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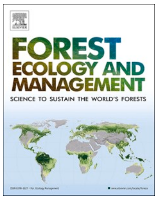

Atlantic Forest recovery after long-term eucalyptus plantations: The role of zoochoric and shade-tolerant tree species on carbon stock

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ABSTRACT

Currently, about a third of the world's forest areas that have been deforested are regrowing. These second-growth forests (SGF) promote carbon stocks and tree species richness recovery (co-benefits recovery), which is central to mitigating the negative impact of climate change and loss of biodiversity. In Brazil's Atlantic Forest, second-growth forests that are regrowing after long-term land use can recover diversity and carbon and can have important carbon-tree diversity co-benefits. Thus, we evaluate the recovery of tree species richness and above-ground carbon stock (AGC) in SGF that are regrowing after a long-period of eucalyptus plantations. For this we sampled 43 SGF with stand ages varying from 1–32 years after eucalyptus plantations cutting and three reference old-growth forests (OGF). We considered all individuals with more than 15 cm of circumference at breast height in one 20 × 50 m plot by patch. We identified all tree species, which were categorized into functional attributes, such as zoochoric and non-zoochoric, pioneer and shade-tolerant, and fleshy and dry fruits species. There were marked differences in species richness and AGC between OGF and SGF, but SGFs were not different between then. However, in 32 years these second-growth forests recovered ~38% of species richness and ~14% of carbon stock of old-growth forests. In addition, there was a carbon-biodiversity co-benefits mainly between zoochoric and shade-tolerant species richness. These results showed that these second-growth forests could naturally recover biodiversity and AGC. Possibly, this is due to the connectivity provided by land-use for eucalyptus plantations that induces favorable conditions for the recruitment of zoochoric and shade-tolerant species and thus for the recovery of biodiversity and AGC after eucalyptus cutting. Thus, this second-growth forest management can contribute to Atlantic Forest biodiversity conservation and carbon stock initiatives.

1. Introduction

Currently, about a third of the world's forest areas have been deforested are second-growth forests (SGF) with different successional stages (Hansen et al., 2013; Arroyo-Rodríguez et al., 2017). These SGF are important reservoir of biodiversity which provides multiples ecosystem services, such as carbon dynamic and stock, and non-timber forestry resources (food, medicines, fibers) as a sustainable livelihood (Chazdon et al., 2016; Klemick, 2011; Roberts et al., 2018). Furthermore, SGF can promote carbon-biodiversity co-benefits, i.e., carbon stock recovery along with a positive relationship with tree species richness (Liang et al., 2016; Matos et al., 2020; Osuri et al., 2020). Thus, SGF become central to mitigate the impact of climate change and biodiversity loss on a global scale (Gellie et al., 2018; Hansen et al., 2020). However, anthropogenic disturbances (i.e., land-use change for logging, agriculture, pasture) can affect negatively the recovery of

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biodiversity, carbon stock and ecosystems services along tropical forest (Fernandes Neto et al., 2019; Jakovac et al., 2015; Sloan et al., 2015; Villa et al., 2018). In this context, understanding how these SGF can contribute to biodiversity and carbon stock recovery under different forest types and land-use is an scenarios important issues in tropical forest ecology management and conservation (e.g., Matos et al., 2020; Rozendaal et al., 2019).

Studies on SGF in different ecological contexts have been compared mainly changes in tree community diversity and structure using as reference the old-growth forests (OGF) and estimating the recovery rate (e.g., Rozendaal et al., 2019; Poorter et al., 2019). Furthermore, beyond these stand-age dependent forest attributes, the variation in the relative importance of functional attributes (i.e., seed dispersal syndrome, fruit types, regeneration strategies) on carbon during natural regeneration of SGF (Jakovac et al., 2015; Poorter et al., 2016; Pyles et al., 2018; Rodrigues et al., 2019; Santo-Silva et al., 2016, 2013), can also be important to estimate the recovery rate. However, the few studies that analyze the contribution of different functional attributes on carbon recovery are based on a community scale (considering all tree species). For example, early successional stages of SGF that are re-growing after disturbances harbor predominantly fast-growth and light-demanding pioneer species with short life cycles between 10 and 15 years (Chazdon, 2014; Guariguata and Ostertag, 2001; Chazdon 2014; Villa et al., 2018,2019) along with dominance of anemochoric and autochoric (non-zoochoric) pioneer species (Chazdon 2014; Santo-Silva et al., 2016). Then, shade-tolerant and long-lived species gradually dominate the forest canopy, along late-successional stages and OGF (Chazdon, 2014; Poorter et al., 2019). The non-zoochoric species occurrence also decreases during late-successional stages, while the dominance of zoochoric species increases in OGF (e.g. Santo-Silva et al., 2016). Thus, these changes in tree species richness consequently influences the carbon stock (Osuri et al., 2014; Safar et al., 2020) and possibly carbon-biodiversity co-benefits.

In this context, as one of Earth's most biodiverse regions, Brazilian Atlantic Forest is an important biome to investigate carbon-biodiversity co-benefits changes along forest succession. This ecological region is one of the world's hotspots for biodiversity conservation (Myers et al., 2000) and suffered a drastic reduction in forest cover with only 12.5% of forest remnants (considering areas with more than 3 ha; Scarano and Ceotto 2015). A recent study showed that after 20 years of regeneration, the second-growth forests on Atlantic Forest have recovered on average 52% of total species richness and 16% of carbon stock compared to old-growth forests (Safar et al., 2020). Moreover, co-benefit between above-ground carbon stock and biodiversity has been found after 30 years of Atlantic Forest succession, which recovered an average of 76% of species richness and 20% of carbon stock of the old-growth forest (Matos et al., 2020). Although carbon recovery is slow in these second-growth forests, there is a high positive relationship between carbon and biodiversity, which can be an important strategy to reducing emissions from deforestation and forest degradation, and conserve biodiversity (Matos et al., 2020; McCarthy et al., 2012). However, evaluating the forest recovery and carbon-biodiversity co-benefits after a long-term land-use and the relative contribution of functional attributes in the Atlantic Forest are still necessary to improve management and conservation criteria.

