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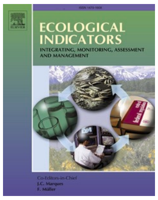

Original Articles

Functional richness mediates landscape and management effects on tree biomass and soil fertility during secondary forest succession

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ABSTRACT

Secondary forests can play a critical role in conserving plant biodiversity and sequestering carbon. However, intensive past management, fragmentation, and initial soil fertility can hinder forest recovery during secondary succession, especially in terms of tree species selection. In turn, tree species selection can negatively impact soil fertility recovery and may slow down the succession process, but the direct and indirect effects between these factors remain unclear. To assess the complex interactions among landscape, previous management, soil and vegetation, 27 secondary forests of varying ages, previously used for eucalyptus plantations, located in diverse landscape configurations within the Atlantic Forest biome, were examined. Key variables, such as planting frequency, cutting frequency, forest cover in the landscape, patch isolation between fragments, functional richness, tree aboveground biomass (AGB), soil sum of bases, soil organic matter, and soil phosphorus concentration were used to construct a structural equation model to evaluate the direct and indirect effects of landscape and previous management on forest development. Cutting frequency and patch isolation had a negative direct effect on functional richness. Additionally, a strong positive direct effect of functional diversity on aboveground biomass and soil sum of bases was found. Thus, cutting frequency and patch isolation had negative indirect effects on biomass and soil sum of bases (a proxy for soil fertility), mediated by functional richness. These findings underscore the significance of integrating plant functional diversity into restoration strategies to preserve ecosystem functioning and efficiently recover biodiversity, tree biomass, and soil fertility in secondary forests.

1. Introduction

Secondary forests are typically established after habitat conversion and are vital for biodiversity recovery and climate change mitigation due to their role as carbon sinks (Edwards et al., 2019; Gardner et al., 2009). However, secondary forests are often growing in areas with an intensive land use history and fragmented landscapes (Arroyo-Rodríguez et al., 2017). These factors can hinder biodiversity gains and carbon sequestration during forest succession (van Breugel et al., 2019), mainly due to management impact on local environments and the barriers imposed by the landscape on life migration (Coelho et al., 2022a; Villa et al., 2018). Together with the increase in biodiversity and biomass during forest succession, it is expected an increase in soil fertility and enhanced soil biological functions (Teixeira et al., 2020). Therefore, soil fertility indicators are increasingly recognized as key to monitoring the success of restoration strategies, although this is rarely done (Mendes et al., 2019). Despite the growing number of studies about the effects of secondary forest succession on ecosystem functioning (Matos et al., 2020; Teixeira et al., 2020; Van Der Sande et al., 2023), some complex ecological relationships remain unknown, such as the effects of previous management and landscape configuration on plant biomass, soil fertility, and thus, in ecosystem functioning. Understanding these gaps is important to improve conservation and restoration strategies, especially in highly diverse and threatened biomes, such as

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the Atlantic Forest (Colli-Silva et al., 2020; Guedes Pinto and Voivodic, 2021).

Previous land management practices can negatively impact tree species diversity and biomass of secondary forests worldwide, mainly because of microenvironment depletion (Veldkamp et al., 2020; Villa et al., 2020). The frequent cycles of planting and harvesting, for example, involve management practices such as soil revolving, weeding, or herbicide application, which can disrupt the microenvironmental conditions essential for maintaining soil fertility in forest ecosystems (Jakovac et al., 2017; Villa et al., 2018). In addition, intensive previous management can avoid the germination and establishment of species sensitive to light, high temperatures, and dry environments, resulting in a limited recovery of plant diversity and biomass during secondary succession (Chazdon and Guariguata, 2016; Guariguata and Ostertag, 2001; Zhang et al., 2014). Thus, the negative effect on the vegetation can also hinder the recovery of soil fertility (Teixeira et al., 2020) as a positive influence of biodiversity and tree biomass on the recovery of soil functions is expected (Teixeira et al., 2020).

Landscapes where most secondary forests are situated are characterized by reduced forest cover and isolated remaining fragments (Matos et al., 2020; Sloan et al., 2015). These modifications can alter regional environmental conditions, such as average temperature and precipitation, due to the increase of non-forest and non-natural areas (De Frenne et al., 2021; Frelich et al., 2020). Moreover, fragmentation reduces animal population sizes and disrupts animal movement and seed dispersal between fragments (Ibáñez et al., 2014; Morán-López et al., 2015). As a result, the landscape acts as an environmental filter for plant communities, making it challenging for species with larger fruits and seeds to disperse between fragments and decreasing their occurrence within the overall landscape, including in regenerating areas (Ewers and Didham, 2006; Tscharntke et al., 2012b). These species are primarily zoochorous (with seeds dispersed by animals) and shade-tolerant, and they play an important role in maintaining the carbon stocks of forest fragments (Coelho et al., 2022b). Consequently, more isolated second forest fragments exhibit lower biodiversity and reduced biomass, which in turn can limit soil recovery capacity (Bello et al., 2015; Coelho et al., 2022a; Magnago et al., 2015). Therefore, landscape configuration may also have an indirect impact on soil fertility during secondary succession, although this hypothesis has not been tested.

Situated within the most densely populated region of the country, the Brazilian Atlantic Forest has been subject to conversion and intensive land use practices since the colonization era (Nazareno et al., 2012). Only 31 % of the original area has remained under natural vegetation cover due to conversion into pastures (39 %), agriculture (28 %), a mosaic of land uses (27 %), and silviculture (6 %; MapBiomas, 2022). The intense land-use history and fragmentation have resulted in an increased number of threatened species, requiring the development of effective conservation strategies for the Atlantic Forest (de Lima et al., 2020). Furthermore, due to requirements of the Brazilian Forest Code and Brazilian commitments related to the United Nations Decade of Restoration (to restore 12 million ha of forest), there is a strong demand for forest restoration efforts in this biome (Dockendorff et al., 2022; Soares-filho et al., 2014). Fortunately, the Atlantic Forest has shown a certain potential for the natural recovery of biodiversity and tree biomass (Coelho et al., 2022b; Matos et al., 2020; Safar et al., 2020). However, the rates of diversity and biomass recovery can differ due to previous management intensities and landscape configurations, which can also have consequences for soil fertility recovery and ecosystem functioning.

Tree biomass and soil fertility recovery are key for ecosystem services provision during secondary forest succession. Therefore, a better understanding of the effects of previous management intensity and landscape configuration on soil and vegetation development can inform conservation and restoration strategies and support their successful implementation. The objective of this article is to investigate the effects of previous silvicultural management intensity and landscape configuration on tree diversity, tree biomass, and soil fertility during secondary succession. The hypothesis is that previous management intensity (e.g., planting frequency and cutting frequency) and landscape configuration variables (e.g., patch isolation and reduced forest cover) have a negative impact on tree biodiversity and biomass, and thus an indirect negative impact on soil fertility in secondary forests, mediated by changes in tree diversity and biomass.

2. Material and methods

2.1. Study area

This study was conducted in a Semi-deciduous Tropical Forest located within the Atlantic Forest domain, encompassing the municipalities of São José do Goiabal, Dionísio, and Timóteo, which are part of the ArcelorMittal BioForest areas (19°51′36.28″S; 42°38′24.96″W). These municipalities have between 144,381 km2 and 339,375 km2, and a population size between 5.396 and 81.579 of people (IBGE, 2024). The region is known as “Vale do Aço”, contains several steel-producing industries, as well as charcoal production, with a vast area of eucalyptus planting (de Oliveira-Junior et al., 2020). The region experiences an Aw climate, classified as hot and humid according to the Köppen classification, with distinct rainy and dry periods. The average annual precipitation in the area is 1450 mm, and the mean annual temperature ranges from 20 to 23 °C (Alvares et al., 2013). The dominant soil classes are Red-Yellow Latosol in hilltops and mountainsides and Red-Yellow Podzol in upper fluvial terraces (de Oliveira-Junior et al., 2020; dos Santos et al., 2018).

