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Multiple drivers influence tree species diversity and above-ground carbon stock in second-growth Atlantic forests: Implications for the passive restoration

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ABSTRACT

Second-growth forests (SGF) are critical components for limiting biodiversity loss and climate change mitigation. However, these forests were established after anthropic disturbances such as land use for planting, and in highly human-modified landscapes. These interventions can decrease the ability of biological communities to recover naturally, and it is necessary to understand how multiple drivers, from local scale to landscape scale influence the diversity and carbon stock of these forests in natural regeneration. For this, we used data from 37 SGF growing on areas previously used for eucalyptus plantations in the Brazilian Atlantic Forest, after the last cut cycle. For each SGF, the forest tree species diversity was calculated based on the Hills number, and we also calculated the above-ground carbon stock. Then, we evaluated the influence of multiple environmental factors on these indexes: soil properties, past-management intensity, patch configuration, and landscape composition. Little influence of soil properties was found, only soil fertility negatively influenced above-ground carbon stock. However, past-management intensity negatively influenced tree species diversity and carbon stock. The isolation of other forests and tree species propagules source distance (>500 ha) also negatively influenced the diversity of species. This is probably due to the favoring of tree pioneer species in highly human-modified landscapes because they are more tolerant of environmental changes, less dependent on animal dispersal, and have low carbon stock capacity. Thus, areas with higher past-management intensity and more isolated areas are less effective for passive restoration and may require intervention to recover tree diversity and carbon stock in the Atlantic Forest. The approach, which had not yet been applied in the Atlantic Forest, brought similar results to that found in other forests, and serves as a theoretical basis for choosing priority areas for passive restoration in the biome.

1. Introduction

The rapid growth of the world's population and the demand for natural resources has led to the worldwide replacement of old-growth forests for agricultural systems, mining, and other human activities (Nazareno et al., 2012). Currently, about one-third of the deforested areas undergoes regeneration processes and develop, temporally (i.e. due to fallow time on plantations) or permanently (i.e. because of land abandonment or due to restoration initiatives), into second-growth forests (Arroyo-Rodríguez et al., 2017; Hansen et al., 2013). These forests are important because they protect soils from erosive processes, provide products to local populations, and contribute to the

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maintenance of biodiversity and ecosystem services, such as carbon sequestration (Chazdon et al., 2016; Klemick, 2011; Villa et al., 2020b). Thus, the main initiative for biodiversity conservation and climate change mitigation in the world is the restauration of deforested areas (Ivanova et al., 2020). However, these areas are usually located in landscapes with strong anthropic influences (Arroyo-Rodríguez et al., 2017). The regeneration (recover processes of forest structure) of this areas depends, among other factors, on the previous or current management intensity and the landscape configuration (Jakovac et al., 2015; Sloan et al., 2015). Thus, it is important to know how multiple drivers influence forest regeneration in human-modified landscapes to choose priority areas for restoration.

Global initiatives foresee the deployment of large-scale second-growth forests worldwide. These initiatives were discussed at the Paris Climate Agreement and reinforced at the 2014 United Nations Climate Summit in New York, when more than 130 governments, private companies, civil society and indigenous peoples pledged to restore more than 350 million hectares of forests globally by 2030 (Brancalion et al., 2019; Ivanova et al., 2020; Uriarte and Chazdon, 2016). Thus, the United Nations' Decade on Ecosystem Restoration (2021–2030) was established. This ambitious goal would be met primarily by the forest planting methods that could cost up to US$ 837 billion over 15 years. However, natural or assisted regeneration (both passive restoration methods) can make this goal possible on a large scale by offering better cost benefits (Uriarte and Chazdon, 2016).

Along tropical forest succession, there is an increase in species richness, crown height, stem density and basal area of the trees, meanwhile the canopy opening and abundance of herbs, shrubs and lianas decrease (Chazdon, 2014; Finegan, 1996). The neotropical second-growth forests take an average of 20 years to recover 80 percent of species richness and 50 percent of above-ground carbon stock (AGC) of old-growth forests (Oberleitner et al., 2021; Rozendaal et al., 2019). These forest recovery rates depend mainly on soil properties and climatic conditions (Guariguata and Ostertag, 2001; Rozendaal et al., 2019). However, in a scenario of human-modified landscapes the past-management effect can decrease the recovery rate and successional trajectories, because the disturbance can alter local environment conditions (Guariguata and Ostertag, 2001; Jakovac et al., 2015; Villa et al., 2018). For example, increasing the frequency of land use cycles (i.e. logging, shifting cultivation, plantation) and shortening the fallow period in the same forest area (i.e. five or more SC cycles) induce a land-use intensification and degradation (Jakovac et al., 2017; Styger et al., 2007; Villa et al., 2018), expanding agricultural frontiers on a local-scale, and reducing the forest resilience (Jakovac et al., 2015; Kingwell-Banham and Fuller, 2012; Villa et al., 2020a). In addition, the landscape configuration (e.g., patch size and isolation) and composition of these SGFs can also induce dispersal limitation, due to distance to old-growth forests and matrix dissimilarity, slowing down the forest recovery (Matos et al., 2020; Pérez-Cárdenas et al., 2020). Thus, the recovery of species and AGC during regeneration in human-modified landscapes may be slower or does not happen naturally (Safar et al., 2020).

The Atlantic Forest is the second-largest tropical forest in America and represents one of the world's hotspots for biodiversity conservation (Myers et al., 2000). This forest has a long history of deforestation and land use from the country's colonization in the 16th century to the present, resulting in a highly fragmented biome (Nazareno et al., 2012; Tabarelli et al., 2010a). Therefore, the Atlantic Forest has many areas to be restored with different soil properties, management intensity and landscape configurations. There are pacts aimed at recovering millions of hectares of Atlantic Forest, such as the Pact for the Restoration of the Atlantic Forest (15 Mha until 2050) and Brazil's Determined National Contribution to the Paris Climate Agreement (12 Mha until 2030), which includes the Atlantic Forest (Rosa et al., 2021). Parts of these areas have been used for eucalyptus (*Eucalyptus* sp.) plantations, one of the main land uses in the Atlantic Forest region (Gonçalvez et al., 2013). It is known that after eucalyptus cutting these areas regenerate naturally (Brancalion et al., 2019, 2020) and can recover in 32 years 38 percent of species richness and 14 percent of the AGC of nearby old-growth forests (Coelho et al., 2022). Due to the structural similarity of eucalyptus planting with natural forests, there is a movement of seed-dispersing animals and similar environmental conditions during the land use (Carrilho et al., 2017). This allows the establishment of these species in the soil seed bank as well as the regeneration of old-growth forest species (Barlow et al., 2007; Bertacchi et al., 2016; Carrilho et al., 2017; Zhang et al., 2014). Thus, these areas can be considered for passive restoration, but we do not know how multiple drivers affect species richness and aboveground carbon stock after last cut of eucalyptus plantations in the Atlantic Forest biome.

In this context, considering the demand for restoration of Brazil's Atlantic Forests, we investigate how multiple drivers influence stand age dependent forest attributes in a human-modified Atlantic Forest landscape. Specifically, we evaluated how soil properties, past-management intensity, local configuration, and landscape composition influence tree diversity and AGC. We hypothesized that after last cut of eucalyptus plantations: (i) soil properties would have an influence on tree species diversity and AGC recovery; (ii) the past-management intensity would negatively affect the tree species diversity and AGC; (iii) patch size would positively affect while isolation of forests and tree species propagules source distance would negatively affect the tree species diversity and AGC recovery; and that (iv) forest and eucalyptus forest cover in the landscape would positively affect tree species and AGC recovery. In addition, we suggested how choose priority areas for passive restoration in the Atlantic Forest domain after long-term land use. For this we used 35 s-growth forests of different stand ages (3–32 years) after at least 30 years of use for eucalyptus plantations with different, soil properties, past-management intensity, patch characteristics and landscape composition. This approach has not yet been applied in the Atlantic Forest and can generate theoretical knowledge about priority areas for passive restoration in the biome.

2. Material and methods

2.1. Study area

The study area was near the largest fragment of the Atlantic Forest in the state of Minas Gerais, Rio Doce State Park, between the municipalities of São José do Goiabal, Dionísio and Timóteo (19°50′57.25″S; 42°39′11.71″W; Fig. 1a). The region is included in the Atlantic Forest domain, and according to the Brazilian vegetation classification, contains *submontane semideciduous seasonal forests* (Veloso et al., 1991). The region has mean annual precipitation of 1450 mm, mean temperature ranging between 20 and 23 °C with well-defined periods of rain and drought, and two dominant soil classes: Red-Yellow Latosol in hilltops and mountainsides and Red-Yellow Podsol upper fluvial terraces (Alvares et al., 2013; Lopes et al., 2002; Santos et al., 2018). This region is very developed e economically important, mainly by land use for agriculture, livestock, and eucalyptus plantation (Oliveira-Junior et al., 2020; Scarano and Ceotto, 2015).