Here, we evaluated the tree species richness and carbon stock recovery and the carbon-tree species richness co-benefits along Atlantic Forest succession after a long-term of eucalyptus plantation. Thus, we postulate three main research questions: (i) What is the difference in tree species richness and above-ground carbon stock (AGC) between second-growth forests and nearby old-growth forests? (ii) Are these second-growth forests recovering tree species richness and AGC along stand age? and (iii) Is there co-benefit between tree species richness (total and by functional attributes) and AGC in these second-growth forests?

2. Material and methods

2.1. Study area

This study was carried out in a semideciduous seasonal Atlantic Forest in the Rio Doce Basin (19°48′29″S; 42°37′40″W), beside to Rio Doce State Park in Minas Gerais State, Brazil (Fig. 1A). The study area is specifically between Dionísio, São José do Goiabal, São Pedro dos Ferros, and Timóteo, municipalities of the Minas Gerais state (Fig. 1B). This region has a long land-use history which consisted mainly in converting natural habitat to agriculture, livestock and planted forests (de Oliveira-Junior et al., 2020; Scarano and Ceotto, 2015). Thus, these forests are found on hilltops and mountainsides mainly as SGFs (i.e., forests that are regrowing after anthropogenic disturbance) in small remnant fragments representing <12% of the original forest (Scarano and Ceotto, 2015). The regional climate, according to Köppen classification is Aw with mean annual precipitation of 1450 mm and mean temperature ranging between 20 and 23 °C (Alvares et al., 2013). The study area presents Red-Yellow Latosol that covers hilltops and mountainsides (dos Santos et al., 2018).

Specifically, our study area has a complex landscape configuration represented mainly by second-growth forests patches with different stand age (3–32 years old), and old-growth forest patches (Fig. 1C, and Table A1 from Appendices). The second-growth forests sampled were inserted in areas previously occupied by eucalyptus plantation with at least 30 years of land-use. These areas are owned by ArcelorMittal BioFlorestas Ltda, which also provided the exact SGF stand age (time between the last eucalyptus cutting in each area and the SGF sampling date). The OGF remnants in the study area occur inside the Rio Doce State Park that is protected since 1962 by Forest Institute of Minas Gerais State.

2.2. Sampling design and tree inventory

We sampled 43 forest patches of second-growth forests at different stand ages after eucalyptus cutting and three old-growth forest patches in the study area. At each forest patch (SGF and OGF), from January to March 2018, one plot of 20 × 50 m (0.1 ha) was randomly installed. Then, all tree individuals with a diameter at breast height (DBH) $\geq$ 4.8 cm and 1.30 m above ground height were sampled (Magnago et al., 2014; Matos et al., 2016). We sampled a total of 4.6 ha of second-growth forests and 0.3 ha of old-growth forests. For those species difficult to identify in the field, their specimens were collected and identified at the Herbarium of the Federal University of Viçosa (VIC) according to Angiosperm Phylogeny Group IV (APG IV, 2016).

2.3. Above-ground carbon quantification

We calculated the biomass of each individual sampled using the equation suggested by Chave et al. (2014):

$$\text{AGBest} = \exp[-1.803\text{–}0.976E + 0.976\ln(\rho) + 2.673\ln(\text{D}) - 0.0299[\ln(\text{D})]^2]$$

where AGBest is the estimated above-ground biomass (Mg), E is a measure of environmental stress; ρ is wood density (g/cm^3) and D (cm) is the diameter of the tree at breast height. This analysis were carried out using the "BIOMASS" package for R (Réjou-Méchain et al., 2017). The environmental stress was obtained in this package using geographic coordinate of each patch. The value for wood density (g/cm^3) was obtained from Global Wood Density database (GWD; Zanne et al., 2009). For species that were not included in the GWD (4%) or when they were identified only at the genus level (2.8%), we used the average density of wood for all species of the same genus included in the database (see Magnago et al., 2014; Matos et al., 2020). Finally, we considered the above-ground carbon stock value for each second-growth forest and old-growth forest as 50% of total AGBest of each sampled plot (Malhi et al.,

