

Brazilian Atlantic forest carbon stocks undergoing active restoration after bauxite mining exploration: an approach based on functional attributes

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Research

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Abstract

Background: Tropical forests are important carbon sinks at the global scale. They are important reservoirs of terrestrial carbon and play a fundamental role in global climate regulation. We evaluated the tree species diversity and dominance patterns in stem and carbon stocks in a Brazilian Atlantic forest restored after bauxite mining exploration in the state of Minas Gerais, south-eastern Brazil.

Methods: Aboveground carbon was estimated for a permanent 1-ha forest restored after 14 years, measuring all trees with a circumference at breast height (CBH) ≥ 15 cm, planted during restoration. We studied species richness, community composition and stem- and carbon-dominant species based on two categorical functional attributes associated with forest regeneration (successional strategy and dispersal syndrome).

Results: The restored forest obtained a high carbon accumulation (~ 58 Mg ha⁻¹), between two and three times more than second-growth forests with the same or more time for natural regeneration, when compared with other restored Brazilian seasonal semideciduous Atlantic Forest stands. The restored forest presented a marked local carbon dominance, with $\sim 7.5\%$ of the tree species of the community representing 50% of the total aboveground carbon (AGC). Anemochoric and zoochoric species presented a similar pattern of carbon dominance, while the initial second-growth species presented a higher carbon storage capacity than the pioneer species.

Conclusions: Our findings stress the importance of analysing the relative contributions of species, classified by functional attributes and by their dominance, to ecosystem functioning at fine-scale active restoration.

1. Introduction

Tropical forests are home to half of the earth's biodiversity. They are important reservoirs of terrestrial carbon and play a fundamental role in global climate regulation (Bonan 2008; Lewis et al. 2015). They support also the lives of indigenous and non-indigenous communities through non-timber forestry resources, such as food, medicines and fibres (Wood et al. 2016; Roberts et al. 2018). However, land-use changes have caused large-scale deforestation and forest degradation in the tropics (Lewis et al. 2015), significantly contributing to increased carbon emissions (Houghton 2012; Mitchard et al. 2018). During the past two decades, the global net carbon fluxes from deforestation and the degradation of tropical forests were about the same as the total flux from new land use types (Pan et al. 2011). These current tendencies have a considerable impact on the role of tropical forests as carbon sinks in the long term (Brienen et al. 2015). In this context, restoration initiatives are becoming increasingly important and have called for unprecedented levels of forest restoration to counteract decades of rapid deforestation (Crouzeilles et al. 2016; Holl 2017).

Despite the land use changes in tropical forests, forest restoration after anthropogenic disturbances still represents an important reservoir of biodiversity and carbon stocks (Gibson et al. 2011; Chazdon et al.

2016; Rozendaal et al. 2019). Naturally regenerated second-growth forests cover vast areas on a global scale (i.e. 2.4 million km² in Latin America) and play a crucial role in mitigating climate change (FAO 2010; Mitchard et al. 2018). However, active restoration also contributes to enhanced biodiversity and ecosystem services, such as carbon stock storage (Benayas et al. 2009; Rohr et al. 2018). There are several important initiatives that can significantly contribute to the challenge of restoring 3.5 million km² of degraded forests on a global scale by 2030 (i.e. Bonn Challenge) or 20 million hectares in Latin America by 2020 through the 20 × 20 initiative (Jacobs et al. 2015). For this reason, Brazil, as a country with a large proportion of tropical forest area (i.e. Amazon Forest, Atlantic Forest), is also committed to participating in these initiatives.