A total of 27 s-growth forest patches with varying lengths of fallow time after the last eucalyptus harvest were examined in this work. The fallow periods ranged from 3 to 32 years. It is important to note that all patches were originally covered by primary Atlantic Forests that were cleared for charcoal production, followed by the establishment of eucalyptus plantations (Fig. 1). Initially, 35 plots were sampled between January and July of 2018 (see Coelho et al., 2022a). However, to test our hypothesis samples with soils that did not meet the classification criteria for clay soil were excluded from the database (see supplementary material SM1).

2.2. Plant sampling

For each second-growth forest patch, a transect measuring 20x50 meters (0.1 ha) was randomly established. Within this transect, all tree individuals with a diameter at breast height (DBH) of $\geq$ 4.8 cm (measured at 1.30 m above ground height) were sampled, following the methodology described by Matos et al. (2020). Data recorded for each individual included DBH, height, and species name. Species identification was conducted in the field or through collection and later identification based on the Angiosperm Phylogeny Group IV classification system (APG IV, 2016).

2.3. Plant diversity

In this study, two biodiversity dimensions were considered: plant taxonomic and functional diversity. Three Hill numbers, which represent effective measures of species diversity based on their relative abundances, were employed to assess taxonomic diversity (Hsieh et al., 2016; Rother et al., 2019). These diversity indices are parameterized across three orders of “q”, which reflect the increasing importance of abundance from $q = 0$ to $q = 2$: (i) species richness ($q = 0$): a measure that assigns equal weight to both rare and abundant species; (ii) exponential form of Shannon entropy ($q = 1$): which places less emphasis on rare species; and (iii) inverse of Simpson diversity ($q = 2$): which takes into account the relative abundance distribution of species and assigns even less weight to rare species compared to Shannon entropy. Higher values indicate greater evenness in the abundance distribution (Gotelli

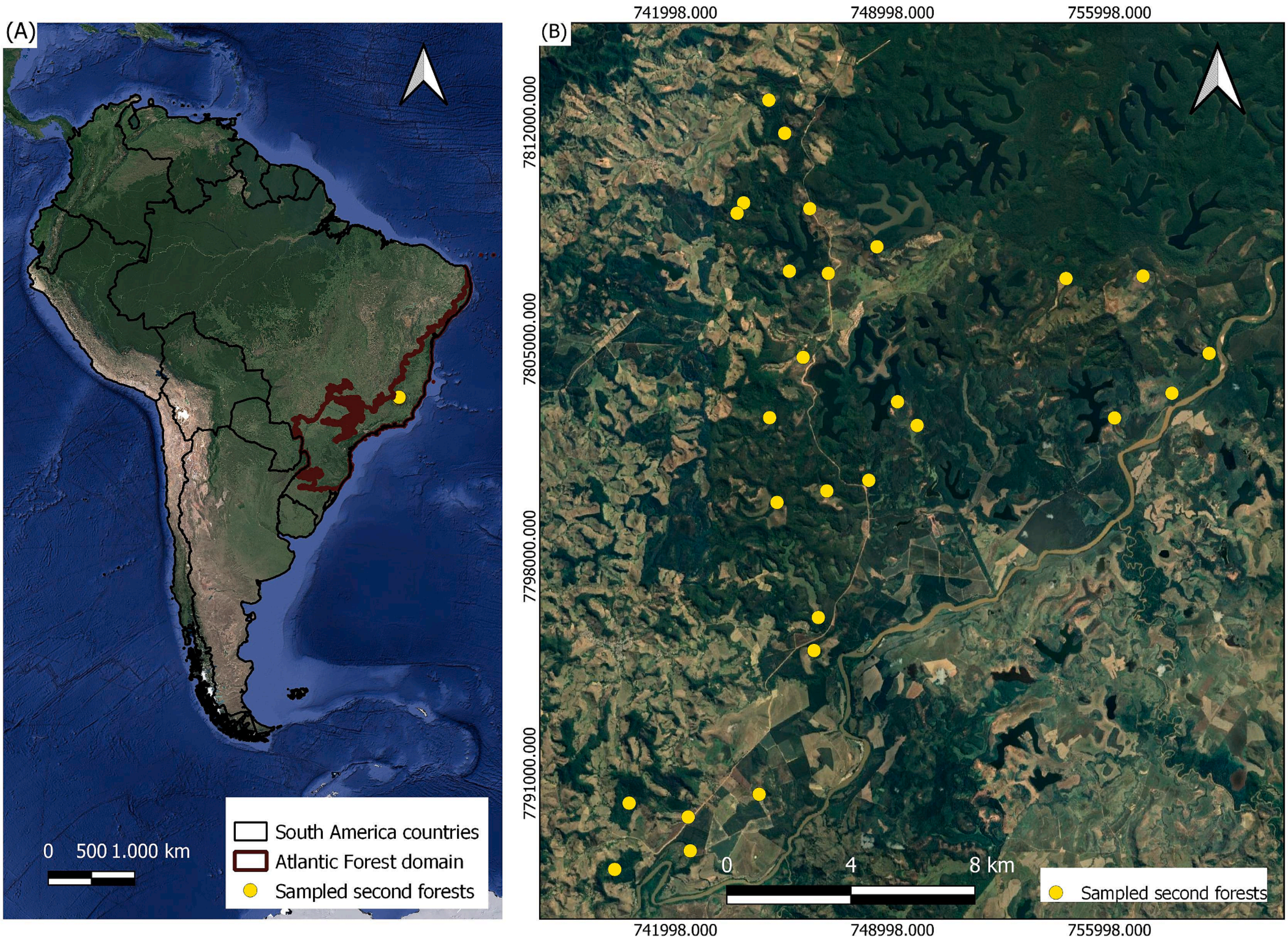

Fig. 1. Localization of study area: (A) South America region with Atlantic Forest domain; (B) sampled second forest patches.

and Chao, 2013; Hill, 1973). These diversity indices were calculated using the “iNEXT” package (Hsieh et al., 2016).

Both vegetative and reproductive traits were considered to evaluate the functional diversity of each fragment. The vegetative attributes encompassed wood density, maximum diameter, maximum height, leaf length, leaf width, and shade tolerance (shade-tolerant or non-shade-tolerant). As for reproductive attributes, seed length, seed width, fruit length, fruit width, fruit type (fleshy or dry), and type of dispersion (zoochorous or non-zoochorous) were examined. Wood density data were obtained from the Global Wood Density database (Zanne et al., 2009). For species diameter and maximum height, the highest values observed within the plots where they occurred were recorded (Coelho et al., 2020). Leaf length and width measurements were retrieved from virtual herbaria, specifically by consulting SpeciesLink, where the attribute values represented the mean measurements derived from five randomly selected exsiccates of the same species from different herbaria (Meira-Neto et al., 2019). Information regarding shade tolerance and reproductive traits was collected from the databases utilized by Magnago et al. (2014) and Matos et al. (2020), as well as from SpeciesLink databases and taxonomic descriptive articles specific to each species.

Using the functional traits, two functional diversity indices considered in this study were calculated: (i) functional richness: the extent of multidimensional functional space occupied by the community; and (ii) functional evenness: the regularity with which the species fill the functional space, considering their relative abundances (Villéger et al., 2008). The functional richness is calculated by algorithms considering the minimum convex hull that includes all species and traits under consideration. Meanwhile, functional evenness is obtained through a sequence of formulas representing the sum of the tree length that connects the dots in three-dimensional space, weighed by abundance (see Villéger et al., 2008 for more details). These indices were computed using the methods and scripts developed by Villéger et al. (2008) and the functions available in the “FD” package (Laliberte and Legendre, 2010). All plant diversity analyses were done using “R” software.