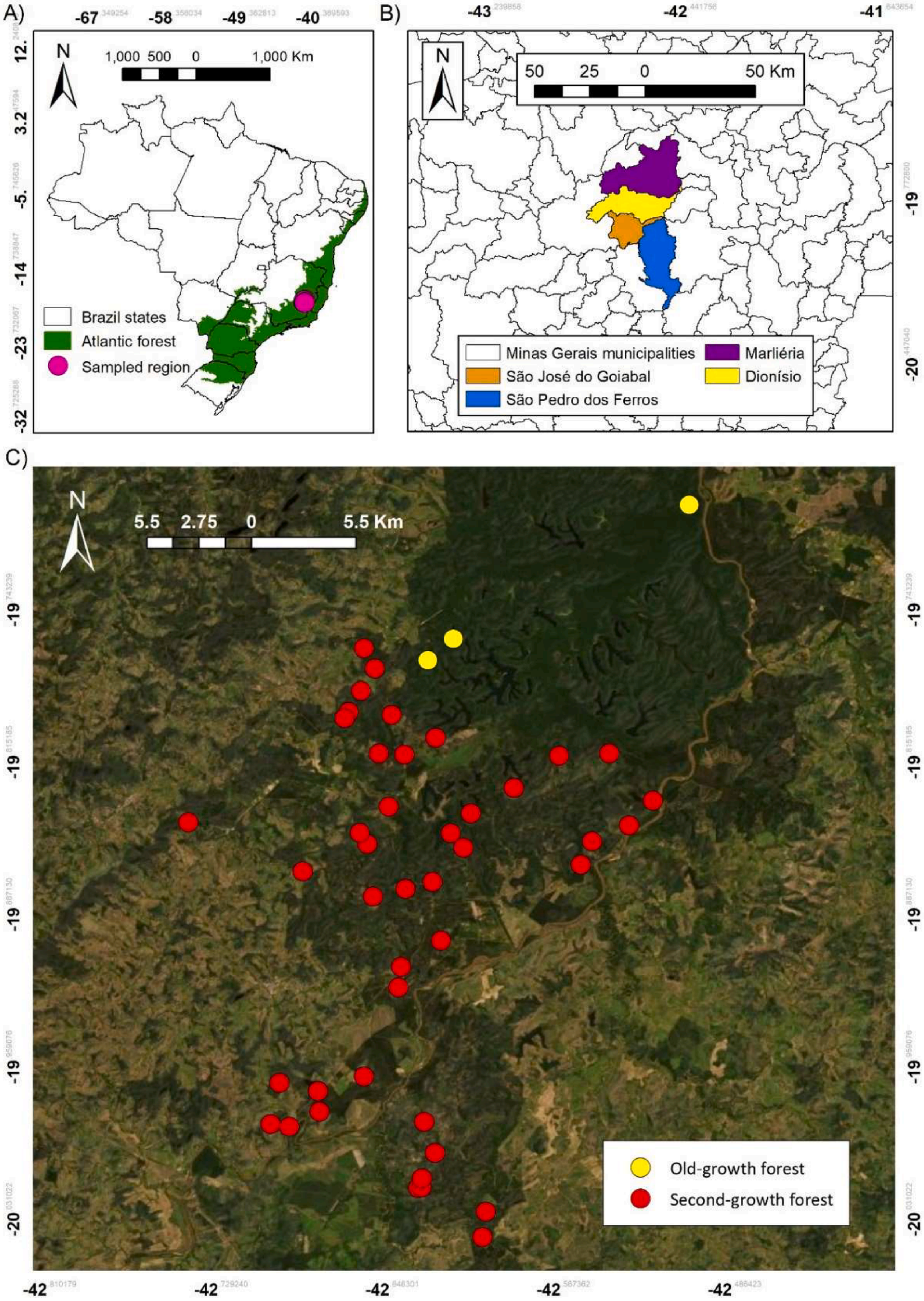

Fig. 1. Localization of the study area and sampling plots in relation to Brazil states (A), Minas Gerais state (B), and forest landscape sampled (C). SGF and OGF sampled plots are indicated with red and yellow dots respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2004).

2.4. *Functional attributes classification*

Each sampled tree species was classified into three functional attributes, successional strategy, fruit type and dispersal syndrome. Each functional attributes were divided into two categories, the successional strategy was categorized into pioneer or shade-tolerant species (Bongers et al., 2009; Magnago et al., 2014). The fruit type was categorized into fleshy fruit or dry fruit. We consider fleshy fruit when accumulate water and many other organic compounds and dry fruit those that do not have these characteristics (Coombe, 1976; Matos et al., 2020). The dispersal syndrome was categorized into zoochoric and non-zoochoric (Magnago et al., 2014; Santo-Silva et al., 2016). The zoochoric species were trees dispersed by animals and non-zoochoric species dispersed by anemochory and autochory. These functional attributes mainly represent the ability to colonize different types of habitats, resist disturbances, and store carbon (Matos et al., 2020; Pérez-Harguindeguy et al., 2013). These traits were obtained for each species from consulting in the data available in the SpeciesLink (for more details see: http://splink.cria.org.br/), by Magnago et al. (2014), and by the database of Matos et al. (2020).

2.5. Data analyses

All analyses were run in R 3.6.0 (R Development Core Team, 2019) and to draw the graphs illustration in this study, we used the "ggplot2" package (Hadley, 2015).

2.5.1. Species richness and carbon stock along Second-Growth forests and Old-Growth forests

To compare the species richness and AGC between forest stand ages we divided them in five stand age categories: (i) SGF_5yr – 14 s-growth forests which comprises areas between three and seven years of succession; (ii) SGF_10yr – 16 s-growth forest which comprises between 8 and 11 years of succession; (iii) SGF_18yr – 6 s-growth forests areas with 18 years of succession; (iv) SGF_30yr – 7 s-growth forests which covers areas between 27 and 32 years of succession; vi) and OGF – three protected old-growth forest patches.

Then, to compare species richness between stand age categories we used an individual-based approach to estimate rarefaction and extrapolation curves using the first $(q = 0)$ Hill number (Chao et al., 2014). Extrapolations were made based on presence/absence in the plots data of species (Colwell et al., 2012), using the "iNEXT" package (Hsieh et al., 2016). The Hill number was estimated as the mean of 100 replicate bootstrapping runs to estimate 95% confidence intervals. Whenever the 95% confidence intervals did not overlap, species numbers differed significantly at $p < 0.05$ (Colwell et al., 2012). Additionally, to compare the variation of community composition across forest stand ages a non-metric multidimensional scaling (NMDS) analysis was performed using 'metaMDS' function based on Jaccard similarities (Clarke, 1993; Oksanen et al., 2018). After checking the stress generated by the NMDS, we corroborate the nonmetric fit based on stress using linear regression (see Fig. A.1 from Appendices). Then, a permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) was used to test differences in species composition by using the 'adonis' function (Oksanen et al., 2018). All different functions of NMDS are available within the "vegan" package (Oksanen et al., 2018).