Restoration costs vary according to different methods and ecosystem types, and generally, the costs are lower for passive restoration (natural regeneration) and higher for active restoration, such as seedling planting (Chazdon, 2014; Holl, 2017). The natural succession of the forest after a disturbance is also known as passive restoration and consists of the management of permanent areas to promote the recovery of diversity, structure and functions (Chazdon et al. 2016; Poorter et al. 2019; Rozendaal et al. 2019). On the contrary, active restoration consists of the implementation of management techniques such as direct planting of seeds or tree seedlings or the transposition of seed banks from old-growth forests (e.g. Zahawi et al. 2013; Ssekuubwa et al. 2019). Active restoration is favoured in areas where natural regeneration is limited, such as isolated areas with extensive deforestation and seed bank loss, low precipitation rates, a long history of land use and increased soil degradation (Holl 2017; Crouzeilles et al. 2017). Both methods can be important and complementary to an integrated management plan and to forest management for restoration purposes (Villa et al. 2017; Martins 2018; Ssekuubwa et al. 2019). However, more research is needed to understand the effects of restoration methods on tree species richness and ecosystem functioning in tropical forests undergoing restoration.

Recent studies have demonstrated the importance of linking ecosystem functioning and tree species diversity in various tropical forests, where some dominant species (i.e. higher basal area) are the most representative species in ecosystem processes (e.g. Bastin et al. 2015; Fauset et al. 2015; Rodrigues et al. 2019a). This phenomenon of a disproportionate influence of a small number of species on ecosystem functioning is also called “hyperdominance” (e.g. Bastin et al. 2015; Rodrigues et al. 2019a) and has been applied to describe the relative contribution to ecosystem services, such as biomass and carbon storage at regional and fine scales (Fauset et al. 2015; Rodrigues et al. 2019a). For instance, a small number of species of tropical forests can be responsible for more than 50% of the total regional biomass production (Bastin et al. 2015; Fauset et al. 2015), also in the fine scale (Rodrigues et al. 2019a). However, little is known about the ecosystem functioning distribution of dominant species during restoration (i.e. carbon stock acquisition), especially on a fine scale in tropical forests. Most studies on ecosystem functioning and tree diversity relationships have focused on carbon stocks as a factor determining ecosystemic processes in balance with the atmosphere (Liang et al. 2017; Poorter et al. 2017).

The maintenance of the carbon stock in forest biomass depends on the tree functional attributes (Poorter et al. 2015; Chazdon et al. 2016), which can determine the natural regeneration trajectory of second-

growth forests after disturbance (Arroyo-Rodríguez et al. 2015; Poorter et al. 2019). These changes during restoration can be evaluated using functional attributes associated with regeneration (e.g. Poorter et al. 2017; 2019), such as seed dispersal syndrome and regeneration strategies (Wright et al. 2005; Reich 2014; Santos-Silva et al. 2016). In this sense, there is strong evidence that during the early stages of tropical forest succession, light-demanding pioneer species dominate (Guariguata and Ostertag 2001; Villa et al. 2018a, 2019) along with non-zoochoric pioneer species (Tabarelli et al. 2010, 2012). Along the succession, the pioneer species are gradually replaced by shade-tolerant species due to decreasing light in the understory (Chazdon 2014; Villa et al. 2018a; Poorter et al. 2019). The frequency of the occurrence of non-zoochoric species also decreases, while the dominance of zoochoric species increases along succession (e.g. Liebsch et al. 2008). Considering species dominance and their relative contribution to ecosystem services based on functional attributes can be an important approach in forest restoration, mainly in human-modified and threatened tropical forests.

The Brazilian Atlantic Forest domain has one of the richest biodiversity and is the most endangered ecosystem in the world (Myers et al., 2000), with approximately only 10% of old-growth forests preserved (Scarano and Ceotto 2015). Land use changes throughout human history resulted in highly fragmented Atlantic forest landscapes, mainly composed of small fragments at different successional stages (Ribeiro et al. 2009). Thus, in this study, we evaluated tree species diversity and dominant species patterns in a Brazilian Atlantic forest restored after bauxite mining in the state of Minas Gerais, south-eastern Brazil. We considered as species diversity the species richness and community composition and as dominant species the number of stem- and carbon-dominant species. Thus, we studied species richness, community composition and stem- and carbon-dominant species, based on two categorical functional attributes associated with forest regeneration (successional strategy and dispersal syndrome). Functional attributes were divided into the following categories: successional strategy (pioneer, early secondary and late secondary species) and dispersal syndrome (anemochoric, autochoric and zoochoric).