2.4. Above-ground tree biomass

The above-ground biomass (AGB) of each individual was calculated using the following allometric equation developed by Chave et al. (2014):

$$AGB = \exp[-1.803 – 0.976E + 0.976\ln(\rho) + 2.673\ln(D) – 0.0299[\ln(D)]^2] \quad (1)$$

In this equation, AGB represents 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* is determined by a linear function of climatic water deficit, temperature seasonality, and precipitation seasonality of each area, which were calculated using the “BIOMASS” package in “R” software. The total above-ground biomass per patch was obtained by summing the AGB values of all trees with a diameter at breast height (DBH) greater than or equal to 5 cm. The resulting value was then converted to megagrams per hectare (Mg/ha). Wood density values (g/cm^3) were sourced from the Global Wood Density database (GWD; Zanne et al., 2009).

2.5. *Previous management intensity*

Land-use history data provided by the landowners was used to assess the previous management intensity. The following variables were considered: (i) planting frequency: the number of times each patch was used for eucalyptus plantation; (ii) cutting frequency: the number of times the eucalyptus plantation was cut by clear-cutting in each patch; (iii) use time: the duration between the first cycle of planting and the last cycle of cutting; (iv) fallow age: the period between the last cutting cycle and the tree sampling during secondary succession.

2.6. *Landscape configuration*

Three metrics related to landscape configuration were considered: (i) patch isolation, which refers to the minimum linear distance in meters between the sampled patch and another natural forest patch; (ii) source distance, which represents the minimum linear distance between each sampled patch and a natural forest patch that is equal to or larger than 500 ha (Matos et al., 2020); and (iii) forest cover, that indicates the percentage of natural forest within the landscape. Both landscape variables were obtained from classified images using the Brazilian Annual Land Use and Land Cover Mapping Project (MapBiomas Collection 5) data for the year 2018. Patch isolation and source distance were measured using ArcGIS software (Environmental Systems Research Institute, Redlands, CA, USA). Forest cover was calculated using FRAGSTAT 4.2 software (McGarigal et al., 2023) within a 2-kilometer radius buffer centered on each transect (Matos et al., 2016). This information was extracted from ArcGIS software, as described in previous studies (Coelho et al., 2020; Matos et al., 2016).

2.7. *Soil fertility*

Ten different soil fertility indicators were measured: (i) P, phosphorus concentration using Melich-1 as extractor; (ii) Mg^{2+}, magnesium concentration extracted in KCl 1 mol/L; (iii) Ca^{2+}, calcium concentration extracted in KCl 1 mol/L; (iv) K, potassium concentration using Melich-1 as extractor; (v) Fe, iron concentration using Melich-1 as extractor; (vi) Al^{3+}, aluminum concentration extracted in KCl 1 mol/L; (vii) pH, a measure of hydrogen ion concentration in water in KCl and CaCl (1:2,5 ratio); (viii) SB, the sum of bases; ix) CEC, cation exchange capacity; and (x) MO, organic matter using Walkley-Black chromic acid wet oxidation method (Mylavarapu et al., 2002; Walkley and Black, 1934). For this, three random samples of 0–20 cm depth were taken in each patch during the same day of vegetation sampling.

2.8. *Data analysis*

2.8.1. *Data treatment*

First, a Pearson correlation matrix was generated among the four variable sets under consideration: previous management intensity, landscape configuration, biodiversity, and soil fertility. These analyses aimed to identify the most representative variables from each set and reduce the number of variables, mainly that correlated (p-value < 0.05). Within the previous management variables, cutting frequency demonstrated a positive correlation with use time ($P = 0.68$; p-value $= 0.0001$) and a negative correlation with fallow age ($P = -0.90$; p-value $= 0.0001$). Conversely, planting frequency did not exhibit correlations (Fig. 3A). Consequently, cutting frequency and planting frequency were chosen as proxies for previous management intensity, as these variables are good representatives of management practices. Regarding the landscape configuration variables, forest cover displayed a negative correlation with source distance ($P = -0.68$; p-value $= 0.0001$), while patch isolation did not demonstrate correlations (Fig. 3B). Therefore, forest cover and patch isolation were selected as proxies for landscape configuration, because forest cover is a proxy of habitat amount, some of the most important variables in landscape ecology (Arroyo-Rodríguez et al., 2020). In the biodiversity set, all variables were highly correlated ($P \geq 0.54$; p-value ≤ 0.0033; Fig. 3C). Hence, functional richness is the sole representative variable since it encompasses both taxonomic diversity and the functional roles of each species (Maira et al., 2015; Mammola et al., 2021). Lastly, within the soil fertility variables, the sum of bases exhibited correlations with almost all variables: negative with Al and Fe ($P \leq -0.76$; p-value ≤ 0.0001) and positive with pH, CEC, Ca, Mg, K ($P \geq 0.72$; p-value ≤ 0.0001). Organic matter only displayed a positive correlation with two variables, Ca and CEC ($P \geq 0.59$; p-value ≤ 0.0096), and phosphorus concentration did not demonstrate any correlations (Fig. 3D). Therefore, the variables sum of bases, organic matter, and phosphorus were selected as proxies for soil fertility. The analysis was conducted using the "Hmisc" package in R software (Harrell and Dunpont, 2019).

2.8.2. *Data analyses*

Structural equation models (SEM; Schreiber, 2006) were constructed to examine the direct effects of selected variables of previous management intensity (cutting frequency and planting frequency) and landscape configuration (forest cover and patch isolation) on tree biodiversity (functional richness), tree biomass, and soil fertility (organic matter, soil sum of bases, and phosphorus concentration. The model also considered the potential direct impact of previous management intensity and landscape configuration variables on soil fertility. The conceptual model with all tested relationships is depicted in Fig. 2.

Various metrics were considered to assess model fit of SEM: the Chi-square ($\chi 2$) p-value, Tucker-Lewis index (TLI), comparative fit index (CFI), standardized root mean square residual (SRMR), root mean square error of approximation (RMSEA) and Akaike information criterium (AIC; Hooper et al., 2008). To ensure that the model accurately represented the associations between variables, the residuals of the correlational units were examined by comparing the observed and model-implied matrices. Additionally, an additional structural equation model was conducted using species richness instead of functional richness, as species richness is a more traditional measure of diversity. An alternative model using latent variables instead of independent variables was also evaluated. The statistical analysis was conducted using the "lavaan" package in R software (Oberski et al., 2023).

3. Results

A structural equation model was built to test the relationships depicted in Fig. 2, according to the initial hypotheses. The results of the selected structural equation model are indicated in Fig. 4. The model was deemed acceptable since the $\chi 2$ p-value was larger than 0.05, indicating that the model-implied matrix did not differ from the observed-implied matrix (Schreiber, 2006; Teixeira et al., 2021). Other model quality indices were adequate, including a TLI of 1.00 (criterion ≥ 0.95), CFI of 1.00 (criterion ≥ 0.95), SRMR of 0.00 (criterion < 0.08), and RMSEA of 0.00 (criterion < 0.06) The strength of causal relationships between variables was evaluated using standardized parameter values, and relationships were deemed significant when the p-value was ≤ 0.05 (Gana and Broc, 2018; Oberski, 2014). The model was considered to neither over-predict nor under-predict the associations between variables, as indicated by residuals lower than 0.1 $|\text{res} < 0.1|$ (Gana and Broc, 2018). A moderate negative effect ($E < -0.3$) of cutting frequency ($E = -0.445$; p-value $= 0.007$) and patch isolation ($E = -0.352$; p-value $= 0.033$) on functional richness was observed. Furthermore, a strong positive effect ($E > 0.7$) of functional richness on tree aboveground biomass ($E = 0.783$; p-value < 0.0001), as well as on soil sum of bases ($E = 0.710$; p-value $= 0.011$) was detected. Consequently, the effect of cutting frequency and patch isolation on tree biomass and soil sum of bases was indirect, mediated by tree functional richness (Fig. 4; supplementary material SM2). The p-value $\chi 2$, TLI, CFI, SRMR, and RMSEA of the alternative model using species richness were similar to those presented in the selected model of functional richness (supplementary