To compare AGC between stand-age categories we tested the normal distribution of all variables using the Shapiro-Wilk test and the Q-Q graph (Fig. A.2 from appendices), and the homogeneity of the variations was evaluated by the Bartlett test (Crawley, 2013). We used Kruskal-Wallis's test followed by a posterior Dunn's test performed with the "dunn.test" package (Dinno, 2017).

2.6. Forest recovery analysis

We calculated the recovery ratio (*Rc*) of the species richness, species richness by categorical functional attributes, AGC, and additionally of species composition in each SGF patch sampled. For species composition was calculated the mean pairwise between SGF and OGF plots based on the Chao-Jaccard index (Rozendaal et al. 2019) in each forest patch sampled. The forest recovery of each community was based on the Eq. (2) proposed by Liu et al. (2019):

$$Rc = \frac{SGF}{OGF} \tag{2}$$

where SGF is the value found in second-growth forests and OGF the average values found of the same variable in the three areas of old-growth forest sampled. Then we used Linear Regression from "stats" package to evaluate the relationship of the species richness recovery, species richness recovery by categorical functional attributes, above-ground carbon stock recovery, and species composition recovery rate along the stand age.

2.6.1. Carbon-biodiversity co-benefits

We applied generalized linear mixed-effects models (GLMMs, with random and fixed effects) to evaluate co-benefits between the above-ground carbon stock and species richness of second-growth forest by categorical functional attributes. Species richness was the response variable (data count), and predictors with fixed effects were carbon stock (continuous explanatory variable) and functional attributes (three discrete explanatory variable). These discrete variables were dispersal syndrome (two levels, zoochoric and non-zoochoric groups), regeneration strategy (two levels, pioneer and shade-tolerant groups), and fruit types (two levels, fleshy and dry groups). The stand age, forest patch and plots were considered as a random effect in all models (Rozendaal et al., 2019). The previous data analysis distribution, the Poisson error distribution was tested after checking the most suitable distribution and link function (Fig. S4 from SM) (Crawley, 2013; Zuur et al., 2009). We constructed a separate model for each categorical functional attribute (i.e., dispersal syndrome, regeneration strategy, fruit types). All models were calculated using the package "lme4" (Bates et al., 2019).

3. Results

3.1. Species richness and carbon stock along second-growth forests and old-growth forests

In the rarefaction and extrapolation curves we found higher species richness in old-growth forests (OGF) than in second-growth forests (SGF) (Fig. 2). However, we did not observe differences between SGFs richness (Fig. 2). In the same way, OGF had higher carbon stock than all the SGF, but all SGF had similar carbon stock values (Fig. 3). Thus, there were differences in carbon stock only between OGF (~130.78 Mg ha^{-1}) and SGF_5yr (~7.08 Mg ha^{-1}; $p < 0.01$), SGF_10yr (~8.73 Mg ha^{-1}; $p < 0.01$), SGF_18yr (~13.64 Mg ha^{-1}; $p < 0.01$), and SGF_30yr (~18.20 Mg ha^{-1}; $p < 0.01$). The NMDS revealed that tree community composition showed marginal differences only between OGF in relation to SGF_10yr (PERMANOVA: $F4,41 = 1.16$, $p < 0.05$), but with a marked overlap and no difference between SGFs (Fig. A.2; Table A.2 from Appendices).

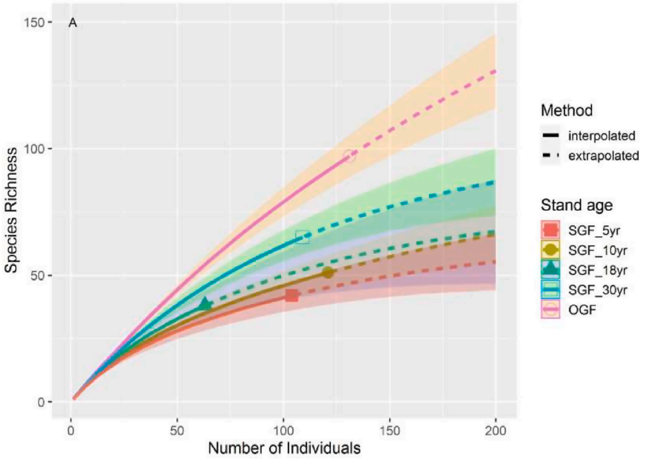

Fig. 2. Rarefaction (solid lines) and extrapolation curves (dashed lines) of woody species diversity based on the first Hill numbers $(q = 0)$ at different stand ages categories (5, 10, 18, and 30 years old) of second-growth forests (SGF) and old-growth forest (OGF).

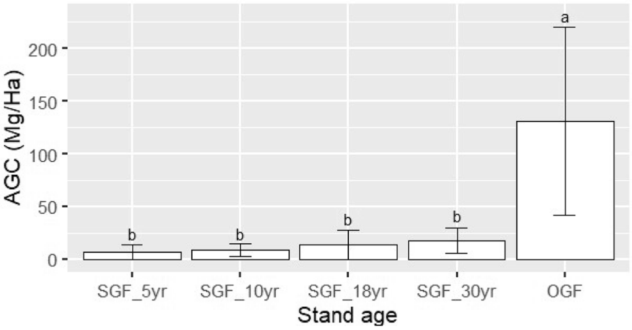

Fig. 3. Differences in aboveground carbon stock (AGC) between second-growth forests (SGF) and old-growth forest patch (OGF). The AGC median value is presented for stand age categories (5, 10, 18, and 30 years old) of second-growth forests and for old-growth forests (OGF). Different letters indicate significant differences (Dunn's test, $p < 0.05$) between stand ages categories.