We addressed three questions: 1) How are the species richness and dominant species pattern separated by functional attributes associated with forest regeneration? 2) Does higher tree species richness determine the occurrence of a higher number of carbon-dominant species? 3) What is the relative importance of tree functional groups among the most stem-dominant and carbon-dominant species? We hypothesised that the same stem-dominant species are not the same carbon-dominant species because species may differ in their contribution to carbon stocks, despite their abundance (number of individuals). This study represents an important contribution to evaluate tree abundance, dominance and diversity patterns by functional attributes as a way to understand ecosystem functioning at a fine scale; this way, we establish criteria for restoration activities in the region.

2. Material And Methods

2.1. Study area

The study was conducted in a seasonal semideciduous Atlantic forest fragment at Descoberto municipality (21°25'35" S and 42°56'08" W), Minas Gerais state, southeastern Brazil (Fig. 1). The study area has a moderate humid tropical climate, with a dry season from May to September and a wet season between December and March. Mean annual relative humidity is ca. 80%, mean annual air temperature is 19°C and mean annual precipitation is 1,340 mm.

The study area is located at an elevation between 283 and 1,381 m, and the relief varies from strongly undulating to mountainous. The site is characterised by two dominant soil classes, Ferralsols and Cambisols (IUSS Working Group WRB, 2015).

2.2. Site description and restoration activities

This study was conducted in a small restoration area established after bauxite exploitation by the Brazilian Company of Aluminum (CBA). The study site covers an area of 1 hectare, and restoration activities started by the planting of seedlings in 2003; the current study was carried out 14 years later in 2017. Generally, bauxite mining is done in small areas (less than 5 ha) as ore deposits mainly occur on hilltops. Prior to mining, the soil surface (fertile layer) was removed, and the material was deposited in a nearby area to be reused afterwards, making use of the inherent soil characteristics (organic matter, seed bank, microorganisms, fertility) and, consequently, facilitating and accelerating the restoration process (Golos and Dixon 2014).

After cessation of the mining process, different techniques to restore these areas have been developed and applied to forest restoration (prior to seedling planting). Here, we highlight the main ones: 1) topographic reconstruction (ground levelling and the use of contour lines to stabilise the terrain); 2) reuse of the surface layer (fertile layer) previously removed before mining; 3) correction of the soil acidity and phosphate fertilisation in the entire area (to improve soil chemical properties); 4) ant control to reduce damages to planted seedlings. Native woody species were used for active forest restoration (Table A.1., Appendix/from Electronic Supplement Material, ESM hereafter).

The restoration area was fenced to avoid any external interference, and subsequently, the seedlings were planted. Species with different successional strategies were used at a spacing of 1 × 1 m; for each seedling, chemical fertilization and hydrogel application were used. After planting, coverage fertilisation around each seedling was employed, in addition to ant control through granulated baits distributed randomly in some points throughout the area.

2.3. Forest inventory and data collection

The 1-ha (100 × 100 m) sampling area was sub-divided into 100 sampling plots of 10 × 10 m. Within each plot, all trees with a circumference at breast height (CBH) ≥ 15 cm were identified to the species level and tagged for tree height measurement using a laser tape measurer. All individuals were identified using specialised literature, through consultation with the Herbarium of the Universidade Federal de Viçosa or by taxonomists. The Angiosperm Phylogeny Group IV (APG IV 2016) was used for taxon classification.

2.4. Functional attributes

We classified all species according to their functional attributes associated with forest regeneration (Wright et al. 2005; Reich 2014). Each functional attribute was divided into three groups according to previous studies (e.g. Tabarelli and Peres 2002; Santo-Silva et al. 2012): for dispersal syndrome, we separated trees into anemochoric (i.e. dispersed abiotically), autochoric (self-dispersal) and zoochoric species (i.e. dispersed by animals). For successional regeneration strategy, we classified species as pioneer, early secondary and late secondary species (Rozendaal and Chazdon 2015). Thus, the species were classified into successional categories (SC) according to Budowski (1965) and adapted by Gandolfi et al. (1995) for Brazilian second-growth forests into: pioneers (P); early secondary (ES); late secondary (LS). Considering the dispersal syndrome (DS), the species were classified according to Pijl (1982) into: dispersal by animals (ZOO); dispersal by wind (ANE); self-dispersal (AUTO). Finally, we selected tree height and wood density to compare successional strategies and dispersal syndromes. Previous studies have used tree height and wood density as functional attributes (Santos et al. 2008; Santo-Silva et al. 2012, 2016).