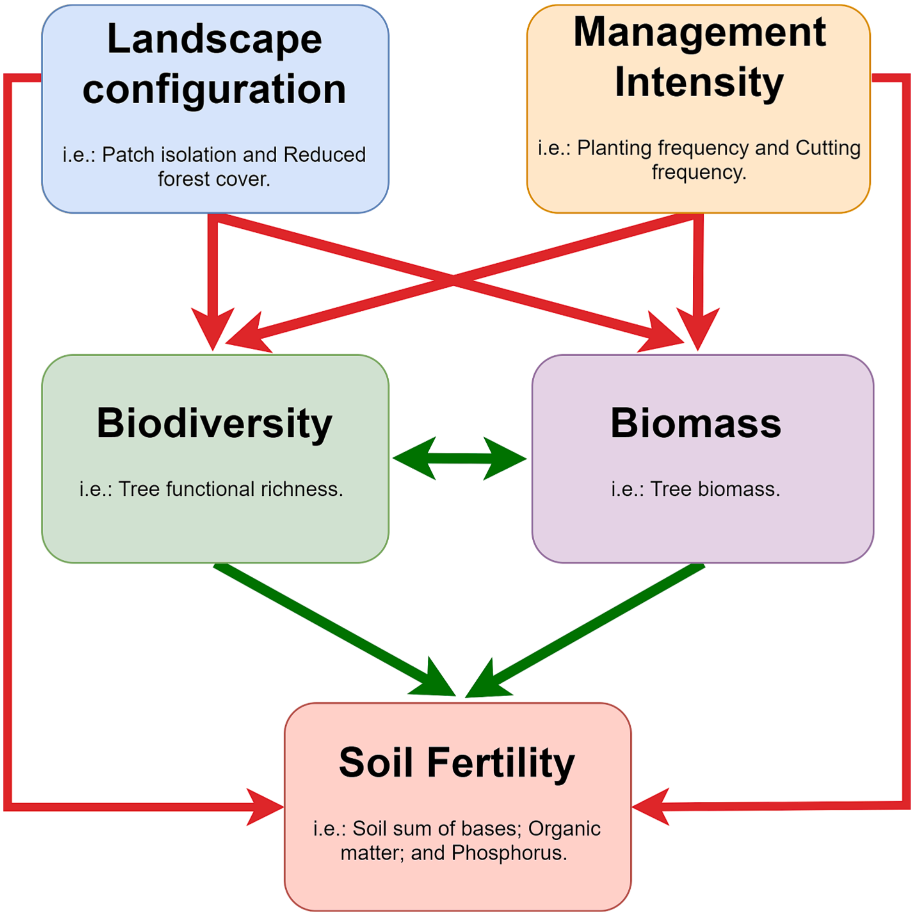

Fig. 2. The conceptual model illustrates the hypothesis tested in this study. Each box represents a set of variables considered in the analysis. Red lines indicate presumed negative influences, while green lines represent presumed positive influences, based on findings from previous studies on forest secondary succession discussed in the introduction. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

material SM3). However, the AIC of the selected model was lower than the model with species richness. A structural equation model with latent variables was also built, however, it did not meet model quality requirements probably due to the high ratio between the total number of variables and the number of observations.

4. Discussion

This study addresses a crucial knowledge gap in Atlantic Forest ecology by investigating the direct and indirect effects of previous management intensity and landscape configuration on tree biodiversity, tree biomass, and soil fertility during secondary succession. The findings reveal that patch isolation and cutting frequency have a negative impact on functional richness, indicating that intensive management and landscape fragmentation can hinder plant diversity recovery during secondary succession. In turn, a positive direct effect of functional richness on plant biomass and soil sum of bases was observed. These results suggest that previous management intensity and landscape fragmentation have negative indirect effects on tree biomass and soil fertility mediated by functional richness, highlighting the importance of (functional) diversity in the regulation of ecosystem functioning.

4.1. Management intensity influences on biodiversity

The negative impact of cutting frequency on functional richness is probably explained because intensive land use practices play an important role in changing habitat structure and quality (Fernandes-Neto et al., 2019; Pyles et al., 2022, 2018). In the case of silviculture, frequent cutting exposes the soil to adverse effects such as intense solar radiation, elevated temperatures, and soil compaction, resulting from altered local climate conditions and human activities in the area (Cook et al., 2016; Zhou et al., 2020). The environmental filtering process eliminates species from the soil seed bank that are unable to germinate and grow under the new environmental conditions, particularly shade-tolerant species that are often specialized and more susceptible to environmental changes (Brancalion et al., 2019; Brockerhoff et al., 2013; Guariguata and Ostertag, 2001; Zhang et al., 2014). As a result, the subsequent loss of shade-tolerant species from the seed bank and the early stages of succession probably contribute to delayed recovery and reduced functional richness in secondary forests previously subjected to intensive silvicultural practices (Coelho et al., 2022b).

4.2. Landscape configuration influences on biodiversity

Like management intensity, patch isolation acts as a functional environmental filter, particularly for dispersal-related traits (Matos et al., 2020; Pérez-Cárdenas et al., 2020). Species with larger fruits and seeds have limited dispersal distances and may not be able to reach more isolated secondary forest patches (Kolb and Diekmann, 2005; Martello et al., 2023; Tscharntke et al., 2012a). Moreover, these species are typically dispersed by animals whose mobility can be hindered by distances between fragments and the complexity of the landscape matrix (Carrié et al., 2017; Schleicher et al., 2011; Zambrano et al., 2019). Consequently, patch isolation diminishes the functional richness of secondary forests due to the exclusion of species with larger fruits and seeds in their regeneration (Arroyo-Rodríguez et al., 2023; Coelho et al.,

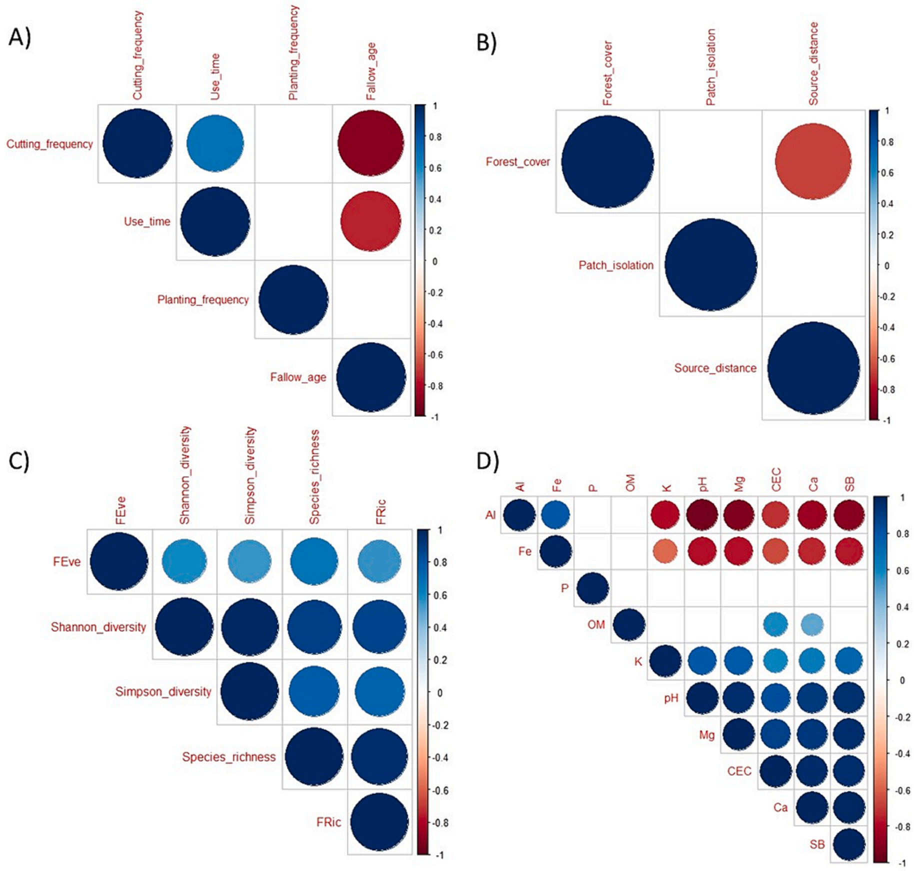

Fig. 3. Correlation matrices for the considered set of variables: (A) previous management intensity; (B) landscape configuration; (C) biodiversity; and (D) soil fertility. Unfilled spaces represent non-significant correlations ($p > 0.05$). FRic, functional richness; P, phosphorus concentration; Mg, magnesium concentration; Ca, calcium concentration; K, potassium concentration; Fe, iron concentration; Al, aluminum concentration; pH, measure of hydrogen ion concentration in water; SB, sum of bases; CEC, cation exchange capacity; MO, organic matter.