3.2. Species richness and carbon recovery

In 32 years, the evaluated SGFs areas recovered on average 38% of the species richness ($t = 3.585$; $p = 0.0008$), and 14% of carbon stock ($t = 3.059$; $p = 0.0039$) of the OGFs (Fig. 4). The species richness recovery according to successional strategy in these 32 years was ~28% for shade-tolerant species ($t = 3.228$; $p = 0.002$) and ~60% for pioneer species ($t = 2.143$; $p = 0.038$) of the OGF (Fig. 5). The species richness according to the fruit types, showed a recovery rate of ~34% for fleshy fruit species ($t = 3.221$; $p = 0.002$) and ~32% for dry fruit species ($t = 2.495$; $p = 0.016$). By dispersal syndrome, the recovery was ~35% for zoochoric species richness ($t = 3.382$; $p = 0.001$) but the richness recovery of non-zoochoric species did not change (Fig. 5). The AGC relative recovery according to successional strategy was ~42% ($t = 3.822$; $p = 0.0004$) for pioneer species but the carbon recovery of shade-tolerant species did not change along SGF stand age (Fig. 5). The relative carbon recovery was ~7% ($t = 2.988$; $p = 0.004$) for fleshy fruit species and ~20% ($t = 2.314$; $p = 0.025$) for dry fruit species. Finally, the carbon relative recovery was ~12% ($t = 2.444$; $p = 0.018$) for zoochoric species but the carbon recovery of non-zoochoric species did not change across the stand age (Fig. 5). There was no significant recovery of Jaccard similarity with time (see Fig. A.4 from appendices).

3.3. Carbon-biodiversity co-benefits

Our tested models showed a significant positive relationship between AGC and species richness of evaluated SGFs in all categorical functional attributes (Fig. 6). Thus, the variation in aboveground carbon stock had the strongest positive effect on the variation of species richness of dispersal syndromes (Est. $= 0.09$, $z = 3.03$, $p < 0.002$, $R^2 = 0.71$), fruit types (Est. $= 0.01$, $z = 0.16$, $p < 0.001$, $R^2 = 0.64$) and regeneration strategy (Est. $= 0.08$, $z = 3.23$, $p < 0.001$, $R^2 = 0.73$). When analyzed by categorical functional attributes, we observed that zoochoric species (Est. $= 1.01$, $z = 8.6$, $p < 0.001$, $R^2 = 0.54$) and shade-tolerant species (Est. $= 0.96$, $z = 8.82$, $p < 0.001$, $R^2 = 0.73$) have a strong and positive relationship between AGC and species richness, but fleshy fruits species do not have this relationship (Est. $= 0.01$, $z = 0.16$, $p = 0.87$, $R^2 = 0.14$).

4. Discussion

Our results demonstrate significant rates of Atlantic Forest recovery after a long period of eucalyptus plantation management and highlight the implications for carbon-biodiversity co-benefits. Furthermore, we revealed the relationship between stand age-dependent functional attributes and ecosystem functioning based on carbon stock (e.g., co-benefits) along forest succession. Previous studies in Atlantic Forest have found that deforestation, disturbance, and edge effect promote a replacement of shade tolerant tree species by pioneer species (Pütz et al., 2011; Tabarelli et al., 2010). These species replacement could negatively affect the species richness and AGC (de Paula et al., 2011; Pütz et al., 2014). Here, we found a significant species richness and AGC recovery, but approximately half of what was found for species recovery and 6% less than found for carbon recovery in other Atlantic Forest recovery studies (Matos et al., 2020; Safar et al., 2020). Similarly, the relationship between specific functional attributes (i.e., successional strategy, fruit type, dispersal syndrome) and ecosystem functioning based on co-benefits between AGC and species richness tend to reach the values observed in old-growth forest fragments. Thus, here we discuss the recovery rate and the differences in functional attribute responses along with forest succession, suggesting that these SGF are recovering species richness and AGC; and that zoochoric and shade-tolerant tree species are responsible for a strong and positive relationship between AGC and species richness in these fragmented forest patches.