2.2. Study plots

Were used data from 42 s-growth forest patches previously used for eucalyptus planting in fallow time after the last cutting. The land-use history of these patches was made available by the landowner company. Thus, we excluded 7 patches with different land-use before eucalyptus planting, like livestock and coffee planting. All the remaining 35 patches were primary forest cleared for charcoal production and later used for eucalyptus planting. The first eucalyptus planting cycle in these areas was soon after the primary forest clearing. The fallow age times range from 3 to 32 years after the last cutting cycle (see Fig. 1e an example of a second-growth forest with 8 years of fallow age) and the

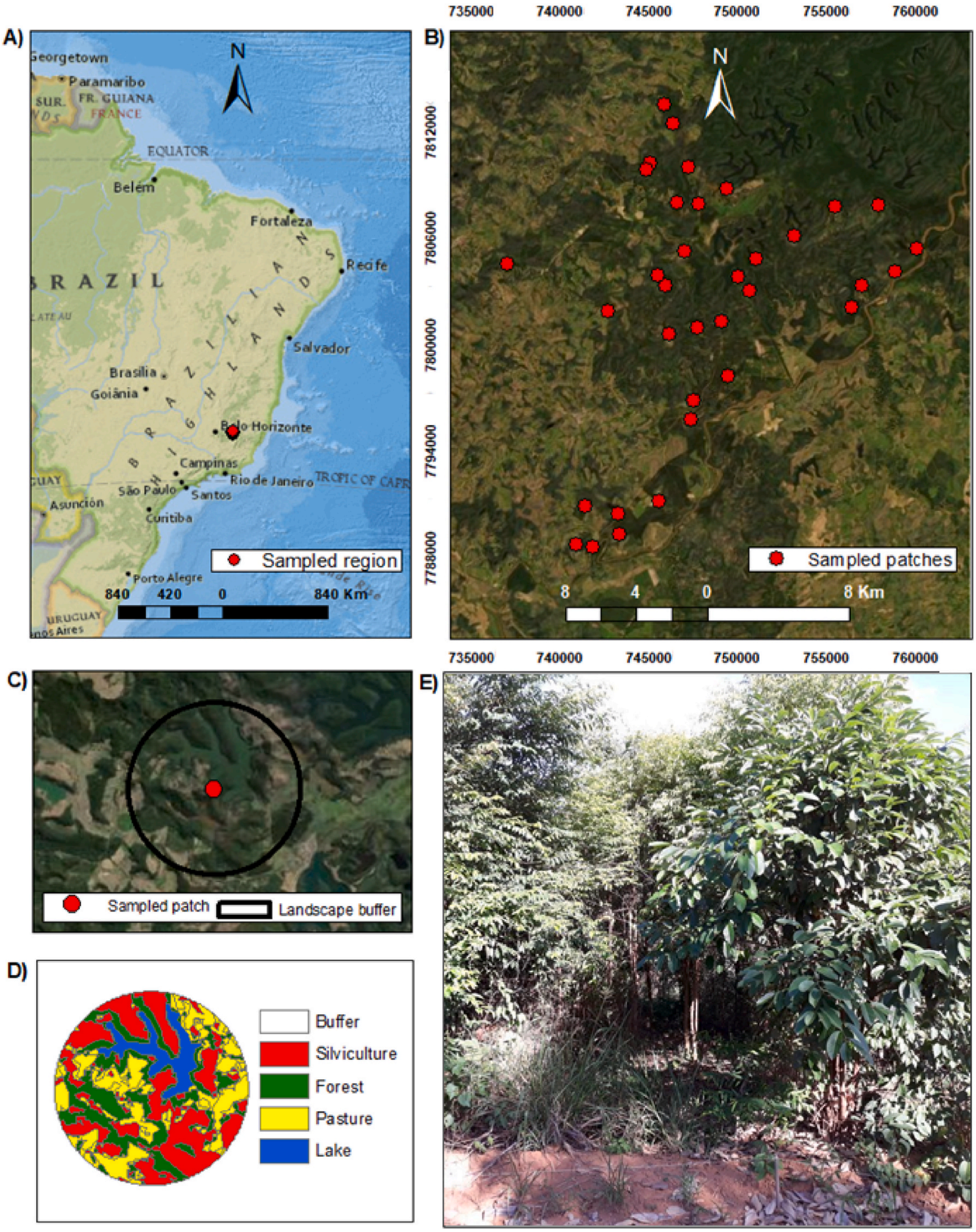

Fig. 1. Map of location and characteristics of the sampled patches. A) Region sampled in the state of Minas Gerais, Brazil; B) Second-growth forests sampled near to the state park of Rio Doce; C) Example of the 2 km buffer created from each sampling point for collecting landscape composition variables; D) Example of the 2 km buffer cutout on the classified image of MapBiomas collection 5 of 2018 for the quantification of forest and silviculture cover; E) second-growth forest sampled at the point represented in C) and D) with 8 years-old of fallow.

size of the areas varied between 13 ha and 199 ha. We avoided patches with more than four eucalyptus regenerating individuals.

2.3. Tree sampling

In each second-growth forest, we sampled one plot of 20 × 50 m (0.1 ha). Within each plot, both the shrub and arboreal strata were sampled, including all individuals rooted within our plots ≥4.8 cm in diameter at breast height (1.30 m above ground height) following Matos et al. (2020). For tree individuals that were not identified at the site, we collected leaves and any reproductive parts, and these were then classified into morphospecies and subsequently identified by morphological comparison in the Herbarium of Viçosa (VIC) or by botanical experts for their families following APG IV (2016). The botanical material collected in the reproductive stage was deposited in the Herbarium of the Federal University of Viçosa, Minas Gerais (VIC).

2.4. Tree diversity

To measure the tree species diversity we used three Hill numbers (effective number of species) based on species relative abundances (Hsieh et al., 2016; Rother et al., 2019). These diversity indexes are parameterized in three orders of q: i) $q = 0$ - species richness, measure that give the same weight to rare species and to abundant ones; ii) $q = 1$ - exponential form of Shannon entropy, measure of species diversity giving less weight to rare species; and iii) $q = 2$ - inverse of Simpson diversity, measure of the relative abundance distribution of species giving even less weight to rare species than Shannon, where higher values indicate evenness on abundance distribution (Gotelli and Chao, 2013; Hill, 1973; Jost, 2006). These indexes were calculated in "iNEXT" package (Hsieh et al., 2016) and the equations are described in Jost (2006).

2.5. Above-ground carbon stock

First, we calculated the above-ground biomass of each individual with the allometric equation improved by Chave et al. (2014) in equation (1):

$$AGB = \exp[-1.803 – 0.976E + 0.976\ln(\rho) + 2.673\ln(D) – 0.0299[\ln(D)]^2] \text{(Eq. 1)}$$

where AGB is the estimated above-ground biomass, E is a measure of environmental stress; ρ is wood density (g/cm3) and D (cm) is the tree's diameter at breast height. The value of E was obtained according to the geographic coordinates of each area using the "BIOMASS" package where we calculated AGBest (Réjou-Méchain et al., 2017). The total AGB per patch was the sum of the AGBs of all trees having DBH $\geq$5 cm, which was then converted to megagrams per hectare (Mg ha^{-1}). The value for wood density (g/cm3) was obtained from Global Wood Density database (GWD; Zanne et al., 2009). For species with wood density that have not been recorded in GWD we made an average with the species of the same genus recorded (Magnago et al., 2014; Matos et al., 2020). Second, we obtained the carbon stock assuming that the carbon concentration of a tree's different organs is assumed to be approximately 50 percent of the biomass (Malhi et al., 2004).

2.6. Environment explanatory variables

2.6.1. Plot scale variables

Plot drivers were grouped into two categories, such as soil properties and past-management intensity. We considered ten properties-related soil: i) P - phosphorus concentration; ii) Mg^{2+} - magnesium concentration; iii) Ca^{2+} - calcium concentration; iv) K - potassium concentration; v) Fe - iron concentration; vi) Al^{3+} - aluminum concentration; vii) pH - measure of hydrogen ion concentration; viii) clay - percentage of clay; ix) sand - percentage of sand; and x) silt - percentage of silt in the soil sample. For this, three random samples of 0–20 cm depth were taken in each patch. The three samples were later homogenized and analyzed by Soil Department of Federal University of Viçosa, following the protocol of Santos et al. (2018).

For past-management intensity were considered the data of land-use history of the patches improved by the landowner company: i) planting cycle - numbers of times that each patch was used by eucalyptus plantation; ii) cutting cycle - number of times that the eucalyptus plantation was cutting in each patch by clear-cut; iii) use time - time between de first cycle planting and last cycle cutting; and iv) fallow age - time between the last cutting cycle and the tree sampling along secondary succession. These variables-related management intensity and land-use history have been used in previous studies (Jakovac et al., 2015; Pérez-Cárdenas et al., 2020; Villa et al., 2018).

We summarized the soil properties variables and past-management intensity of the plots performing two principal component analyses (PCA) based on correlation matrix separately using "FactorMiner" package (Lê et al., 2008). The soil properties PCA was composed by concentrations of phosphorus, magnesium, calcium, potassium, iron, aluminum, pH, and percentages of clay, sand, and silt. Meanwhile, the past-management intensity PCA was composed by planting cycle, cutting cycle, use time, and fallow age. Then, we analyzed how many axes of PCA were important to retain in models for both variables sets applying the Horn's parallel analysis with 600 iterations and retaining the axes with an adjusted eigenvalue >1 (see Jakovac et al., 2015). These parallel analyses were processed using "Paran" package (Dinno, 2018). Thus, were retained only one axis as proxy for past-management intensity and two axes as proxy for soil properties. We called the first PCA axis of the soil properties as soil fertility and the second PCA axis as soil texture because strong correlation with chemical and physical properties, respectively (see more information in the results part).