2.5. Estimation of aboveground carbon

Aboveground carbon (AGC) was estimated from the initial calculations of aboveground biomass (AGB). We calculated the AGB of individual stems using a general allometric equation, based on tree DBH (cm), height (H, m) and wood density (ρ , g cm⁻³) (Chave et al. 2014). We used Neotropical data from the Global Wood Density Database to obtain the wood density of each species, using genus or family averages whenever species-level information was not available. Tree height was measured with a laser tape. The AGB was calculated as follows:

$$AGB = 0.0673 (\rho \times DBH^2 \times H)^{0.976}$$

The total AGB per plot was the sum of the AGBs of all trees with a DBH \geq 10 cm, which was then converted into megagrams per hectare (Mg ha⁻¹) (Rodrigues et al. 2019a, 2019b). Species-level biomass was calculated as the sum of the biomass of all stems from a given species. Finally, AGC storage was calculated by multiplying AGB with a conversion factor of 0.5, assuming that 50% of the total tree biomass is carbon (Ali et al. 2016).

2.6. Data analysis

All analyses were carried out in the R Environment (R Core Team 2018). Species richness was evaluated using individual-based rarefaction and extrapolation curves, which were constructed using the first (species richness, $q = 0$) Hill number (Chao et al. 2014). Extrapolations were made from the abundance data, considering functional groups that accumulate more than 500 observed individuals twice and functional groups that only accumulate up to 250 individuals fourfold. Individual-based rarefaction/extrapolations curves were computed using the 'iNEXT' package (Hsieh et al. 2016). Rarefaction was estimated as the mean of 100 replicate bootstrapping runs to estimate 95% confidence intervals (e.g. Campos et al. 2018; Rodrigues et al. 2019; 2019b). Whenever the 95% confidence intervals did not overlap, species numbers differed significantly at $P < 0.05$ (Colwell et al. 2012).

Non-metric multidimensional scaling (NMDS), an analysis to evaluate community composition differences among functional groups by using the Euclidean distance, was applied in the “vegan” package (Oksanen et al. 2017). In addition, we performed permutational multivariate analysis of variance using distance matrices (PERMANOVA, 9,999 permutations) to determine differences in species composition by functional groups, using the “vegan” package (Oksanen et al. 2017).

Structural attributes (height and wood density) and aboveground carbon as variables were checked for normal distribution. Thus, we tested homogeneity of variances by Bartlett’s test, QQ-plots and histograms of residuals to assess normality, using the “dplyr” package (Crawley 2013; Hadley et al. 2018). To compare means of the variables (i.e. wood density, tree height) among functional attributes, we used the Kruskal-Wallis test (for non-normally distributed data), followed by a posterior Dunn test (Dinno 2017). We also used one-way ANOVA to compare means of aboveground carbon (for normally distributed data), followed by a posterior Tukey test (Crawley 2013). All these analyses were performed with the “stats” and “dunn.test” packages (Dinno 2017).

According to Rodrigues et al., (2019), we evaluated the number of stem-dominant and carbon-dominant species in the study area. In this sense, we considered as ‘carbon dominants’ the species that accumulated 50% of the total carbon when ranked by decreasing order of contribution to the total AGC and as ‘stem dominants’ the species that accumulated 50% of the total number of individuals in the tree community (Bastin et al. 2015; Fauset et al. 2015; Rodrigues et al. 2019). However, since the same stem-dominant species are not the same as the biomass-dominant species, because species may differ in their contribution to ecosystem functioning (Rodrigues et al. 2019), we estimated the maximum number of species required to account for 50% of carbon in the study area. Thus, we also calculated the contribution of stem dominants to the total carbon and regressed the percentage contribution of each species to the carbon of the whole dataset against their percentage contribution to the number of stems of the whole dataset (Fauset et al. 2015; Rodrigues et al. 2019). Abundance corresponds to the number of individuals.