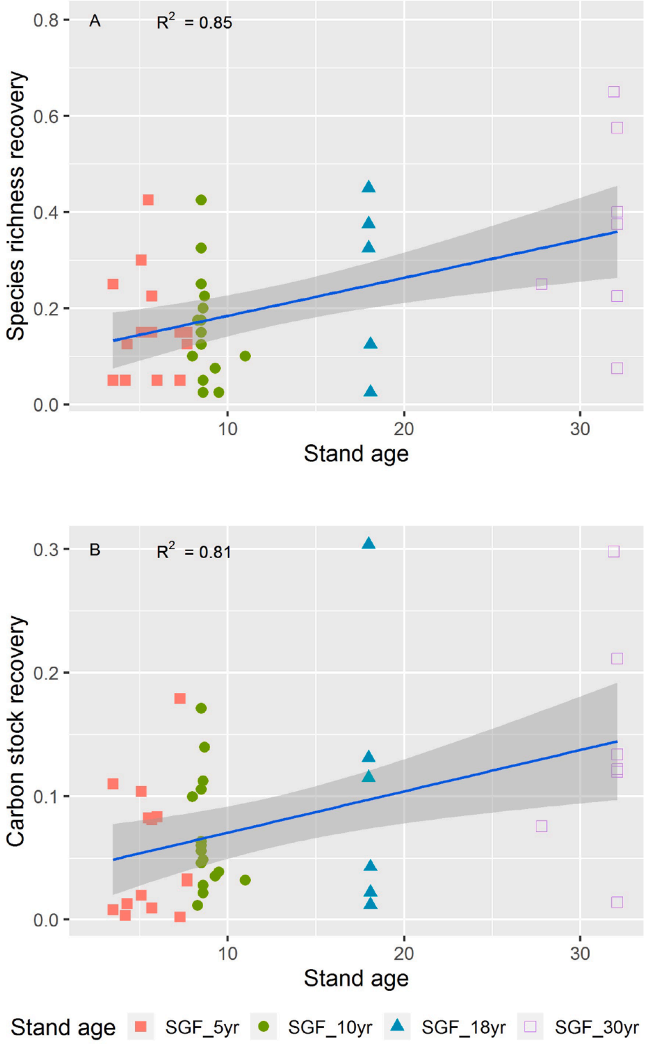

Fig. 4. Relationships between species richness relative recovery (A; equation of regression: $y = 0.10 + 0.007x$) and aboveground carbon relative recovery (B; equation of regression: $y = 0.03 + 0.003x$) with second-growth forests stand age. The dots are the observed data, the lines are the predictions from the model, and the shaded area is the 95% confidence interval.

There were marked differences in species richness and carbon stock between OGF and SGFs. However, we did not find differences between stand age categories of SGFs. OGFs have greater species richness and AGC because they had a long time to grow and to gain shade-tolerant species. This is an expected result due to early successional stages

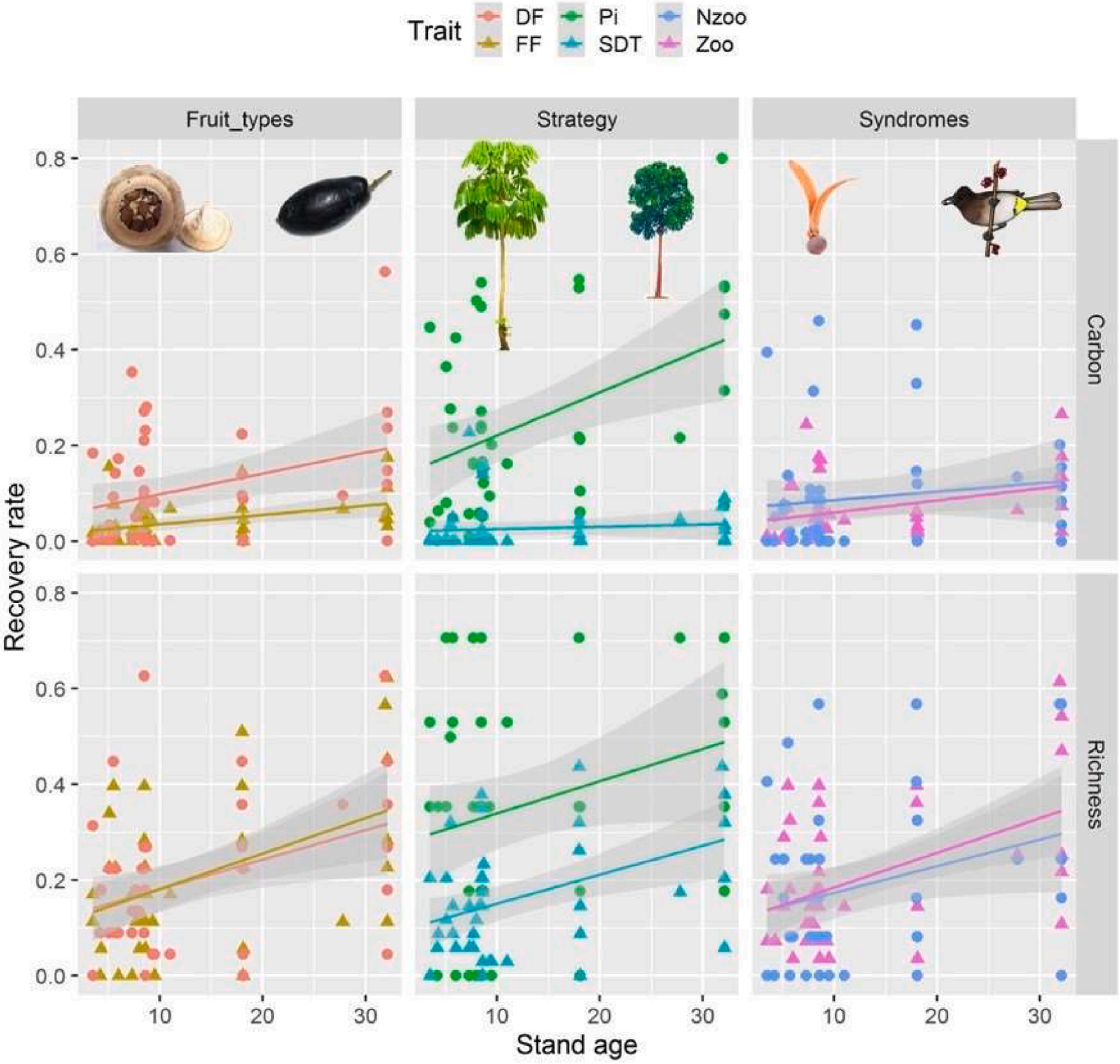

Fig. 5. Relationships between species richness and aboveground carbon relative recovery by functional attributes along second-growth forest stand age. We considered three functional attributes: fruit types, fleshy fruits (FF) or dry fruits (DF); regeneration strategy, pioneer (Pi) or shade-tolerant (SDT); and dispersal syndromes, zoochoric (Zoo) and non-zoochoric (Nzoo). The dots are the observed data, the lines are the predictions from the model, and the shaded area is the 95% confidence interval.

dominated by fast-growth and light-demanding pioneer species with short life cycles and less carbon stock (Guariguata and Ostertag, 2001; Villa et al., 2019). These results highlight the importance of OGFs for species conservation and carbon storage. Furthermore, they show that SGFs growing after long-term eucalyptus plantations at the same age can have very distinct indexes of species richness and AGC.