2022a; Safar et al., 2022).

4.3. Biodiversity influences on biomass and soil fertility

The positive effect of functional richness on tree biomass and soil sum of bases aligns with numerous studies that have demonstrated a positive co-benefit relationship between diversity and biomass (Gilroy et al., 2014; Magnago et al., 2015; Osuri et al., 2020) and between diversity and soil functioning (Teixeira et al., 2020; Villa et al., 2021). As succession progresses, environmental changes in the regenerating area allow the establishment of shade-tolerant species, generally characterized by large fresh fruits and zoochoric dispersal, representing a high proportion of biomass among forest species (Bello et al., 2015; Coelho et al., 2022b; Safar et al., 2022). Similarly, there is an increase in plant species with higher wood density, maximum diameter, maximum height, leaf dry matter content, and leaf thickness (Fernandes-Neto et al., 2019; Poorter et al., 2021; Teixeira et al., 2020). The increase in functional diversity enables more efficient utilization of diverse resources, such as water, nutrients, and light, leading to enhanced resource capture and greater biomass accumulation in the ecosystem (Balvanera et al., 2006; Rodrigues et al., 2023; Tilman et al., 1997). In addition, a diverse plant community with various litter quality and decomposition rates can accelerate nutrient cycling, leading to increased soil nutrients, and thus in soil fertility indices, here indicated by the influence on soil sum of bases (Bautista-Cruz and del Castillo, 2005; Teixeira et al., 2020; Zhang et al., 2018).

No significant effect of biodiversity and biomass on soil organic matter and phosphorus concentrations was observed. The recovery of soil organic matter during secondary succession remains a topic of debate. While some studies show an increase in soil organic matter in early successional stages (Deng et al., 2013; Robinson et al., 2015), others report no significant recovery (Rodríguez-León et al., 2021; Yesilonis et al., 2016). For soil phosphorus concentration, the pattern is also not clear. Some studies reported an increase in soil phosphorus concentration during secondary succession (Hughes et al., 1999; Robinson et al., 2015), while others found no significant recovery (Rodríguez-León et al., 2021; Safar et al., 2019; Yesilonis et al., 2016), or a decrease along secondary succession (Li et al., 2013). Thus, more studies need to be carried out to better understand the changes in soil organic matter and phosphorus concentration during secondary succession.

4.4. Management and landscape influences on biomass and soil fertility

The findings indicated that the impact of management intensity and landscape fragmentation on tree biomass and soil sum of bases is indirect and mediated by functional diversity. This corroborates that anthropogenic factors act as an environmental filter on biodiversity, decreasing functional diversity, and causing loss of ecosystem functions and processes (Magnago et al., 2014; Poorter et al., 2021; Ribeiro et al., 2019; Villa et al., 2021). Soil fertility plays a vital role as an essential ecosystem function, influencing seed germination, the presence of soil fauna and microbiota, and ultimately, the survival of plants (Sylvain and Wall, 2011; Teixeira et al., 2020). Additionally, biomass stock is a crucial function in the ecosystem, enhancing energy for various trophic levels and sequestering atmospheric carbon for climate stability (Favero et al., 2020). This study underscores the early phases of ecosystem

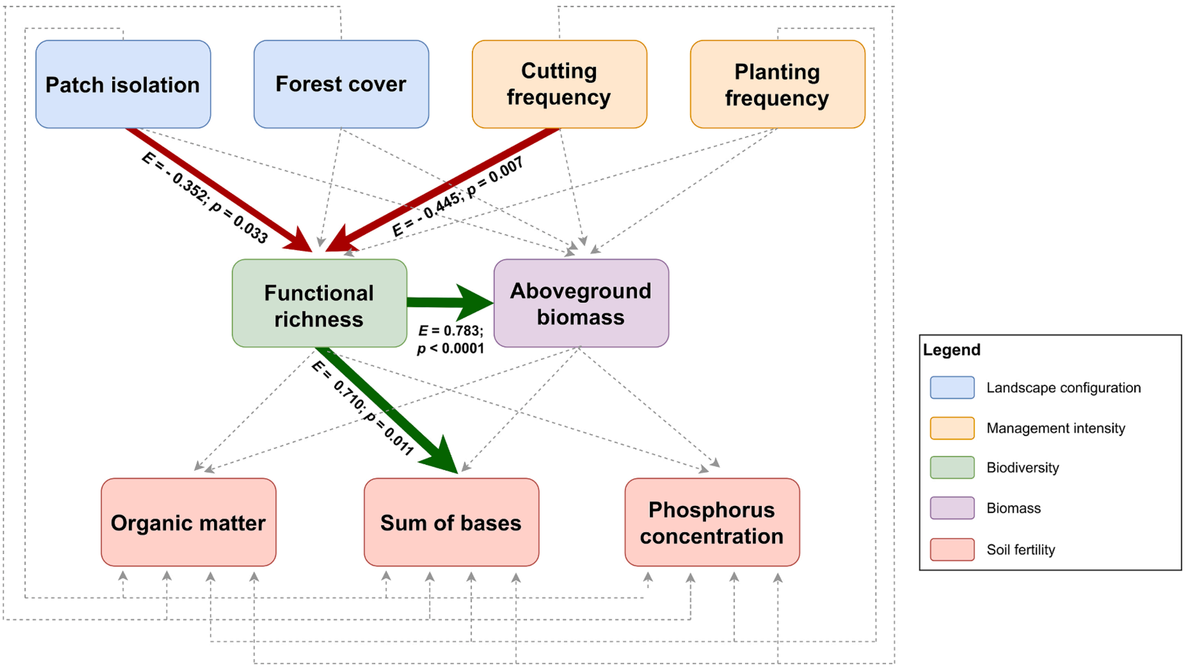

Fig. 4. The structural equation models illustrate the direct and indirect effects of previous management intensity (cutting frequency and planting frequency) and landscape configuration (patch isolation and forest cover) on tree diversity (functional richness), tree biomass, and soil fertility (sum of bases, organic matter, and phosphorus concentration) in Atlantic secondary forests following long-term eucalyptus plantation. Significant negative influences are depicted by red lines, while significant positive influences or correlations are represented by green lines. Dotted lines indicate tested relations that were found to be insignificant. *E* is the coefficient estimate of the tested relation in the structural model equation and *p* is the exceedance probability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

degradation triggered by anthropogenic influence on management and landscape configuration. These factors can trigger a cascading effect, resulting in the loss of biodiversity and essential ecosystem functions (Park and Razafindratsima, 2019).

4.5. Application in conservation and restoration strategies

The findings highlight the need to improve connectivity between forest remnants to allow seed dispersion between them and the maintenance and recovery of plant diversity in tropical forests (Arroyo-Rodríguez et al., 2023). Secondly, areas with lower previous management intensity and fragmentation should be prioritized for passive restoration efforts in tropical forests because of the higher capacity to recover the functional composition of primary forests (Coelho et al., 2022a; Pyles et al., 2022). Finally, functional diversity should be monitored during both passive and active restoration, as interventions like seed sowing or planting seedlings of underrepresented traits, especially zoochoric species with larger fruits and seeds and shade-tolerant species, may be necessary to enhance ecosystem functioning and the overall restoration success (Aerts and Honnay, 2011; Carlucci et al., 2020).