2.6.2. Patch and landscape scale variables

For patch configuration and landscape composition characteristics we used patch-scale and patch-landscape approaches, respectively (Matos et al., 2020; Pérez-Cárdenas et al., 2021). Thus, we measured three patch-scale variables in independent patches: i) patch size - area in hectares (ha); ii) patch isolation - the shortest linear distance in meters between the patch sampled and another natural forest patch; and iii) source distance - the minor linear distance between each patch sampled and some natural forest patch $\geq$500 ha. We collected two patch-landscape metrics for landscape composition considering a circular buffer of 2 km: i) forest cover - percentage of forest cover in the landscape; and ii) silviculture cover - percentage of planted forests in the landscape. Patch configuration and landscape composition metrics were obtained by classified images improved by Brazilian Annual Land Use and Land Cover Mapping Project (MapBiomas Collection 5) referent to 2018. The patch isolation and source distance were measured in ArcGis software (Environmental Systems Research Institute, Redlands, CA, USA). The patch area, forest cover and silviculture cover were calculated in "FRAGSTAT 4.2" software (McGarial et al., 2012) in a buffer of 2 km of radius since the center of each plot (Coelho et al., 2020; Matos et al., 2016) was extracted from "ArcGis" software (Fig. 1c and d).

2.7. Statistical analyses

We applied the Moran's I test to check for the potential influence of spatial autocorrelation in diversity and carbon stock of the sampled transects. For this, we used the "spdep" package (Bivand and Piras, 2015) and the significance was determined by the Monte-Carlo permutation test (1000 permutations). Thus, we did not find a geographical correlation between our sampled transects. We tested the data distribution by the Shapiro-Wilk test and the distributions of the residuals were normal for all parameters. Thus, to evaluate the influences of past-management intensity, soil properties, local configuration and landscape composition on diversity and carbon stock (response variables) we used generalized linear models (GLM) with Gassian distribution, following equation (2):

$$\begin{aligned}\text{Diversity or AGC} \sim\ & \text{Soil fertility} + \text{Soil texture} + \text{Past} \\ & - \text{management intensity} + \text{Patch area} \\ & + \text{Patch isolation} + \text{Source distance} \\ & + \text{Forest cover} + \text{Silviculture cover}\end{aligned} \qquad (2)$$

where soil fertility was the first PCA axis of soil properties, soil texture the second PCA axis of soil properties, and past-management intensity was the first PCA axis of past-management intensity PCA. Using an information-theoretic approach and multi-model inference (Burnham et al., 2011) in the "MuMIn" package (Barton, 2017) we calculated Akaike's information criterion (AICc indicated for small samples), by the combination of all candidate models. Were applied

Spearman correlation analyses to avoid variables with correlations >0.6 in the same candidate models. We considered the models with $\Delta AICc \leq 5$ as the best models to explain the variation of variables responses and calculated the average models (Burnham and Anderson, 2002; Matos et al., 2020). In addition, we obtained the independent contribution of each environmental predictor from the sum of Akaike weights of average models (Burnham et al., 2011).

3. Results

3.1. Environmental variables treatment

In this study, 3.5 ha of sampled secondary forest area were included. A total of 1103 tree individuals were sampled, distributed among 84 species. The sampled soils were generally acidic pH, with very varied chemical and physical characteristics (Table 1). For the soil properties, two axes were retained in the PCA: the first axis (adjusted eigenvalue = 5.293; explained 62.6 percent of the variation) was positively correlated with pH, Mg^{2+}, Ca^{2+}, K, P, and silt percentage, and negatively correlated with Fe, Al^{3+}, and clay percentage; and the second axis (adjusted eigenvalue = 1.144; explained 17.6 percent of the variation) was positively correlated with P, silt and clay percentages, and negatively correlated with sand percentage. Thus, we related the first axis to soil fertility, because strong correlation with nutrient contents, and the second axis to soil texture, because strong correlation with physical characteristics (see SM1, SM2, SM3 and SM4 in supplementary material for more information).

The fallow age of our second-growth forests varied between 3 and 32 years and the use time for eucalyptus plantation varied between 16 and 50 years. During the time of use these areas had 1 to 3 planting cycles, and 2 to 4 cutting cycles. Only the first axis of past-management intensity PCA was retained in the Horn's parallel analyses (adjusted eigenvalue = 2.170, explained 64.2 percent of the variation). This axis was positively correlated with cutting cycle and use time, and negatively correlated with follow age (see SM5, SM6, SM7 and SM8 in supplementary material for more information).

Table 1
Environmental variables used to evaluate influences in secondary succession in this work and correlation with PCA axis selected and variables.

Variable sets	Unit	Minimum	Maximum	PCA axis 1	PCA axis 2
Soil Properties					
pH	(H2O)	3.48	6.41	0.968[a]	−0.0531
Mg^{2+}	cmol/dm^3	0.05	1.23	0.9268[a]	0.1509
Ca^{2+}	cmol/dm^3	0.32	6.36	0.9127[a]	0.1074
K	mg/dm^3	11	195	0.8503[a]	0.1087
P	mg/dm^3	1.3	9.9	0.5122[a]	0.4112[a]
Fe	mg/dm^3	17.4	104.4	−0.8115[a]	0.2475
Al^{3+}	cmol/dm^3	2.2	8.7	−0.8994[a]	0.0563
Silt	%	0.006	0.341	0.688[a]	0.6258[a]
Clay	%	0.295	0.757	−0.7823[a]	0.4947[a]
Sand	%	0.104	0.632	0.3066	−0.9184[a]
Explained variation by PCA	%	-	-	*62.6*	*17.6*
Past-Management Intensity					
Planting cycle	Number	1	3	−0.0900	0.9921[a]
Cutting cycle	Number	2	4	0.9376[a]	−0.05
Use time	Years	16	50	0.8691[a]	0.15
Fallow age	Years	3	32	−0.9626[a]	−0.01
Explained variation by PCA	%	-	-	*64.2*	*25.2*
Patch Configuration					
Patch area	ha	13.4	199	–	–
Patch isolation	m	25	698	–	–
Source distance	m	25	21632	–	–
Landscape composition					
Forest cover	%	5.011	54.610	–	–
Silviculture Cover	%	9.746	62.156	–	–

[a] Significance values of correlation ($p < 0.05$).

The patch configuration and landscape composition were also quite varied among the secondary forests sampled. The area of forests ranged from 13.4 to 199 ha, and the isolation from 25 to 698 m. The source patch larger than 500 ha was the same for all SGFs, the Rio do Doce state park, ranging source distance from 25 to 21,632 m. The landscape composition varied between 5 and 54 percent of forest cover and 9 to 62 percent of eucalyptus cover (see SM9 and SM10 in supplementary material for more information).

3.2. Effects of multiple drivers in tree species diversity and carbon stock

The diversity parameters and above-ground carbon stock were influenced by the environmental variables (Fig. 2). Species richness ($q = 0$) was negatively influenced by past-management intensity ($\beta = -0.426 \pm 0.153$ *SE*, $z = 2.679$, $p = 0.007$) and patch isolation ($\beta = -0.428 \pm 0.157$ *SE*, $z = 2.618$, $p = 0.009$). The exponential Shannon ($q = 1$) was negatively influenced by past-management intensity ($\beta = -0.451 \pm 0.170$ *SE*, $z = 2.554$, $p = 0.011$) and patch isolation ($\beta = -0.357 \pm 0.168$, $z = 2.05$, $p = 0.040$), and positively influenced by source distance ($\beta = 0.347 \pm 0.168$ *SE*, $z = 1.96$, $p = 0.05$). The inverse of Simpson ($q = 2$) was also negatively influenced by past-management intensity ($\beta = -0.411 \pm 0.173$ *SE*, $z = 2.296$, $p = 0.021$) and positively influenced by source distance ($\beta = 0.385 \pm 0.178$ *SE*, $z = 1.76$, $p = 0.078$). Finally, above-ground carbon stock was negatively influenced by past-management intensity ($\beta = -0.347 \pm 0.153$ *SE*, $z = 2.175$, $p = 0.029$) and soil fertility ($\beta = -0.396 \pm 0.153$ *SE*, $z = 2.49$, $p = 0.012$). Patch isolation and past-management intensity had negative effect in all evaluated parameters. However, source distance had positive effect in exponential of Shannon and negative effect in inverse of Simpson. Patch area, soil texture, forest cover, and silviculture cover, were not significant response variables in any model (see SM11, SM12, SM13 and SM14 in supplementary material for more information).

In all diversity parameters, past-management intensity was the most important variable, following the sum of Akaike weights of average models (Fig. 3). The other two variables more important for species richness were patch isolation and soil fertility. For exponential Shannon were patch isolation and source distance, and for inverse of Simpson were source distance and patch isolation, in this order. For above-ground carbon stock, soil fertility was the variable with higher independent contribution, followed by past-management intensity and forest cover. Patch area, soil texture, and silviculture cover were not the most important variables in any model.