The recovery of species richness and carbon stock was demonstrated along stand age, where second-growth forests recovered 38% of species richness and 14% of AGC in three decades. The recovery of carbon stock is generally slower than the recovery of tree species richness (Bello et al., 2015; Matos et al., 2020; Safar et al., 2020) explaining the marked AGC difference between OGFs and SGFs found here. Neotropical forests take a median time of two decades to recover 80% of species richness (Rozendaal et al., 2019), and little more than 50% of carbon stock of old-growth forest (Oberleitner et al., 2021; Poorter et al., 2016). However, specifically in the Atlantic Forest, some studies have found a lower recovery rate: 52% of species richness and 16% of carbon stock in 20 years (Safar et al., 2020) and 76% of species richness and 20% of carbon stock in 30 years (Matos et al., 2020). Here, we found even slower recovery rates. These different recovery rates can be explained because Atlantic Forest biome are highly fragmented and both studies (Safar et al., 2020; Matos et al., 2020) were carried out in secondary forests on different land-use type and history, including second-growth forests growing after the clear cut of native forests. Fragmentation makes it difficult to disperse propagules between forest fragments and regenerating areas, decreasing the recovery of species in the landscape (Pérez-Cárdenas et al., 2021). In the same way, the secondary succession process may be slower depending on the frequency, intensification and duration of the land use, because these factors affect seed bank and soil fertility (Jakovac et al., 2015; Pyles et al., 2018; Villa et al., 2018). In the case of the land-use history for eucalyptus plantations, we know that the longer the time of use and the higher the number of plantation cycles there is a soil nutrient decreasing and less understory diversity of plant species in SGF that are regrowing after eucalyptus cutting (Cook et al., 2016; Zhou et al., 2020).

We presume that factor related to habitat filtering and spatial factor related to dispersal limitation (e.g., Villa et al., 2021) can be strong drivers of forest recovery (Pérez-Cardenas et al., 2021) and should be better explored in landscapes with eucalyptus plantations. Probably, some eucalyptus plantations were distributed nearby OGF patches, increasing the forest patch connectivity through eucalyptus plantation by the canopy strata (Brancalion et al., 2020). This connectivity can

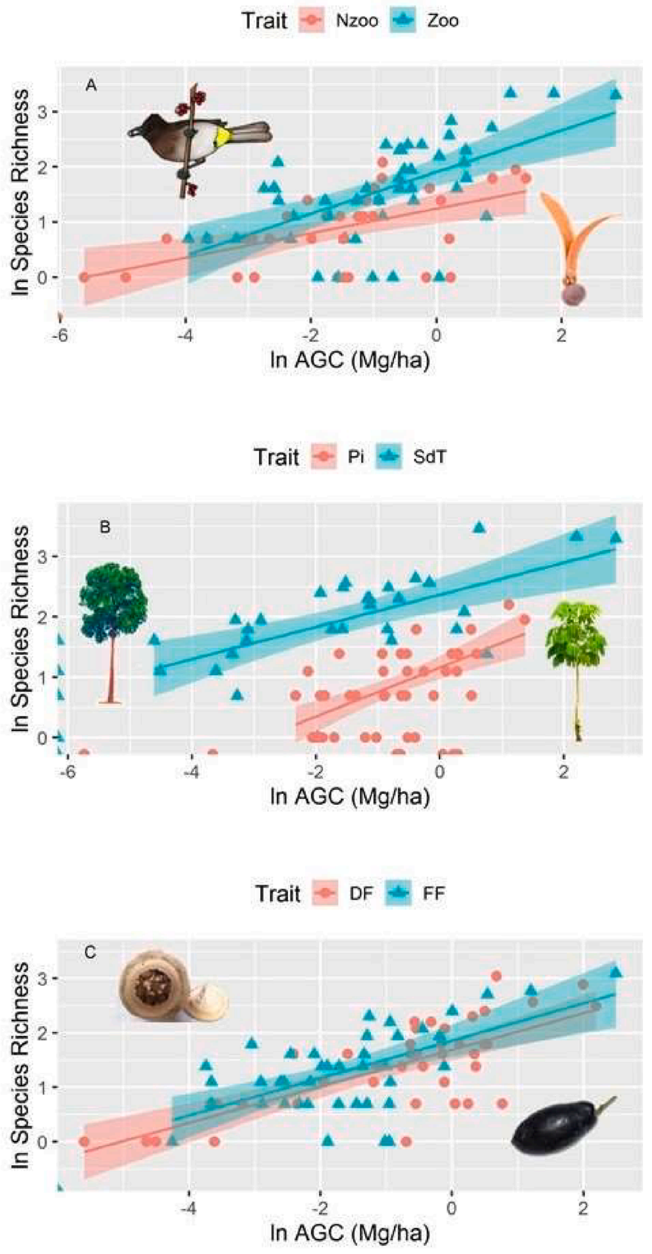

Fig. 6. Relationships between aboveground carbon stock (AGC) and species richness of the evaluated second-growth forests by categorical functional attributes: (A) dispersal syndromes, zoochoric (Zoo) or non-zoochoric (Nzoo) tree species); (B) regeneration strategy, pioneer (Pi) or shade-tolerant (SdT); and C) fruit types, fleshy fruits (FF) or dry fruits (DF). Solid lines represent fitted (predicted) values of the models, and the shaded polygons the 95 % associated with the modeled predictions.

induce favorable conditions for animal movement attracting more seed dispersing fauna (Barlow et al., 2007; Bertacchi et al., 2016; Brancalion et al., 2019; Carrilho et al., 2017) and for recruitment of shade-tolerant species that become common in late-successional stages (Poorter et al., 2019; Rozendaal et al., 2019; Santo-Silva et al., 2016; Villa et al., 2021). These conditions maintain part of species richness of OGFs in eucalyptus plantations' seed bank (Brockerhoff et al., 2013; Gabriel et al., 2013; Zhang et al., 2014) which can explain similar species richness in SGFs with distinct age categories and the significant species richness relative recovery after eucalyptus cutting.