The species rank curves were based on both species abundance and AGC distribution (Magurran 2004; Rodrigues et al. 2019). To obtain species rank curves, all species were ranked from the most to the least abundant ones (e.g. Rodrigues et al. 2019). Likewise, we adjusted a proportional AGC accumulation curve for the entire tree community to make inferences about functional redundancy (e.g. Lohbeck et al. 2016). Thus, the species rank curves using the ‘radfit’ function of the “vegan” package were obtained (Oksanen et al. 2018).

Finally, we tested the main effects of species richness on aboveground carbon via covariance analysis (ANCOVA). Predictor variables were grouped into three categories, i.e. species richness (continuous explanatory variable), dispersal syndrome and successional regeneration strategy (categorical explanatory variable). The dispersal syndrome included three levels (i.e. anemochoric, autochoric and zoochoric species), and the successional regeneration strategy also had three levels (pioneer, early secondary and late secondary species). This analysis was done with logarithmised data to maintain homoscedasticity (Crawley 2013). For graphics illustration we used the package ‘ggplot2’ (Hadley, 2015).

3. Results

A total of 1,664 trees, classified into 65 species, were recorded in the forest 14 years after active restoration. We observed 668 trees of 29 zoochoric species, 622 trees of 22 anemochoric species and 349 trees of 12 autochoric species. Further, there were 855 trees of 29 early secondary species, 535 trees of 24 pioneer species and 258 trees of 12 late secondary species (Table A.1., from ESM). We found a predominance of early secondary (~ 83.3% of the total community) and zoochoric species (~ 81.1% of the total community).

3.1. Species richness and community composition

We found significant differences between the species richness patterns of the different functional attribute groups using individual-based rarefaction and extrapolation curves (Fig. 2).

The rarefaction and extrapolation curves showed that groups early secondary and zoochory functional attributes presented the highest number of accumulated individuals and species richness. However, the early secondary and autochoric species rapidly achieved an asymptote of rarefaction curves (Fig. 2). The NMDS revealed that tree species composition varied considerably among functional attribute groups (Fig. 3).

3.2. Community structural attributes and aboveground carbon

Community structural attributes (height and wood density) and aboveground carbon showed differences among species by successional strategies and dispersal syndrome groups (Fig. 4).

Tree height showed differences among successional strategies ($\chi^2 = 93.03$, $df = 2$, $p < 0.001$) and dispersal syndromes ($\chi^2 = 15.04$, $df = 2$, $p < 0.001$). The WD showed differences among successional strategies ($\chi^2 = 172.20$, $df = 2$, $p < 0.001$) and dispersal syndromes ($\chi^2 = 38.26$, $df = 2$, $p < 0.01$), and the AGC showed differences among successional strategies (ANOVA, $p < 0.05$) and dispersal syndromes (ANOVA, $p < 0.05$).

3.3. Aboveground carbon and species abundance distribution

Overall, the restored forest stored 57.79 Mg carbon ha⁻¹. The highest AGC storage was found for early secondary species (33 Mg ha⁻¹), followed by pioneer species (20.87 Mg ha⁻¹) and late secondary species (3.70 Mg ha⁻¹). In terms of dispersal syndromes, the highest AGC storage was observed in zoochoric species (23.40 Mg ha⁻¹), followed by anemochoric (19.30 Mg ha⁻¹) and autochoric species (14.80 Mg ha⁻¹).

In addition, we found five species (7.5% of the total community) accounting for 50.7% of the total AGC in the regenerated site (Fig. 5), with different successional strategies and dispersal syndromes (Fig. 6).