4. Discussion

Our study indicates how multiple drivers influence the above-ground carbon stock and diversity after long-term land use history in human-modified Atlantic Forest landscape. We found a limited effect of soil properties in the evaluated parameters: soil fertility negatively influenced the AGC, but soil properties did not influence the diversity parameters. It is a counterintuitive result, considering that soil properties are determinant for tree diversity and carbon stock (Rodrigues et al., 2018). In addition, generally the more fertile soil, the higher the growth of plants and thus the larger carbon stock (Rodrigues et al., 2019). On the other hand, as expected, we found a negative effect of past-management intensity, isolation and source distance on tree species diversity and carbon stock. These factors probably favor pioneer species, which are more tolerant to environmental changes, little dependent on animal dispersal, and low AGC capacity (Pérez-Cárdenas et al., 2021; Villa et al., 2018). Thus, we found that past-management intensity and landscape configuration is more important than soil properties in

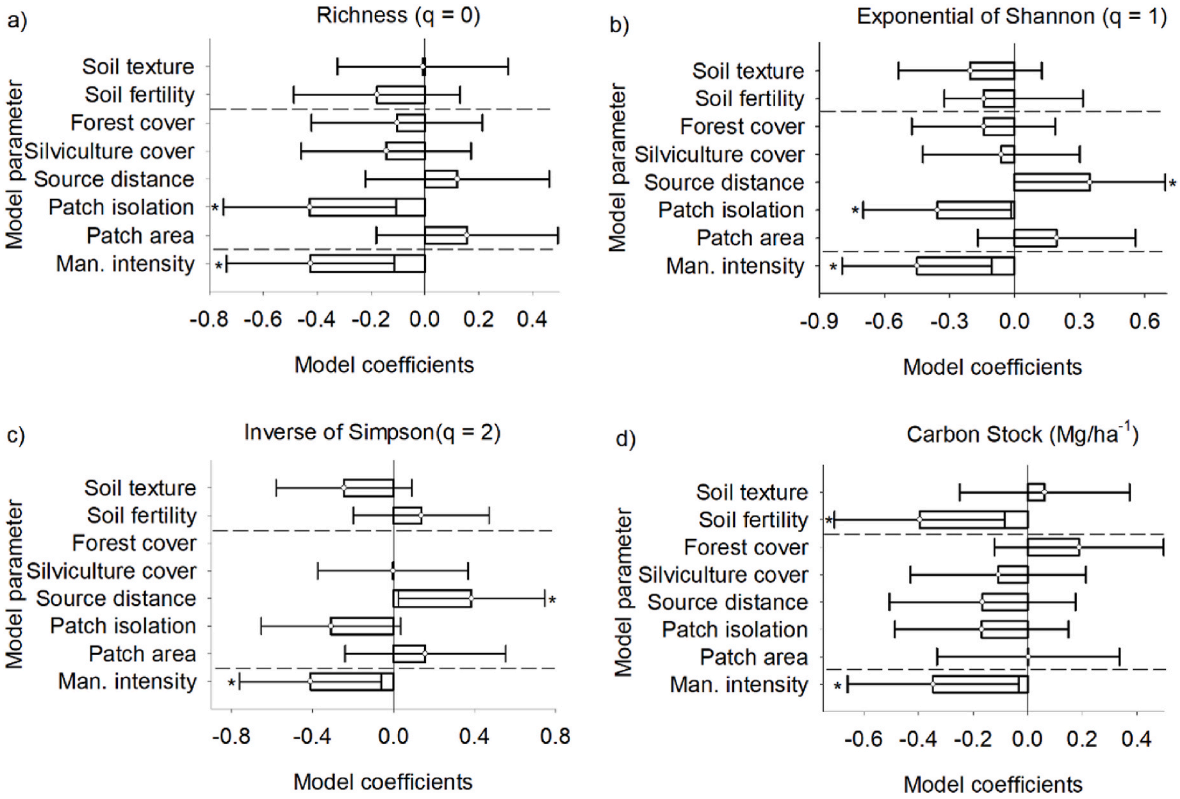

Fig. 2. Multiple drivers influence species richness (q = 0), exponential Shannon diversity (q = 1), inverse of Simpson diversity (q = 2), and above-ground carbon stock considering models with values of ΔAICc ≤5. The position of the bars represents positive or negative effect and error bars represent the (±) adjusted standard errors obtained after average models analysis. If the error bar is crossing the line of zero the variable is not significant. The significant influences are shown by (*).

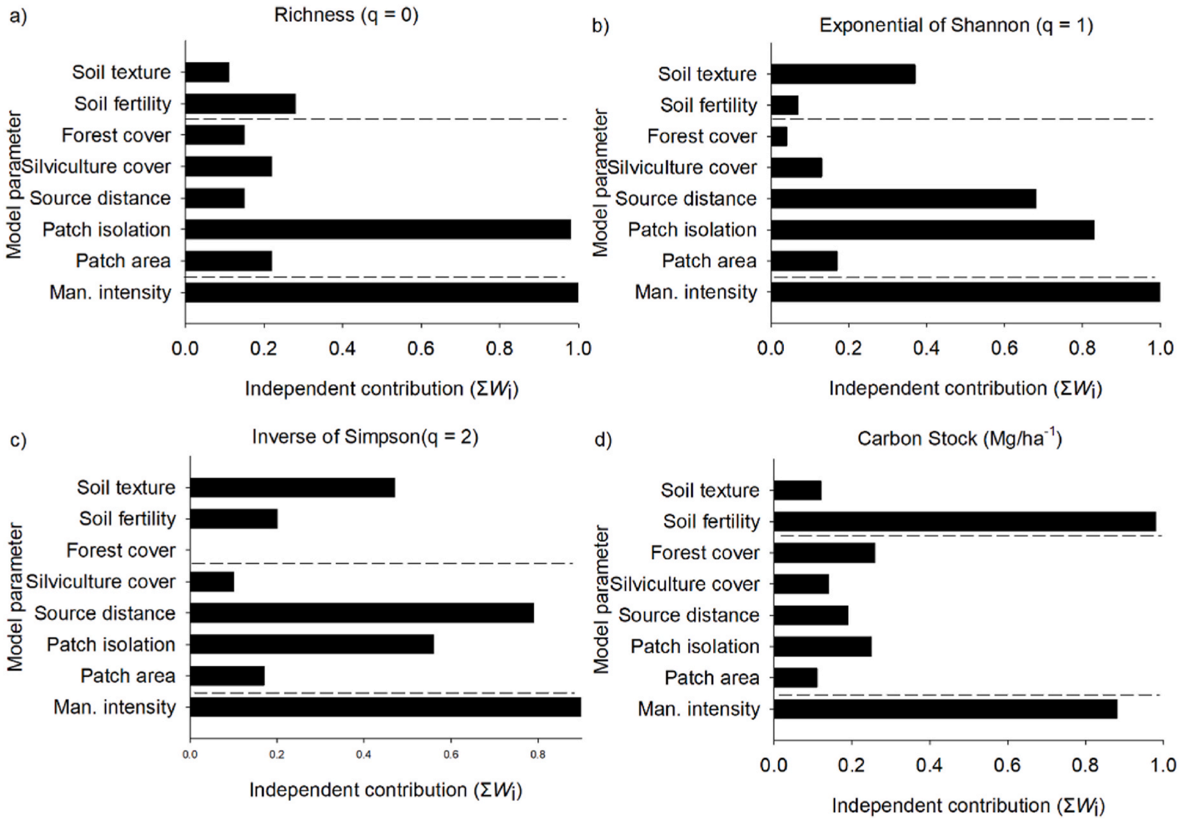

Fig. 3. Sum of independent contribution of each environmental variable on species richness (q = 0), exponential Shannon diversity (q = 1), inverse of Simpson diversity (q = 2), and above-ground carbon stock considering models with values of ΔAICc ≤5.

Atlantic Forest succession. Our results corroborate with results found in other forests (Jakovac et al., 2015; Pérez-Cárdenas et al., 2020) and indicate priority areas for passive restoration in the Atlantic Forest: those with lower intensity of past-management and with lower isolation and source distance.

4.1. Plot driver effects on tree species diversity and AGC

In the literature, contrary to our results, soil properties are important predictors that explain tree species diversity and carbon stock variation in the most ecosystems including the Atlantic Forest (Cantidio and Souza, 2019; Neri et al., 2013; Punchi-Manage et al., 2013; Rodrigues et al., 2018). Generally, the less soil acidity (i.e. the higher pH), the higher the concentration of nutrients, the greater the fertility, and thus the greater the diversity and AGC (Gastauer and Meira-Neto, 2014). In this study, the soil fertility axis value is positively correlated with pH, Mg^{2+}, Ca^{2+}, K, P, and negatively correlated with Fe and Al^{3+} concentrations, confirming soil fertility patterns. However, soil properties, specifically soil fertility, influenced only AGC in our study in a negative way: we found lower carbon stock in areas with higher nutrients concentrations. This result was also found by another study in the Amazon domain and can be explained by the high level of potassium in the soil, responsible for the increasing of exchanging cations concentrations and for selection of species with lower wood density, consequently with lower amounts of carbon stock (Quesada et al., 2012). The limited effect of soil properties on tree species diversity regeneration was also found for Amazon domain, indicating more importance of past-management intensity and landscape configurations after long-term land use (Jakovac et al., 2015).

The results show that soil fertility negatively influenced aboveground carbon stock. However, we observed a weak relationship of soil fertility with above-ground carbon stock in the tested model compared to the non-significant positive direct effects of soil texture (Ali et al., 2019a). Thus, we presume that the relative importance of other factors that negatively affect AGC could override the effects of soil properties, such as a weak soil effect. Soil nutrients determine resource availability (Paoli et al., 2005), whereas soil textural properties determine the water availability for plant growth and survival (Ali et al., 2019b; Toledo et al., 2012). Furthermore, soil nutrients may influence aboveground biomass indirectly by resulting from interspecific competition for available resource use in natural forests (Peña-Claros et al., 2012).

