,11% de perda de carbono). Terceiro, as iniciativas com o objetivo de mitigar as mudanças climáticas por meio da restauração de florestas ecossistemas poderiam se beneficiar da inclusão de espécies com maior WD, sementes mais pesadas e folhas maiores. Em quarto lugar, a relação entre a diversidade taxonômica e funcional e os estoques de carbono foi fraco na Mata Atlântica, revelando que as políticas de conservação focadas apenas no carbono podem não proteger a biodiversidade. Em quinto lugar, as políticas de conservação de carbono devem levar em conta aspectos metodológicos pois estes podem levar a erros na estimativa de carbono e, consequentemente, baixa eficiência das ações de mitigação do clima. Assim, o uso de “boas práticas de medição para estimativa de estoques de carbono florestal” deve ser levado em consideração nos relatórios de estoque de carbono. Por fim, provamos que as estimativas dos estoques de carbono da Mata Atlântica podem ser expandidas pela utilização de equações alométricas baseadas em área basal e densidade de árvores do povoamento. As equações desenvolvidas aqui explicaram 85,2%-96,2% das variações dos estoques de carbono com menos de 6,5% de erros de estimativa.