The species *Inga vera* (early secondary and zoochoric) and *Anadenanthera peregrina* (early secondary and anemochoric) contributed most to the AGC (28.79% of the total community). Overall, the early secondary species were the main carbon-dominant species in the restored forest (Table 1).

3.4. Effects of tree richness on aboveground carbon

The AGC varied significantly with the positive effects of species richness ($F_{1,280} = 88.37, P < 0.001$) as well as the significant differences by the effects of successional strategy groups ($F_{1,280} = 6.76; P < 0.01$). There was a significant relationship between aboveground carbon and species richness in the dispersal syndrome group ($F_{1,289} = 21.34; P < 0.001$).

4. Discussion

Our results show how the forest under restoration reached a high carbon accumulation ($\sim 58 \text{ Mg ha}^{-1}$) within only 14 years, despite of the previous disturbance by bauxite mining and when compared with other restored Brazilian seasonal semideciduous Atlantic Forest stands (e.g. Ribeiro et al. 2009; 2010; Torres et al. 2013). Our site can store between two to three times more AGC compared to another second-growth forest of the same region (i.e. seasonal semideciduous Atlantic forest at Viçosa municipality) after anthropogenic disturbances, mainly due to agriculture. For example, a 20-year-old second-growth forest, established after eucalyptus cultivation in Viçosa, stored ca. 38 Mg ha^{-1} , almost two times less AGC than our study site (Torres et al. 2013). On the other hand, a 30-year-old second-growth forest, established on a pasture in Mata do seu Nico, stored ca. 19 Mg ha^{-1} , almost three times less AGC than our study site (Ribeiro et al. 2010). In old-growth forests of the same region, the AGC was only 30% higher (83 Mg ha^{-1}) than in our stand (Ribeiro et al. 2009). Because of the previous mining activities, we expected a low carbon stock. However, as previously discussed, there are factors with possible positive effects on regeneration, such as landscape variables (seed sources, distance of forests patches), the occurrence of seed dispersers and the efficiency of the restoration method.

4.1. Species richness and community composition by functional attributes

We observed significant differences in species richness and community composition pattern when comparing functional attributes. The tree community was dominated by zoochoric and early secondary species in terms of richness and abundance. Thus, contrasting patterns were revealed in comparison with other second-growth forests during the early regeneration phases (10–20 years old), where there is commonly a higher abundance of pioneer and anemochoric species (Tabarelli et al. 2012; Chazdon 2014), mainly in highly fragmented forest landscapes (Tabarelli and Peres 2002; Santo-Silva et al. 2016). Thus, via tree seedling planting, it was possible to accelerate the restoration process, since the zoochoric

species and the dominant initial secondary species were planted in the area after cessation of the mining activities. Therefore, in former mining areas, via seedling planting, it is possible to define the former species composition and the distribution of these species in ecological groups and dispersion syndromes.

Different studies have shown that variations in the ecosystem functioning recovery of tropical forests (i.e. biomass stock) depend on their relationship with diversity (e.g. Poorter et al. 2015, 2017). However, in human-modified forest landscapes, the intensity and duration of disturbances (land use changes) are considered one of the main anthropogenic drivers that determine the recovery of diversity and ecosystem functioning patterns (Poorter et al. 2016, Villa et al. 2018b, Rozendaal et al. 2019), as well as the methods implemented for ecological restoration (Crouzeilles et al. 2016). Despite this, there is still little research to elucidate the effects of these drivers on the biodiversity-ecosystem functioning relationship in tropical forests, especially analysing ecosystem processes, for example, carbon storage. In this context, we assume that there are three important factors that may significantly contribute to the diversity and species composition patterns observed in the restored forest stand; furthermore, higher tree abundance and richness of zoochoric species also play an important role.