5. Conclusion

This study provides insights into the effects of management intensity and landscape configuration on functional diversity, tree biomass, and soil fertility during secondary succession. The negative effects of patch isolation and cutting frequency on functional richness highlight the role of management and landscape fragmentation as environmental filters decreasing functional plant diversity of ecosystems. These anthropogenic effects have indirect impacts on forest biomass and soil sum of bases, which are mediated by changes in tree functional richness. By recognizing the influence of functional diversity in regulating ecosystem functioning, managers and policymakers can make informed decisions to promote sustainable practices that enhance biodiversity and ecosystem services. Incorporating these findings into conservation and restoration strategies can lead to more effective management approaches that promote functional diversity and support the long-term sustainability of Atlantic Forest ecosystems.

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CRediT authorship contribution statement

Alex Josélio Pires Coelho: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Heitor Mancini Teixeira:** Writing – review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **Pita Verweij:** Writing – review & editing, Conceptualization. **Fabio Antônio Ribeiro Matos:** Methodology. **Pedro Manuel Villa:** Writing – review & editing, Methodology. **João Augusto Alves Meira-Neto:** Writing – review & editing, Supervision, Funding acquisition.

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.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2024.112029.

References

Aerts, R., Honnay, O., 2011. Forest restoration, biodiversity and ecosystem functioning 1–21. https://doi.org/https://doi.org/10.1186/1472-6785-11-29.

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

An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV, 2016. Bot. J. Linn. Soc. 181, 1–20. https://doi.org/10.1111/boj.12385.

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.

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J.I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I.R., Melo, F.P.L., Morante-Filho, J.C., Santos, B.A., Arasa-Gisbert, R., Arce-Peña, N., Cervantes-López, M.J., Cudney-Valenzuela, S., Galán-Acedo, C., San-José, M., Vieira, I.C.G., Slik, J.W.F., Nowakowski, A.J., Tscharntke, T., 2020. Designing optimal human-modified landscapes for forest biodiversity conservation. Ecol. Lett. 23, 1404–1420. https://doi.org/10.1111/ele.13535.

Arroyo-Rodríguez, V., Rito, K.F., Farfán, M., Navía, I.C., Mora, F., Arreola-Villa, F., Balvanera, P., Bongers, F., Castellanos-Castro, C., Catharino, E.L.M., Chazdon, R.L., Dupuy-Rada, J.M., Ferguson, B.G., Foster, P.F., González-Valdivia, N., Griffith, D.M., Hernández-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Jong, B.H.J., Letcher, S. G., May-Pat, F., Meave, J.A., Ochoa-Gaona, S., Meirelles, G.S., Muñiz-Castro, M.A., Muñoz, R., Powers, J.S., Rocha, G.P.E., Rosário, R.P.G., Santos, B.A., Simon, M.F., Tabarelli, M., Tun-Dzul, F., van den Berg, E., Vieira, D.L.M., Williams-Linera, G., Martínez-Ramos, M., 2023. Landscape-scale forest cover drives the predictability of forest regeneration across the Neotropics. Proc. r. Soc. B Biol. Sci. 290 https://doi.org/10.1098/rspb.2022.2203.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.-S., Nakashizuka, T., Raffaelli, D., Schmid, B., 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services 1146–1156. https://doi.org/10.1111/j.1461-0248.2006.00963.x.

Bautista-Cruz, A., del Castillo, R.F., 2005. Soil Changes During Secondary Succession in a Tropical Montane Cloud Forest Area 906–914. https://doi.org/10.2136/sssaj2004.0130.

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.

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.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Ferraz, S.F.B., 2013. Role of eucalypt and other planted forests in biodiversity conservation and the provision of biodiversity-related ecosystem services. For. Ecol. Manage. 301, 43–50. https://doi.org/10.1016/j.foreco.2012.09.018.

Carlucci, M.B., Brancalion, P.H.S., Rodrigues, R.R., Loyola, R., Cianciaruso, M.V., 2020. Functional traits and ecosystem services in ecological restoration. Restor. Ecol. 28, 1372–1383. https://doi.org/10.1111/rec.13279.

Carrié, R., Andrieu, E., Cunningham, S.A., Lentini, P.E., Loreau, M., Ouin, A., 2017. Relationships among ecological traits of wild bee communities along gradients of habitat amount and fragmentation 85–97. https://doi.org/10.1111/ecog.02632.

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. Glob. Chang. Biol. 20, 3177–3190. https://doi.org/10.1111/gcb.12629.

Chazdon, R.L., Guariguata, M.R., 2016. Natural regeneration as a tool for large-scale forest restoration in the tropics: prospects and challenges. Biotropica 48, 716–730. https://doi.org/10.1111/btp.12381.

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, 0123456789 Biodivers. Conserv.. https://doi.org/10.1007/s10531-020-02013-6.

Coelho, A.J.P., Matos, F.A.R., Villa, P.M., Heringer, G., Pontara, V., de Paula Almado, R., Alves Meira-Neto, J.A., 2022a. Multiple drivers influence tree species diversity and above-ground carbon stock in second-growth Atlantic forests: Implications for passive restoration. J. Environ. Manage. 318, 115588 https://doi.org/10.1016/j.jenvman.2022.115588.

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., 2022b. 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.

Colli-Silva, M., Reginato, M., Cabral, A., Forzza, R.C., Pirani, J.R., Vasconcelos, T.N.d.C., 2020. Evaluating shortfalls and spatial accuracy of biodiversity documentation in the Atlantic Forest, the most diverse and threatened Brazilian phytogeographic domain. Taxon 69, 567–577. https://doi.org/10.1002/tax.12239.

Cook, R.L., Binkley, D., Luiz, J., 2016. Forest Ecology and Management Eucalyptus plantation effects on soil carbon after 20 years and three rotations in Brazil. For. Ecol. Manage. 359, 92–98. https://doi.org/10.1016/j.foreco.2015.09.035.

De Frenne, P., Lenoir, J., Luoto, M., Scheffers, B.R., Zellweger, F., Aalto, J., Ashcroft, M. B., Christiansen, D.M., Decocq, G., De Pauw, K., Govaert, S., Greiser, C., Gril, E., Hampe, A., Jucker, T., Klinges, D.H., Koelemeijer, I.A., Lembrechts, J.J., Marrec, R., Meeussen, C., Ogée, J., Tyystjärvi, V., Vangansbeke, P., Hylander, K., 2021. Forest microclimates and climate change: Importance, drivers and future research agenda. Glob. Chang. Biol. 27, 2279–2297. https://doi.org/10.1111/gcb.15569.

de Lima, R.A.F., Oliveira, A.A., Pitta, G.R., de Gasper, A.L., Vibrans, A.C., Chave, J., ter Steege, H., Prado, P.I., 2020. The erosion of biodiversity and biomass in the Atlantic Forest biodiversity hotspot. Nat. Commun. 11, 1–16. https://doi.org/10.1038/s41467-020-20217-w.

de Oliveira-Junior, N.D., 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.

Deng, L., Wang, K.B., Chen, M.L., Shangguan, Z.P., Sweeney, S., 2013. Soil organic carbon storage capacity positively related to forest succession on the Loess Plateau, China. Catena 110, 1–7. https://doi.org/10.1016/j.catena.2013.06.016.

Dockendorff, C., Fuss, S., Agra, R., Guye, V., Herrera, D., Kraxner, F., 2022. Committed to restoring tropical forests: an overview of Brazil's and Indonesia's restoration targets and policies. Environ. Res. Lett. 17 https://doi.org/10.1088/1748-9326/ac8ab2.

dos Santos, H.G., Jacomine, P.K.T., dos Anjos, L.H.C., de Oliveira, V.A., Lumbreras, J.F., Coelho, M.R., de Almeida, J.A., de Araújo-Filho, J.C., de Oliveira, J.B., Cunha, T.J.F., 2018. Sistema brasileiro de classificação de solos, 5. ed. rev. ed,. Embrapa Solos.

Edwards, D.P., Socolar, J.B., Mills, S.C., Burivalova, Z., Koh, L.P., Wilcove, D.S., 2019. Conservation of Tropical Forests in the Anthropocene. Curr. Biol. 29, R1008–R1020. https://doi.org/10.1016/j.cub.2019.08.026.