The disturbances caused by the management practices (e.g., soil preparation before planting and harvesting after crop growth) cause changes in soil properties, in its seed bank, and thus in the resilience of ecosystems (de Avila et al., 2018; Jakovac et al., 2016; Lawrence et al., 2007; Randriamalala et al., 2015). In our study, the past-management intensity did not affect soil properties (there was no significant correlation between soil acidity or soil texture with past-management intensity) but affected tree species diversity and carbon stock. This is because disturbances generate drastic changes in the environment favoring pioneer species, which survive under various environmental conditions, with faster life cycles, and lower carbon stocks (Tabarelli et al., 2010b; Villa et al., 2018). The successive planting and cutting cycles more often expose the soil seed bank to high solar irradiation and temperatures, making it difficult for species sensitive to these factors to establish (Holp, 1999), the so-called shade-tolerant species. The decrease of shade-tolerant species can explain loss of species richness and AGC, because they are the main responsible for AGC in old-growth forests (Bello et al., 2015; Stephenson et al., 2014) and for increasing AGC during secondary succession (Coelho et al., 2022). These favoring of pioneer species may also explain the decrease in exponential Shannon and inverse of Simpson, caused by the increase of dominance of some species.

4.2. Patch and landscape driver effects on tree species diversity and AGC

The isolation of regenerating areas can be a limiting factor for the tree species recolonization. The distance of forest fragments can difficult the arrival of seeds in regenerating areas (Arroyo-Rodríguez et al., 2017; Ewers and Didham, 2006). Seeds dispersed by wind also have their dispersal range limited by seed shape and mass: seeds of larger masses and less aerodynamics reach shorter distances (Collevatti et al., 2010; Cote et al., 2017). In addition, this depends on the survival home range of a seed dispersing animal population: smaller species typically have a smaller home range and move for short distances (Jetz et al., 2004; Pardini, 2004). The movement of some species can be even more difficult because inhospitable environments (e.g., pastures) (Antongiovanni and Metzger, 2005; Zambrano et al., 2019). Thus, isolation decreases the recolonization chance of some species affecting species richness and Shannon diversity in areas during regeneration.

Our results showed that the increased distance of the source patch increased the exponential Shannon and inverse of Simpson diversity indexes. This means that the increase in the source distance generates a decrease in rare species and species dominance. The source patches are important in fragmented landscapes, because they have larger sizes (considered in this work fragments with more than 500 ha), and capable of housing greater diversity and populations of plants and dispersing animals (Fahrig, 2003, 2007). Thus, these fragments are sources of propagules for the maintenance of diversity in smaller fragments where there is a decrease in populations size and species extinctions (Bello et al., 2015; Ewers and Didham, 2006; Magnago et al., 2015; Pardini et al., 2010), as well as for areas in regeneration. This can be explained because rare species are generally more abundant in larger fragments because they are more sensitive to variations in environmental conditions (Gámez-Virués et al., 2015; Magnago et al., 2015; Solar et al., 2015). For example, some shade-tolerant species may not survive or germinate in environments with high solar irradiations, common conditions in smaller fragments that have most of the habitat under edge influences, or areas in early regeneration stages (Magnago et al., 2015; Paula et al., 2011; Villa et al., 2018). Thus, the farther from large patches (source distance), the lower the chance of recolonization by rare species in small patches or areas under regeneration, which can explain de positive effect in exponential Shannon diversity and inverse of Simpson diversity.

We expected that the patch area, as well as the composition of the landscape, would influence regeneration after the long-term eucalyptus planting. Matos et al. (2020) found a positive effect of patch area on tree species diversity and AGC recovery. Similarly, Pérez-Cárdenas et al. (2021) and Jakovac et al. (2015) found greater diversity in areas with greater forest cover and lower AGC in areas with higher pasture cover, respectively. The higher natural habitat amount in the landscape, greater connectivity between the patches and the capacity to conserve populations in the landscape, maintaining seed dispersal patterns (Fahrig, 2013; Tscharntke et al., 2012). We also expected positive effects of silviculture cover, since eucalyptus is a matrix more similar to tropical forests and allows fauna movement between plantations, increasing connectivity between forest fragments (Barlow et al., 2007; Brancalion et al., 2019; Carrilho et al., 2017). However, our data showed that these factors did not affect and had little importance in tree species diversity and carbon stock in regenerating areas after long-term eucalyptus planting.

4.3. Implication on passive restoration priority areas

There is a great demand for ecosystems restoration in the world and in Brazil, either for carbon emission reduction targets or even environmental legislation of the countries (Soares-filho et al., 2014; Strassburg et al., 2020; Uriarte and Chazdon, 2016). Considering the intensive land use for different activities in the Atlantic Forest and its high degree of fragmentation, part of the priority areas and available areas for restoration in Brazil is in this biome (Nazareno et al., 2012; Scarano and Ceotto, 2015). In this sense, our study provides theoretical knowledge for the choice of areas with higher potential to recover tree species diversity and AGC, mainly for areas previously used for a long time for eucalyptus plantation. It is known that these areas regenerate naturally, but we indicate that areas with lower past-management intensity and less isolated from other forest patches, have greater capacity to recover tree species diversity and carbon stock. Thus, these areas reduce the costs of forest restoration, reducing the need for human interventions.

Authors' contributions

AJPC, JAAMN, and FARM conceived the ideas and designed methodology; AJPC and RPA collected the data; AJPC, FARM, PMV, GH, VP, RPA, and JAAMN analyzed the data; AJPC, FARM and JAAMN led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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 data

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References

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

Ali, A., Lin, S.L., He, J.K., Kong, F.M., Yu, J.H., Jiang, H.S., 2019b. Climatic water availability is the main limiting factor of biotic attributes across large-scale elevational gradients in tropical forests. Sci. Total Environ. 647, 1211–1221. https://doi.org/10.1016/j.scitotenv.2018.08.072.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L., Sparovek, G., 2013. Koppen's climate classification map for Brazil. Meteorol. Zeitschrift 22, 711–728. https://doi.org/10.1127/0941-2948/2013/0507.

Antongiovanni, M., Metzger, J.P., 2005. Influence of matrix habitats on the occurrence of insectivorous bird species in Amazonian forest fragments. Biol. Conserv. 122, 441–451. https://doi.org/10.1016/j.biocon.2004.09.005.

Apg, I.V., 2016. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. Bot. J. Linn. Soc. 181, 1–20.

Arroyo-Rodríguez, V., Melo, F.P.L., Martínez-Ramos, M., Bongers, F., Chazdon, R.L., Meave, J.A., Norden, N., Santos, B.A., Leal, I.R., Tabarelli, M., 2017. Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. Biol. Rev. 92, 326–340. https://doi.org/10.1111/brv.12231.

Barlow, J., Gardner, T.A., Araujo, I.S., Ávila-Pires, T.C., Bonaldo, A.B., Costa, J.E., Esposito, M.C., Ferreira, L.V., Hawes, J., Hernandez, M.I.M., Hoogmoed, M.S., Leite, R.N., Lo-Man-Hung, N.F., Malcolm, J.R., Martins, M.B., Mestre, L.A.M., Miranda-Santos, R., Nunes-Gutjahr, A.L., Overal, W.L., Parry, L., Peters, S.L., Ribeiro, M.A., Da Silva, M.N.F., Da Silva Motta, C., Peres, C.A., 2007. Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proc. Natl. Acad. Sci. U. S. A 104, 18555–18560. https://doi.org/10.1073/pnas.0703333104.

Barton, K., 2017. 'MuMIn': multi-model inference. R package version 1.40.0. https://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf. (Accessed 15 June 2020) (date last accessed).

Bello, C., Galetti, M., Pizo, M.A., Magnago, L.F.S., Rocha, M.F., Lima, R.A.F., Peres, C.A., Ovaskainen, O., Jordano, P., 2015. Defaunation affects carbon storage in tropical forests. Sci. Adv. 1, 1–11. https://doi.org/10.1126/sciadv.1501105.

Bertacchi, M.I.F., Amazonas, N.T., Brancalion, P.H.S., Brondani, G.E., de Oliveira, A.C.S., de Pascoa, M.A.R., Rodrigues, R.R., 2016. Establishment of tree seedlings in the understory of restoration plantations: natural regeneration and enrichment plantings. Restor. Ecol. 24, 100–108. https://doi.org/10.1111/rec.12290.

Bivand, R., Piras, G., 2015. Comparing implementations of estimation methods for spatial econometrics. J. Stat. Software 63, 1–36. https://doi.org/10.18637/jss.v063.i18.

Brancalion, P.H.S., Campoe, O., Mendes, J.C.T., Noel, C., Moreira, G.G., van Melis, J., Stape, J.L., Guillemot, J., 2019. Intensive silviculture enhances biomass accumulation and tree diversity recovery in tropical forest restoration. Ecol. Appl. 29, 1–12. https://doi.org/10.1002/eap.1847.

Brancalion, P.H.S., Amazonas, N.T., Chazdon, R.L., van Melis, J., Rodrigues, R.R., Silva, C.C., Sorrini, T.B., Holl, K.D., 2020. Exotic eucalypts: from demonized trees to allies of tropical forest restoration? J. Appl. Ecol. 57, 55–66. https://doi.org/10.1111/1365-2664.13513.

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

Burnham, K.P., Anderson, D.R., Huyvaert, K.P., 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behav. Ecol. Sociobiol. 65, 23–35. https://doi.org/10.1007/s00265-010-1029-6.