The spatial factor can also explain the same AGC pattern between stand age categories of second-growth forests. Probably, there is a functional attributes convergence, where light-demanding pioneer and shade-tolerant species or non-zoochoric and zoochoric species can coexist since the beginning of succession, in areas previously occupied by eucalyptus plantations. Previous studies have reported a tendency for large shade-tolerant and zoochoric tree species to have larger fruits and seeds, which have a positive relationship to aboveground carbon stock (Bello et al., 2015; Peres et al., 2016). This tendency has been observed mainly in old-growth forests where carbon stocks are greatest due to shade-tolerant and zoochoric tree species (Stephenson et al., 2014). Thus, the presence of these species since the beginning of succession allows higher carbon indexes in some areas, preventing the differentiation of carbon stock between SGF categories. Curiously, for shade-tolerant species, there was no significant recovery in the SGF in terms of carbon stock and only 28% in terms of species richness in 32 years. This result reinforces the coexistence of pioneer and shade-tolerant species since the beginning of the succession and explains the greater carbon stock in the evaluated OGFs.

The co-benefit relationship between aboveground carbon stock and tree species richness along with Atlantic Forest succession highlights the importance of zoochoric and shade-tolerant tree species on carbon stock. These results are congruent with other results found for the Atlantic Forest (Magnago et al., 2015; Matos et al., 2020) and Amazon forest (Lennox et al., 2018), indicating that the recovery of carbon stock along succession also recover the tree species richness. In addition, our results indicate that carbon and species richness recovery in these forest patches are following patterns found in OGF that are dominated by larger sized species with larger seeds, which are dispersed by vertebrates (Tabarelli et al., 2010; Tabarelli and Peres, 2002) and have higher carbon stock potential (Bello et al., 2015). These species become less abundant in fragmented and SGF causing a decrease in carbon stock (Magnago et al., 2016, 2015; Pyles et al., 2018), but they remain the main species responsible for carbon stock along secondary succession as showed here by the stronger positive relationship between zoochoric and shade-tolerant species richness with AGC.

Our results suggest that the long-term eucalyptus plantation probably reduce forest recovery as other land-use types, such as logging and cultivation intensification in tropical forest (de Avila et al., 2018; Jakovac et al., 2015; Villa et al., 2018; Xu et al., 2015). However, we show here that areas previously occupied by eucalyptus plantations can be considered for passive restoration methods based on co-benefits, and actions to reduce carbon emissions due to forest degradation. Furthermore, evidence shows that eucalyptus did not negatively affect the natural regeneration of native woody species before or after eucalyptus cutting: the natural regeneration species richness and planted non-pioneer growth were similar across treatments in the post-logging period (Brancalion et al., 2020). In the same way, another study showed that there is no trade-off between above-ground carbon accumulation by planted trees and the spontaneous regeneration of tree species (Brancalion et al., 2019).

This study demonstrated that the stronger co-benefits between zoochoric and shade-tolerant species and AGC can be an important approach for applied forest management, which can be used for the identification of key species that promote the recovery of aboveground carbon stock along active and passive restoration in human-modified tropical landscapes. Thus, knowing the forest regeneration by functional groups, and their relative contribution to the co-benefit, it is possible to control natural succession by quantifying and managing the relative proportion of species and number of individuals that simultaneously contribute to the AGC increase. Therefore, our study reveals that zoochoric and shade-tolerant species can shape AGC stock in our studied forests. Finally, we emphasize the relevance of the trait-based approach in current research to understand forests functioning and trait functional composition (role of key species) for the carbon storage increase and recovery in the threatened Atlantic Forest.

5. Conclusions

Our study demonstrated that after long-term eucalyptus plantations the second-growth forests have way less species richness and carbon stock than nearby old-growth forests, and they cannot be differentiated in species richness and AGC by stand age categories. However, there is a significant but slower relative recovery rate of richness and carbon stock when compared with other studies in neotropical second-growth forests. In addition, we showed that there is a co-benefit between above-ground carbon stock and species richness, mainly zoochoric and shade-tolerant species. The slower recovery rate can be explained by low fertility of areas after intensive land use. However, probably the connectivity provided by eucalyptus plantations between forest fragments and the canopy strata allow the establishment of the OGF species in the soil seed bank during land-use time. Thus, zoochoric and shade-tolerant species can coexist in this second-growth forests since the beginning of succession, allowing similar species richness and above-ground carbon stock in different stand age categories, and a significant recovery of these attributes along stand age. Thus, our study indicates that passive restoration may be applicable on areas previously used for eucalyptus plantation to recover the tree species richness and above-ground carbon stock. Furthermore, the occurrence of zoochoric and shade-tolerant species can be key species to increase carbon stock along forest recovery process.

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CRediT authorship contribution statement

Alex Josélio Pires Coelho: Conceptualization, Data curation, Formal analysis, Methodology, Writing – original draft, Writing – review & editing. **Pedro Manuel Villa:** Formal analysis, Writing – review & editing. **Fabio Antônio Ribeiro Matos:** Conceptualization, Formal analysis, Methodology, Writing – review & editing. **Gustavo Heringer:** Formal analysis, Writing – review & editing. **Marcelo Leandro Bueno:** Formal analysis, Writing – review & editing. **Roosevelt Paula Almado:** Methodology, Writing – review & editing. **João Augusto Alves Meira-Neto:** Formal analysis, Funding acquisition, Project administration, Resources, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119789.

Appendix C. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119789.

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