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

Favero, A., Daigneault, A., Sohngen, B., 2020. Forests: Carbon sequestration, biomass energy, or both? Sci. Adv. 6, 1–13. https://doi.org/10.1126/sciadv.aay6792.

Fernandes-Neto, J.G., Costa, F.R.C., Williamson, G.B., Mesquita, R.C.G., 2019. Alternative functional trajectories along succession after different land uses in central Amazonia. J. Appl. Ecol. https://doi.org/10.1111/1365-2664.13484.

Frelich, L.E., Jogiste, K., Stanturf, J., Jansons, A., Vodde, F., 2020. Are secondary forests ready for climate change? It depends on magnitude of climate change, landscape diversity and ecosystem legacies. Forests 11, 1–15. https://doi.org/10.3390/f11090965.

Gana, K., Broc, G., 2018. Structural Equation Modeling With Lavaan. John Wiley & Sons.

Gardner, T.A., Barlow, J., Chazdon, R., Ewers, R.M., Harvey, C.A., Peres, C.A., Sodhi, N. S., 2009. Prospects for tropical forest biodiversity in a human-modified world. Ecol. Lett. 12, 561–582. https://doi.org/10.1111/j.1461-0248.2009.01294.x.

Gilroy, J.J., Woodcock, P., Edwards, F.A., Wheeler, C., Baptiste, B.L.G., Medina Uribe, C. A., Haugaasen, T., Edwards, D.P., 2014. Cheap carbon and biodiversity co-benefits from forest regeneration in a hotspot of endemism. Nat. Clim. Chang. 4, 503–507. https://doi.org/10.1038/nclimate2200.

Gotelli, N.J., Chao, A., 2013. Measuring and Estimating Species Richness, Species Diversity, And Biotic Similarity From Sampling Data, Encyclopedia Of Biodiversity, second ed. Elsevier Ltd. 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.

Guedes Pinto, L.F., Voivodic, M., 2021. Reverse the tipping point of the Atlantic Forest for mitigation. Nat. Clim. Chang. 11, 364–365. https://doi.org/10.1038/s41558-021-01035-4.

Harrell, F.E., Dunpont, C., 2019. Hmisc Version 4.2-0 428.

Hill, M.O., 1973. Diversity and Evenness: A Unifying Notation and Its Consequences. Ecology 54, 427–432. https://doi.org/10.2307/1934352.

Hooper, D., Coughlan, J., Mullen, M.R., 2008. Structural equation modelling: guidelines for determining model fit. Electron. J. Bus. Res. Methods 6, 53–60.

Hsieh, T.C., Ma, K.H., Chao, A., 2016., 2016. iNEXT: iNterpolation and EXTrapolation for species diversity.

Hughes, R.F., Kauffman, J.B., Jaramillo, V.J., 1999. Biomass, carbon, and nutrient dynamics of secondary forests in a humid tropical Region of Mexico. Ecology 80, 1892–1907. https://doi.org/10.1890/0012-9658(1999)080[1892:BCANDO]2.0.CO;2.

Ibáñez, I., Katz, D.S.W., Peltier, D., Wolf, S.M., Connor Barrie, B.T., 2014. Assessing the integrated effects of landscape fragmentation on plants and plant communities: The challenge of multiprocess-multiresponse dynamics. J. Ecol. 102, 882–895. https://doi.org/10.1111/1365-2745.12223.

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.

Kolb, A., Diekmann, M., 2005. Effects of life-history traits on responses of plant species to forest fragmentation. Conserv. Biol. 19, 929–938. https://doi.org/10.1111/j.1523-1739.2005.00065.x.

Laliberte, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. Ecology 91, 299–305. https://doi.org/10.1890/08-2244.1.

Li, Y., Yang, F., Ou, Y., Zhang, D., Liu, J., Chu, G., Zhang, Y., Otieno, D., Zhou, G., 2013. Changes in forest soil properties in different successional stages in lower tropical China. PLoS One 8, 1–10. https://doi.org/10.1371/journal.pone.0081359.

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

Maira, L., Laureto, O., Vinicius, M., Soares, D., Samia, M., 2015. Essays and Perspectives Functional diversity : an overview of its history and applicability. Nat. Conserv. 13, 112–116. https://doi.org/10.1016/j.ncon.2015.11.001.

Mammola, S., Carmona, C.P., Guillerme, T., Cardoso, P., 2021. Concepts and applications in functional diversity 1869–1885. https://doi.org/10.1111/1365-2435.13882.

Martello, F., dos Santos, J.S., Silva-Neto, C.M., Cássia-Silva, C., Siqueira, K.N., de Ataíde, M.V.R., Ribeiro, M.C., Collevatti, R.G., 2023. Landscape structure shapes the diversity of plant reproductive traits in agricultural landscapes in the Brazilian Cerrado. Agric. Ecosyst. Environ. 341 https://doi.org/10.1016/j.agee.2022.108216.

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. Glob. Chang. Biol. 26, 509–522. https://doi.org/10.1111/gcb.14824.

McGarigal, K., Cushman, S.A., Ene, E.. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical Maps. Computer software program; available at the following web site. https://www.fragstats.org.

Meira-Neto, J.A.A., Nunes Cândido, H.M., Miazaki, Â., Pontara, V., Bueno, M.L., Solar, R., Gastauer, M., 2019. Drivers of the growth–survival trade-off in a tropical forest. J. Veg. Sci. 30, 1184–1194. https://doi.org/10.1111/jvs.12810.

Mendes, M.S., Latawiec, A.E., Sansevero, J.B.B., Crouzeilles, R., Moraes, L.F.D., Castro, A., Alves-Pinto, H.N., Brancalion, P.H.S., Rodrigues, R.R., Chazdon, R.L., Barros, F.S.M., Santos, J., Iribarrem, A., Mata, S., Lemgruber, L., Rodrigues, A., Korys, K., Strassburg, B.B.N., 2019. Look down—there is a gap—the need to include soil data in Atlantic Forest restoration. Restor. Ecol. 27, 361–370. https://doi.org/10.1111/rec.12875.

Morán-López, T., Fernández, M., Alonso, C.L., Flores-Rentería, D., Valladares, F., Díaz, M., 2015. Effects of forest fragmentation on the oak-rodent mutualism. Oikos 124, 1482–1491. https://doi.org/10.1111/oik.02061.

Mylavarapu, R.S., Sanchez, J.F., Nguyen, J.H., Bartos, J.M., 2002. Evaluation of Mehlich-1 and Mehlich-3 extraction procedures for plant nutrients in acid mineral soils of Florida. Commun. Soil Sci. Plant Anal. 33, 807–820. https://doi.org/10.1081/CSS-120003067.

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.

Oberski, D., 2014. Lavaan.survey: An R package for complex survey analysis of structural equation models. J. Stat. Softw. 57, 1–27. https://doi.org/10.18637/jss.v057.i01.

Oberski, D., Byrnes, J., Vanbrabant, L., Savalei, V., Merkle, E., Hallquist, M., Barendse, M., Scharf, F., 2023. Package ‘ lavaan .’.

Osuri, A.M., Machado, S., Ratnam, J., Sankaran, M., Ayyappan, N., Muthuramkumar, S., Parthasarathy, N., Pélissier, R., Ramesh, B.R., DeFries, R., Naeem, S., 2020. Tree diversity and carbon storage cobenefits in tropical human-dominated landscapes. Conserv. Lett. 1–9 https://doi.org/10.1111/conl.12699.

Park, D.S., Razafindratsima, O.H., 2019. Anthropogenic threats can have cascading homogenizing effects on the phylogenetic and functional diversity of tropical ecosystems. Ecography (cop.) 42, 148–161. https://doi.org/10.1111/ecog.03825.

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.

Poorter, L., Craven, D., Jakovac, C.C., Sande, M.T. Van Der, Amissah, L., Bongers, F., Chazdon, R.L., Farrior, C.E., Kambach, S., Meave, J.A., 2021. Multidimensional tropical forest recovery 1–8.