Cantidio, L.S., Souza, A.F., 2019. Aridity, soil and biome stability influence plant ecoregions in the Atlantic Forest, a biodiversity hotspot in South America. Ecography 42. https://doi.org/10.1111/ecog.04564, 1887–1898.

Carrilho, M., Teixeira, D., Santos-Reis, M., Rosalino, L.M., 2017. Small mammal abundance in Mediterranean Eucalyptus plantations: how shrub cover can really make a difference. For. Ecol. Manage. 391, 256–263. https://doi.org/10.1016/j.foreco.2017.01.032.

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

Chazdon, R.L., 2014. Second Growth: the Promise of Tropical Forest Regeneration in an Age of Deforestation. University of Chicago Press.

Chazdon, R.L., Broadbent, E.N., Rozendaal, D.M.A., Bongers, F., María, A., Zambrano, A., Aide, T.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Craven, D., Almeida-cortez, J.S., Cabral, G.A.L., Jong, B. De, Denslow, J.S., Dent, D.H., Dewalt, S.J., Dupuy, J.M., Durán, S.M., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Lohbeck, M., Muscarella, R., Nunes, Y.R.F., Ochoa-gaona, S., Orihuela-belmonte, E., Peña-claros, M., Ruíz, J., Saldarriaga, J.G., Sanchez-azofeifa, A., Schwartz, N.B., Steininger, M.K., 2016. Carbon Sequestration Potential of Second-Growth Forest Regeneration in the Latin American Tropics.

Coelho, A.J.P., Magnago, L.F.S., Matos, F.A.R., Mota, N.M., Diniz, É.S., Meira-Neto, J.A. A., 2020. Effects of anthropogenic disturbances on biodiversity and biomass stock of Cerrado, the Brazilian savanna. Biodivers. Conserv., 0123456789 https://doi.org/10.1007/s10531-020-02013-6.

Coelho, A.J.P., Villa, P.M., Matos, F.A.R., Heringer, G., Bueno, M.L., de Paula Almado, R., Meira-Neto, J.A.A., 2022. Atlantic Forest recovery after long-term eucalyptus plantations: the role of zoochoric and shade-tolerant tree species on carbon stock. For. Ecol. Manage. 503, 119789 https://doi.org/10.1016/j.foreco.2021.119789.

Collevatti, R.G., Lima, J.S., Soares, T.N., Telles, M.P. de C., 2010. Spatial genetic structure and life history traits in cerrado tree species: inferences for conservation. Nat. Conserv. 8, 54–59. https://doi.org/10.4322/natcon.00801008.

Cote, J., Bestion, E., Jacob, S., Travis, J., Legrand, D., Baguette, M., 2017. Evolution of Dispersal Strategies and Dispersal Syndromes in Fragmented Landscapes, pp. 56–73. https://doi.org/10.1111/ecog.02538.

de Avila, A.L., van der Sande, M.T., Dormann, C.F., Peña-Claros, M., Poorter, L., Mazzei, L., Ruschel, A.R., Silva, J.N.M., de Carvalho, J.O.P., Bauhus, J., 2018. Disturbance intensity is a stronger driver of biomass recovery than remaining tree-community attributes in a managed Amazonian forest. J. Appl. Ecol. 55, 1647–1657. https://doi.org/10.1111/1365-2664.13134.

Dinno, A., 2018. Paran: Horn's test of principal components/factors. http://alexisdinno.com/Software/files/PA_for_PCA_vs_FA.pdf.

Ewers, R., Didham, R., 2006. Confounding factors in the detection of species responses to habitat fragmentation. Biol. Rev. Camb. Phil. Soc. 81, 117–142. https://doi.org/10.1017/s1464793105006949.

Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. Annu. Rev. Ecol. Environ. Syst. 34, 487–515. https://doi.org/10.1146/132419.

Fahrig, L., 2007. Non-optimal animal movement in human-altered landscapes. Funct. Ecol. 21, 1003–1015. https://doi.org/10.1111/j.1365-2435.2007.01326.x.

Fahrig, L., 2013. Rethinking patch size and isolation effects: the habitat amount hypothesis. J. Biogeogr. 40, 1649–1663. https://doi.org/10.1111/jbi.12130.

Finegan, B., 1996. Pattern and Process in Neotropical Secondary Rain Forests: the First 100 Years of Succession, pp. 793–796.

Gámez-Virués, S., Perović, D.J., Gossner, M.M., Börschig, C., Blüthgen, N., de Jong, H., Simons, N.K., Klein, A.-M., Krauss, J., Maier, G., Scherber, C., Steckel, J., Rothenwöhrer, C., Steffan-Dewenter, I., Weiner, C.N., Weisser, W., Werner, M., Tscharntke, T., Westphal, C., 2015. Landscape simplification filters species traits and drives biotic homogenization. Nat. Commun. 6, 8568. https://doi.org/10.1038/ncomms9568.

Gastauer, M., Meira-Neto, J.A.A., 2014. Interactions, environmental sorting and chance: phylostructure of a tropical forest assembly. Folia Geobot. 49, 443–459. https://doi.org/10.1007/s12224-013-9181-1.

Gonçalvez, J.L. de M., Alvares, C.A., Higa, A.R., Silva, L.D., Alfenas, A.C., Stahl, J., Ferraz, S.F. de B., Lima, W., Brancalion, P., Hubner, A., Bouillet, J.D., Laclau, J., Nouvellon, Y., Epron, D., 2013. Forest Ecology and Management Integrating genetic and silvicultural strategies to minimize abiotic and biotic constraints in Brazilian eucalypt plantations. For. Ecol. Manage. 301, 6–27. https://doi.org/10.1016/j.foreco.2012.12.030.

Gotelli, N.J., Chao, A., 2013. Measuring and estimating species richness, species diversity, and biotic similarity from sampling data. In: Encyclopedia of Biodiversity, second ed. Elsevier Ltd. https://doi.org/10.1016/B978-0-12-384719-5.00424-X.

Guariguata, M.R., Ostertag, R., 2001. Neotropical secondary forest succession : changes in structural and functional characteristics. For. Ecol. Manage. 148, 185–206. https://doi.org/10.1016/S0378-1127(00)00535-1.

Hansen, M.C., Potapov, P.V., Moore, R., Hancher, M., Turubanova, S.A., Tyukavina, A., 2013. High-Resolution Global Maps of 134, 850–854.

Hill, M.O., 1973. Diversity and evenness: a unifying notation and its consequences. Ecology 54, 427–432. https://doi.org/10.2307/1934352.

Holp, K.D., 1999. Factors limiting tropical rain forest regeneration in abandoned pasture : seed rain , seed germination , microclimate , and soil. Biotropica 31, 229–242.

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: iNterpolation and EXTrapolation for species diversity. R package version 2.0.12. https://cran.r-project.org/web/packages/iNEXT/iNEXT.pdfHusson.

Ivanova, A., Zia, A., Ahmad, P., Bastos-Lima, M., 2020. Climate mitigation policies and actions: access and allocation issues. Int. Environ. Agreements Polit. Law Econ. 20, 287–301. https://doi.org/10.1007/s10784-020-09483-7.

Jakovac, C.C., Peña-Claros, M., Kuyper, T.W., Bongers, F., 2015. Loss of secondary-forest resilience by land-use intensification in the Amazon. J. Ecol. 103, 67–77. https://doi.org/10.1111/1365-2745.12298.

Jakovac, C.C., Bongers, F., Kuyper, T.W., Mesquita, R.C.G., Peña-Claros, M., 2016. Land use as a filter for species composition in Amazonian secondary forests. J. Veg. Sci. 27, 1104–1116. https://doi.org/10.1111/jvs.12457.

Jakovac, C.C., Dutrieux, L.P., Siti, L., Peña-Claros, M., Bongers, F., 2017. Spatial and temporal dynamics of shifting cultivation in the middle-Amazonas river: expansion and intensification. PLoS One 12, 1–15. https://doi.org/10.1371/journal.pone.0181092.

Jetz, W., Carbone, C., Fulford, J., Brown, J.H., 2004. The scaling of animal space use. Science (80- 306, 266–268. https://doi.org/10.1126/science.1102138.

Jost, L., 2006. Entropy and diversity. Oikos 113, 363–375. https://doi.org/10.1111/j.2006.0030-1299.14714.x.

Kingwell-Banham, E., Fuller, D.Q., 2012. Shifting cultivators in South Asia: expansion, marginalisation and specialisation over the long term. Quat. Int. 249, 84–95. https://doi.org/10.1016/j.quaint.2011.05.025.

Klemick, H., 2011. Shifting cultivation , forest fallow , and externalities in ecosystem services : evidence from the Eastern Amazon. J. Environ. Econ. Manag. 61, 95–106. https://doi.org/10.1016/j.jeem.2010.07.003.

Lawrence, D., D'Odorico, P., Diekmann, L., DeLonge, M., Das, R., Eaton, J., 2007. Ecological feedbacks following deforestation create the potential for a catastrophic ecosystem shift in tropical dry forest. Proc. Natl. Acad. Sci. U. S. A 104, 20696–20701. https://doi.org/10.1073/pnas.0705005104.

Lê, S., Josse, J., Husson, F., 2008. FactoMineR: An R Package for Multivariate Analysis. J. Stat. Software 25, 1–18. https://doi.org/10.18637/jss.v025.i01.

Lopes, W. de P., Silva, A.F. da, Souza, A.L., de Meira Neto, J.A.A., 2002. Estrutura fitossociólogа de um trecho de vegetação arbórea no Parque Estadual do Rio Doce - Minas Gerais , Brasil. Acta Bot. Brasilica 16, 443–456. https://doi.org/10.1590/s0102-33062002000400007.

Magnago, L.F.S., Edwards, D.P., Edwards, F.A., Magrach, A., Martins, S.V., Laurance, W.F., 2014. Functional attributes change but functional richness is unchanged after fragmentation of Brazilian Atlantic forests. J. Ecol. 102, 475–485. https://doi.org/10.1111/1365-2745.12206.

Magnago, Luiz Fernando S., Magrach, A., Laurance, W.F., Martins, S.V., Meira-Neto, J.A.A., Simonelli, M., Edwards, D.P., 2015a. Would protecting tropical forest fragments provide carbon and biodiversity cobenefits under REDD+? Global Change Biol. 21, 3455–3468. https://doi.org/10.1111/gcb.12937.

Magnago, Luiz Fernando Silva, Rocha, M.F., Meyer, L., Martins, S.V., Meira-Neto, J.A.A., 2015b. Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. Biodivers. Conserv. 24, 2305–2318. https://doi.org/10.1007/s10531-015-0961-1.

Malhi, Y., Baker, T.R., Phillips, O.L., Almeida, S., Alvarez, E., Arroyo, L., Chave, J., Czimczik, C.I., Di Fiore, A., Higuchi, N., Killeen, T.J., Laurance, S.G., Laurance, W.F., Lewis, S.L., Montoya, L.M.M., Monteagudo, A., Neill, D.A., Vargas, P.N., Patino, S., Pitman, N.C.A., Quesada, C.A., Salomao, R., Silva, J.N.M., Lezama, A.T., Martínez, R.V., Terborgh, J., Vinceti, B., Lloyd, J., 2004. The above-ground coarse wood productivity of 104 Neotropical forest plots. Global Change Biol. 10, 563–591. https://doi.org/10.1111/j.1529-8817.2003.00778.x.

Matos, F.A.R., Magnago, L.F.S., Gastauer, M., Carreiras, J.M.B., Simonelli, M., Meira-Neto, J.A.A., Edwards, D.P., 2016. Effects of landscape configuration and composition on phylogenetic diversity of trees in a highly fragmented tropical forest. J. Ecol. https://doi.org/10.1111/1365-2745.12661.

Matos, F.A.R., Magnago, L.F.S., Aquila Chan Miranda, C., de Menezes, L.F.T., Gastauer, M., Safar, N.V.H., Schaefer, C.E.G.R., da Silva, M.P., Simonelli, M., Edwards, F.A., Martins, S.V., Meira-Neto, J.A.A., Edwards, D.P., 2020. Secondary forest fragments offer important carbon and biodiversity cobenefits. Global Change Biol. 26, 509–522. https://doi.org/10.1111/gcb.14824.

McGarial, K., Cushman, S.A., Ene, E., 2012. FRAGSTATS v4: spatial patern analysis program for categorical and continuous maps. Amherst, MA, USA. http://www.umass.edu/landeco/research/fragstats/fragstats.html.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fronseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853–858.

Nazareno, A.G., Feres, J.M., de Carvalho, D., Sebbenn, A.M., Lovejoy, T.E., Laurance, W.F., 2012. Serious new threat to Brazilian forests. Conserv. Biol. 26, 5–6. https://doi.org/10.1111/j.1523-1739.2011.01798.x.

Neri, A.V., Schaefer, C.E.G.R., Souza, A.L., Ferreira-Junior, W.G., Meira-Neto, J.A.A., 2013. Pedology and plant physiognomies in the cerrado, Brazil. An. Acad. Bras. Cienc. 85, 87–102. https://doi.org/10.1590/S0001-37652013000100007.

Oberleitner, F., Egger, C., Oberdorfer, S., Dullinger, S., Wanek, W., Hietz, P., 2021. Recovery of aboveground biomass, species richness and composition in tropical secondary forests in SW Costa Rica. For. Ecol. Manage. 479, 118580 https://doi.org/10.1016/j.foreco.2020.118580.

Oliveira-Junior, N.D. de, Heringer, G., Bueno, M.L., Pontara, V., Meira-Neto, J.A.A., 2020. Prioritizing landscape connectivity of a tropical forest biodiversity hotspot in global change scenario. For. Ecol. Manage. 472 https://doi.org/10.1016/j.foreco.2020.118247.

Paoli, G.D., Curran, L.M., Zak, D.R., 2005. Phosphorus efficiency of Bornean rain forest productivity: evidence against the unimodal efficiency hypothesis. Ecology 86, 1548–1561. https://doi.org/10.1890/04-1126.

Pardini, R., 2004. Effects of forest fragmentation on small mammals. Biodivers. Conserv. 13, 2567–2586.

Pardini, R., de Bueno, A.A., Gardner, T.A., Prado, P.I., Metzger, J.P., 2010. Beyond the fragmentation threshold hypothesis: regime shifts in biodiversity across fragmented landscapes. PLoS One 5. https://doi.org/10.1371/journal.pone.0013666.

Paula, M.D. de, Costa, C.P.A., Tabarelli, M., 2011. Carbon storage in a fragmented landscape of Atlantic forest: the role played by edge-affected habitats and emergent trees. Trop. Conserv. Sci. 4, 349–358. https://doi.org/10.1177/194008291100400310.

Peña-Claros, M., Poorter, L., Alarcón, A., Blate, G., Choque, U., Fredericksen, T.S., Justiniano, M.J., Leaño, C., Licona, J.C., Pariona, W., Putz, F.E., Quevedo, L., Toledo, M., 2012. Soil effects on forest structure and diversity in a moist and a dry tropical forest. Biotropica 44, 276–283. https://doi.org/10.1111/j.1744-7429.2011.00813.x.

Pérez-Cárdenas, N., Mora, F., Arreola, F., Arrollo-Rodríguez, V., Balvanera, P., Navarrete, A., Flores-Casas, A.R., Ortega-Huerta, M.A., 2020. Effects of landscape composition and land use intensity on secondary succession in a Mexican tropical dry forest. For. Ecol. Manage.

Pérez-Cárdenas, N., Mora, F., Arreola-Villa, F., Arroyo-Rodríguez, V., Balvanera, P., Flores-Casas, R., Navarrete-Pacheco, A., Ortega-Huerta, M.A., 2021. Effects of landscape composition and site land-use intensity on secondary succession in a tropical dry forest. For. Ecol. Manage. 482, 118818 https://doi.org/10.1016/j.foreco.2020.118818.

Punchi-Manage, R., Getzin, S., Wiegand, T., Kanagaraj, R., Savitri Gunatilleke, C.V., Nimal Gunatilleke, I.A.U., Wiegand, K., Huth, A., 2013. Effects of topography on structuring local species assemblages in a Sri Lankan mixed dipterocarp forest. J. Ecol. 101, 149–160. https://doi.org/10.1111/1365-2745.12017.

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

Randriamalala, J.R., Hervé, D., Letourmy, P., Carrière, S.M., 2015. Effects of slash-and-burn practices on soil seed banks in secondary forest successions in Madagascar. Agric. Ecosyst. Environ. 199, 312–319. https://doi.org/10.1016/j.agee.2014.09.010.

Réjou-Méchain, M., Tanguy, A., Piponiot, C., Chave, J., Hérault, B., 2017. Biomass: an R Package for estimating above-ground biomass and its uncertainty in tropical forests. Methods Ecol. Evol. 8, 1163–1167. https://doi.org/10.1111/2041-210X.12753.

Rodrigues, P.M.S., Schaefer, C.E.G.R., De Oliveira Silva, J., Ferreira, W.G., Dos Santos, R.M., Neri, A.V., 2018. The influence of soil on vegetation structure and plant diversity in different tropical savannic and forest habitats. J. Plant Ecol. 11, 226–236. https://doi.org/10.1093/jpe/rtw135.

Rodrigues, A.C., Villa, P.M., Neri, A.V., 2019. Fine-scale topography shape richness, community composition, stem and biomass hyperdominant species in Brazilian Atlantic forest. Ecol. Indicat. 102, 208–217. https://doi.org/10.1016/j.ecolind.2019.02.033.

Rosa, M.R., Brancalion, P.H.S., Crouzeilles, R., Tambosi, L.R., Piffer, P.R., Lenti, F.E.B., Hirota, M., Santiami, E., Metzger, J.P., 2021. Hidden destruction of older forests threatens Brazil's Atlantic Forest and challenges restoration programs. Sci. Adv. 7, 1–9. https://doi.org/10.1126/sciadv.abc4547.

Rother, D.C., Liboni, A.P., Magnago, L.F.S., Chao, A., Chazdon, R.L., Rodrigues, R.R., 2019. Ecological restoration increases conservation of taxonomic and functional beta diversity of woody plants in a tropical fragmented landscape. For. Ecol. Manage. 451, 117538 https://doi.org/10.1016/j.foreco.2019.117538.