Pyles, M.V., Prado-Junior, J.A., Magnago, L.F.S., de Paula, A., Meira-Neto, J.A.A., 2018. Loss of biodiversity and shifts in aboveground biomass drivers in tropical rainforests with different disturbance histories. Biodivers. Conserv. 27, 3215–3231. https://doi.org/10.1007/s10531-018-1598-7.

Pyles, M.V., Silva Magnago, L.F., Maia, V.A., Pinho, B.X., Pitta, G., de Gasper, A.L., Vibrans, A.C., dos Santos, R.M., van den Berg, E., Lima, R.A.F., 2022. Human impacts as the main driver of tropical forest carbon. Sci. Adv. 8 https://doi.org/10.1126/sciadv.abl7968.

Ribeiro, E.M.S., Lohbeck, M., Santos, B.A., Arroyo-Rodríguez, V., Tabarelli, M., Leal, I.R., 2019. Functional diversity and composition of Caatinga woody flora are negatively impacted by chronic anthropogenic disturbance. J. Ecol. 107, 2291–2302. https://doi.org/10.1111/1365-2745.13177.

Robinson, S.J.B., van den Berg, E., Meirelles, G.S., Ostle, N., 2015. Factors influencing early secondary succession and ecosystem carbon stocks in Brazilian Atlantic Forest. Biodivers. Conserv. 24, 2273–2291. https://doi.org/10.1007/s10531-015-0982-9.

Rodrigues, A.C., Villa, P.M., Silla, F., Gomes, L.P., Meira-Neto, J.A.A., Torres, C.M.M.E., Neri, A.V., 2023. Functional composition enhances aboveground carbon stock during tropical late-secondary forest succession. Plant Biosyst. 157, 1–11. https://doi.org/10.1080/11263504.2022.2073394.

Rodríguez-León, C.H., Peña-Venegas, C.P., Sterling, A., Castro, D., Mahecha-Virguez, L. K., Virguez-Díaz, Y.R., Silva-Olaya, A.M., 2021. Soil quality restoration during the natural succession of abandoned cattle pastures in deforested landscapes in the Colombian Amazon. Agronomy 11. https://doi.org/10.3390/agronomy11122484.

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.

Safar, N.V.H., Magnago, L.F.S., Rolim, S.G., Schaefer, C.E.G.R., 2019. Atlantic Forest topsoil nutrients can be resistant to disturbance and forest clearing. Biotropica 51, 342–354. https://doi.org/10.1111/btp.12658.

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.

Safar, N., van der Sande, M., Carlos, C.E., Luiz, L.F., Martins, S.V., Simonelli, M., Poorter, L., 2022. Landscape openness has different effects on the structure, diversity and functional composition of Brazilian rainforests. For. Ecol. Manage. 520 https://doi.org/10.1016/j.foreco.2022.120395.

Schleicher, A., Biedermann, R., Kleyer, M., 2011. Dispersal traits determine plant response to habitat connectivity in an urban landscape. Landsc. Ecol. 26, 529–540. https://doi.org/10.1007/s10980-011-9579-1.

Schreiber, J.B., 2006. Modeling and Confirmatory Factor Analysis Results : A Review.

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 363–364.

Sylvain, Z.A., Wall, D.H., 2011. Linking soil biodiversity and vegetation: Implications for a changing planet. Am. J. Bot. 98, 517–527. https://doi.org/10.3732/ajb.1000305.

Teixeira, H.M., Cardoso, I.M., Bianchi, F.J.J.A., da Cruz Silva, A., Jamme, D., Peña-Claros, M., 2020. Linking vegetation and soil functions during secondary forest succession in the Atlantic forest. For. Ecol. Manage. 457, 117696 https://doi.org/10.1016/j.foreco.2019.117696.

Teixeira, H.M., Bianchi, F.J.J.A., Cardoso, I.M., Tittonell, P., Peña-Claros, M., 2021. Impact of agroecological management on plant diversity and soil-based ecosystem services in pasture and coffee systems in the Atlantic forest of Brazil. Agric. Ecosyst. Environ. 305, 107171 https://doi.org/10.1016/j.agee.2020.107171.

Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M., Siemann, E., 1997. The influence of functional diversity and composition on ecosystem processes. Science (80-.) 277, 1300–1302. https://doi.org/10.1126/science.277.5330.1300.

Tscharntke, T., Clough, Y., Wanger, T.C., Jackson, L., Motzke, I., Perfecto, I., Vandermeer, J., Whitbread, A., 2012a. Global food security, biodiversity conservation and the future of agricultural intensification. Biol. Conserv. 151, 53–59. https://doi.org/10.1016/j.biocon.2012.01.068.

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., 2012b. 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.

van Breugel, M., Craven, D., Lai, H.R., Baillon, M., Turner, B.L., Hall, J.S., 2019. Soil nutrients and dispersal limitation shape compositional variation in secondary tropical forests across multiple scales. J. Ecol. 107, 566–581. https://doi.org/10.1111/1365-2745.13126.

Van Der Sande, M.T., Powers, J.S., Kuyper, T.W., Norden, N., Salgado-Negret, B., Silva De Almeida, J., Bongers, F., Delgado, D., Dent, D.H., Derroire, G., Do Espirito Santo, M.M., Dupuy, J.M., Fernandes, G.W., Finegan, B., Gavito, M.E., Hernández-Stefanoni, J.L., Jakovac, C.C., Jones, I.L., Das Dores Magalhães Veloso, M., Meave, J. A., Mora, F., Muñoz, R., Pérez-Cárdenas, N., Piotto, D., Álvarez-Dávila, E., Caceres-Siani, Y., Dalban-Pilon, C., Dourdain, A., Du, D.V., García Villalobos, D., Nunes, Y.R. F., Sanchez-Azofeifa, A., Poorter, L., 2023. Soil resistance and recovery during neotropical forest succession. Philos. Trans. R. Soc. B Biol. Sci. 378 https://doi.org/10.1098/rstb.2021.0074.

Veldkamp, E., Schmidt, M., Powers, J.S., Corre, M.D., 2020. Deforestation and reforestation impacts on soils in the tropics. Nat. Rev. Earth Environ. 1, 590–605. https://doi.org/10.1038/s43017-020-0091-5.

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

Villa, P.M., Martins, S.V., Diniz, É.S., de Oliveira, N., Neto, S., Neri, A.V., Pinto-Junior, H., Nunes, J.A., Bueno, M.L., Ali, A., 2021. Taxonomic and functional beta diversity of woody communities along Amazon forest succession: The relative importance of stand age, soil properties and spatial factor. For. Ecol. Manage. 482, 118885 https://doi.org/10.1016/j.foreco.2020.118885.

Villéger, S., Mason, N.W.H., Mouillot, D., 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. Ecology 89, 2290–2301. https://doi.org/10.1890/07-1206.1.

Walkley, A., Black, I., 1934. An examination of the degtjareff method for determining soil organic matter, and a proposed modification of the chronic acid titration method. Soil Sci. 37, 29–38. https://doi.org/10.1111/j.1365-2745.2010.01664.x.

Yesilonis, I., Szlavecz, K., Pouyat, R., Whigham, D., Xia, L., 2016. Historical land use and stand age effects on forest soil properties in the Mid-Atlantic US. For. Ecol. Manage. 370, 83–92. https://doi.org/10.1016/j.foreco.2016.03.046.

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, W., Ren, C., Deng, J., Zhao, F., Yang, G., Han, X., 2018. Plant functional composition and species diversity a ff ect soil C, N, and P during secondary succession of abandoned farmland on the Loess Plateau. Ecol. Eng. 122, 91–99. https://doi.org/10.1016/j.ecoleng.2018.07.031.

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.

Zhou, X., Zhu, H., Wen, Y., Goodale, U.M., Zhu, Y., Yu, S., Li, C., Li, X., 2020. Intensive management and declines in soil nutrients lead to serious exotic plant invasion in Eucalyptus plantations under successive short-rotation regimes. L. Degrad. Dev. 31, 297–310. https://doi.org/10.1002/ldr.3449.