Rozendaal, D.M.A., Bongers, F., Aide, T.M., Alvarez-Dávila, E., Ascarrunz, N., Balvanera, P., Becknell, J.M., Bentos, T.V., Brancalion, P.H.S., Cabral, G.A.L., Calvo-Rodriguez, S., Chave, J., César, R.G., Chazdon, R.L., Condit, R., Dallinga, J.S., De Almeida-Cortez, J.S., De Jong, B., De Oliveira, A., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Dutrieux, L.P., Espírito-Santo, M.M., Fandino, M.C., Fernandes, G.W., Finegan, B., García, H., Gonzalez, N., Moser, V.G., Hall, J.S., Hernández-Stefanoni, J.L., Hubbell, S., Jakovac, C.C., Hernández, A.J., Junqueira, A.B., Kennard, D., Larpin, D., Letcher, S.G., Licona, J.C., Lebrija-Trejos, E., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P.E.S., Meave, J.A., Mesquita, R.C.G., Mora, F., Müller, S.C., Muñoz, R., De Oliveira Neto, S.N., Norden, N., Nunes, Y.R.F., Ochoa-Gaona, S., Ortiz-Malavassi, E., Ostertag, R., Peña-Claros, M., Pérez-García, E.A., Piotto, D., Powers, J.S., Aguilar-Cano, J., Rodriguez-Buritica, S., Rodríguez-Velázquez, J., Romero-Romero, M.A., Ruíz, J., Sanchez-Azofeifa, A., De Almeida, A.S., Silver, W.L., Schwartz, N.B., Thomas, W.W., Toledo, M., Uriarte, M., De Sá Sampaio, E.V., Van Breugel, M., Van Der Wal, H., Martins, S.V., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Villa, P., Williamson, G.B., Zanini, K.J., Zimmerman, J., Poorter, L., 2019. Biodiversity recovery of Neotropical secondary forests. Sci. Adv. 5 https://doi.org/10.1126/sciadv.aau3114.

Safar, N.V.H., Magnago, L.F.S., Schaefer, C.E.G.R., 2020. Resilience of lowland Atlantic forests in a highly fragmented landscape: insights on the temporal scale of landscape restoration. For. Ecol. Manage. 470–471, 118183 https://doi.org/10.1016/j.foreco.2020.118183.

Santoss dos, H.G., Jacomine, P.K.T., Anjos dos, L.H.C., Oliveiras de, V.A., Lumbreras, J.F., Coelho, M.R., Almeidas de, J.A., Araújo-Filhos de, J.C., Oliveiras de, J.B., Cunha, T.J.F., 2018. Sistema brasileiro de classificação de solos, vol. 5 (ed. rev. ed, Embrapa Solos).

Scarano, F.R., Ceotto, P., 2015. Brazilian Atlantic forest: impact, vulnerability, and adaptation to climate change. Biodivers. Conserv. 24, 2319–2331. https://doi.org/10.1007/s10531-015-0972-y.

Sloan, S., Goosem, M., Laurance, S.G., 2015. Tropical forest regeneration following land abandonment is driven by primary rainforest distribution in an old pastoral region. Landsc. Ecol. https://doi.org/10.1007/s10980-015-0267-4.

Soares-filho, B., Rajão, R., Macedo, M., Carneiro, A., Costa, W., Coe, M., Rodrigues, H., Alencar, A., 2014. Cracking Brazil ' S Forest Code, pp. 363–364.

Solar, R., Barlow, J., Ferreira, J., Berenguer, E., Lees, A.C., Thomson, J.R., Louzada, J., Maus, M., Moura, N.G., Oliveira, V.H.F., Chaul, J.C.M., Schoereder, J.H., Vieira, I.C.G., Mac Nally, R., Gardner, T.A., 2015. How pervasive is biotic homogenization in human-modified tropical forest landscapes? Ecol. Lett. 18, 1108–1118. https://doi.org/10.1111/ele.12494.

Stephenson, N.L., Das, A.J., Condit, R., Russo, S.E., Baker, P.J., Beckman, N.G., Coomes, D.A., Lines, E.R., Morris, W.K., Rüger, N., Álvarez, E., Blundo, C., Bunyavejchewin, S., Chuyong, G., Davies, S.J., Duque, Á., Ewango, C.N., Flores, O., Franklin, J.F., Grau, H.R., Hao, Z., Harmon, M.E., Hubbell, S.P., Kenfack, D., Lin, Y., Makana, J.R., Malizia, A., Malizia, L.R., Pabst, R.J., Pongpattananurak, N., Su, S.H., Sun, I.F., Tan, S., Thomas, D., Van Mantgem, P.J., Wang, X., Wiser, S.K., Zavala, M.A., 2014. Rate of tree carbon accumulation increases continuously with tree size. Nature 507, 90–93. https://doi.org/10.1038/nature12914.

Strassburg, B.B.N., Iribarrem, A., Beyer, H.L., Cordeiro, C.L., Crouzeilles, R., Jakovac, C.C., Braga Junqueira, A., Lacerda, E., Latawiec, A.E., Balmford, A., Brooks, T.M., Butchart, S.H.M., Chazdon, R.L., Erb, K.H., Brancalion, P., Buchanan, G., Cooper, D., Díaz, S., Donald, P.F., Kapos, V., Leclère, D., Miles, L., Obersteiner, M., Plutzar, C., Carlos, C.A., Scarano, F.R., Visconti, P., 2020. Global priority areas for ecosystem restoration. Nature 586, 724–729. https://doi.org/10.1038/s41586-020-2784-9.

Styger, E., Rakotondramasy, H.M., Pfeffer, M.J., Fernandes, E.C.M., Bates, D.M., 2007. Influence of slash-and-burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. Agric. Ecosyst. Environ. 119, 257–269. https://doi.org/10.1016/j.agee.2006.07.012.

Tabarelli, M., Aguiar, A.V., Girão, L.C., Peres, C.A., Lopes, A.V., 2010a. Effects of pioneer tree species hyperabundance on forest fragments in Northeastern Brazil. Conserv. Biol. 24, 1654–1663. https://doi.org/10.1111/j.1523-1739.2010.01529.x.

Tabarelli, M., Aguiar, A.V., Girão, L.C., Peres, C.A., Lopes, A.V., 2010b. Effects of pioneer tree species hyperabundance on forest fragments in Northeastern Brazil. Conserv. Biol. 24, 1654–1663. https://doi.org/10.1111/j.1523-1739.2010.01529.x.

Toledo, M., Peña-Claros, M., Bongers, F., Alarcón, A., Balcázar, J., Chuviña, J., Leaño, C., Licona, J.C., Poorter, L., 2012. Distribution patterns of tropical woody species in response to climatic and edaphic gradients. J. Ecol. 100, 253–263. https://doi.org/10.1111/j.1365-2745.2011.01890.x.

Tscharntke, T., Tylianakis, J.M., Rand, T.A., Didham, R.K., Fahrig, L., Batáry, P., Bengtsson, J., Clough, Y., Crist, T.O., Dormann, C.F., Ewers, R.M., Fründ, J., Holt, R.D., Holzschuh, A., Klein, A.M., Kleijn, D., Kremen, C., Landis, D.A., Laurance, W., Lindenmayer, D., Scherber, C., Sodhi, N., Steffan-Dewenter, I., Thies, C., van der Putten, W.H., Westphal, C., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol. Rev. 87, 661–685. https://doi.org/10.1111/j.1469-185X.2011.00216.x.

Uriarte, M., Chazdon, R.L., 2016. Incorporating natural regeneration in forest landscape restoration in tropical regions: synthesis and key research gaps. Biotropica 48, 915–924. https://doi.org/10.1111/btp.12411.

Veloso, H.P., Rangel Filho, A.L.R., Lima, J.C.A., 1991. Classificação da Vegetação Brasileira Adaptada a um Sistema Universal, Rio de Janeiro, IBGE, Departamento de Recursos Naturais e Estudos Ambientais https://doi.org/ISBN 85-240-0384-7.

Villa, P.M., Venâncio, S., Nolasco, S., Neto, D.O., Cristina, A., Guerreiro, L., Delgado, L., Mota, N., Gastauer, M., 2018. Intensification of shifting cultivation reduces forest resilience in the northern Amazon. For. Ecol. Manage. 430, 312–320. https://doi.org/10.1016/j.foreco.2018.08.014.

Villa, P.M., Ali, A., Martins, S.V., Neto, S.N. de O., Rodrigues, A.C., Teshome, M., Alvim Carvalho, F., Heringer, G., Gastauer, M., 2020a. Stand structural attributes and functional trait composition overrule the effects of functional divergence on aboveground biomass during Amazon forest succession. For. Ecol. Manage. 477, 118481 https://doi.org/10.1016/j.foreco.2020.118481.

Villa, P.M., Martins, S.V., de Oliveira Neto, S.N., Rodrigues, A.C., Hernández, E.P., Kim, D.G., 2020b. Policy forum: shifting cultivation and agroforestry in the Amazon: premises for REDD+. For. Pol. Econ 118. https://doi.org/10.1016/j.forpol.2020.102217.

Zambrano, J., Garzon-Lopez, C.X., Yeager, L., Fortunel, C., Cordeiro, N.J., Beckman, N.G., 2019. The effects of habitat loss and fragmentation on plant functional traits and functional diversity: what do we know so far? Oecologia. https://doi.org/10.1007/s00442-019-04505-x.

Zanne, A.E., Lopez-Gonzalez, G., Coomes, D.A., Ilic, J., Jansen, S., Lewis, S.L., Miller, R.B., Swenson, N.G., Wiemann, M.C., Chave, J., 2009. Data from: towards a Worldwide Wood Economics Spectrum. Dryad.

Zhang, D., Zhang, J., Yang, W., Wu, F., Huang, Y., 2014. Plant and soil seed bank diversity across a range of ages of Eucalyptus grandis plantations afforested on arable lands. Plant Soil 376, 307–325. https://doi.org/10.1007/s11104-013-1954-z.