First, the disturbed forest patch is within a fragment matrix with late successional stages, representing an important seed source of secondary and late succession species, dispersed by animals. Thus, in moderately disturbed forests, close to nearby seed sources (old-growth or late successional stages), tree species richness increases rapidly during succession (Zermeño-Hernández et al. 2015; Baker et al. 2016). Conversely, intensely degraded forests and isolated forest fragments limit the ecological conditions for initial natural regeneration (Chazdon 2014; Zermeño-Hernández et al. 2015). Second, it is likely that the largest proportion of zoochoric species planted in our study area, regardless of the successional stage and landscape fragmentation, suggests that even in these environmental conditions after mining disturbance, seeds are dispersed by animals, contributing to tree diversity maintenance at the local scale. We make this assumption that zoochoric tree species may be limited in the dispersal and colonisation of new second-growth forest patches when their dispersers are locally extinct (Tabarelli and Peres 2002; Peres et al. 2016). Third, we infer that the restoration method application through the removal and protection of the topsoil prior to bauxite extraction, and the subsequent transposition of this layer after the disturbance, provided favourable initial conditions for restoration (i.e., soil fertility, seed bank). According to previous studies, soil seed banks become depleted with the intensification by anthropogenic disturbances, causing a negative alteration (i.e. loss of viability, increased predation) as well as the local loss of seed dispersers (Randriamalala et al. 2015; Markl et al. 2012). All these factors, both environmental and anthropogenic ones, can lead to a decrease in species diversity and community composition and, consequently, a loss of resilience and ecosystem functions of tropical forests (e.g. Poorter et al. 2017; Villa et al. 2018b, Rozendaal et al. 2019).

Our results show that zoochoric species have a higher abundance and richness, but abiotically dispersed species also contribute significantly to carbon accumulation in the restored forest. However, the relative importance of pioneer species in ecosystem functioning is transitory during early successional stages.

For this reason, it is justified that restoration actions focus on typical species of old-growth forests, along with the conservation of forest remnants, to guarantee the conservation of tropical tree species in the long term (Rozendaal et al. 2019). In this sense, we infer that shade-tolerant late secondary species, typical of old-growth forests (e.g. Rozendaal and Chazdon 2015; Poorter et al. 2019), have long life cycles with a higher long-term carbon storage capacity (Brienen et al. 2015) and may be more important for forest restoration due to the stability in the ecosystem function maintenance. These results corroborate the replacement of pioneer species with shade-tolerant and zoochoric species during tropical forest regeneration (Chazdon 2014). However, it has also been reported that forest fragments in human-modified tropical landscapes maintain a typical pattern of initial succession systems (Tabarelli et al. 2008, Pütz et al. 2011) due to a strong influence of ruderal, invasive and light-demanding species because of edge effects (Tabarelli et al. 2012). These negative impacts derived from fragmentation can induce a local extinction of large frugivores, which are dispersers of trees with large seeds, high heights and a high capacity to store carbon (e.g. Peres et al. 2016). In this way, edge effects can also promote the replacement of larger (functionally more important) species by smaller species, also reducing carbon storage (Peres et al. 2016). Our findings demonstrate the importance of active forest restoration and conservation fragments to maintain food resources for seed-dispersing wildlife (e.g. Staggemeier et al. 2017), which, at the same time, can be seed sources of important species in the regeneration of ecosystem functions at the local scale.

4.2. The relation between species richness, dominance and aboveground carbon

Our results show that only five species with different functional attributes (syndrome and strategy) were responsible for more than 50% of the AGC of the tree community. Thus, the relationship between species richness and carbon stock can be linear with few dominant species. This phenomenon of dominance is common in tropical forests and can indirectly affect the relationship between species richness and ecosystem functions (Poorter et al. 2015, 2017; Lohbeck et al. 2016). However, in our study, there was a non-linear trend when analysing the whole tree community, where the AGC remained constant regardless of the increase in the number of species. This result leads us to infer that a functional redundancy may prevail, where the ecosystem function (i.e. carbon stock accumulation) remains relatively constant regardless of the increase in species richness (Lohbeck et al. 2016; Poorter et al. 2017; Rodrigues et al. 2019). Thus, different tree species perform equivalent functions within the community (Lohbeck et al. 2016; Poorter et al. 2017). This relationship can present an asymptotic tendency when a high dominance of few species with higher contribution in the AGC storage prevails, together with the presence of many species with lower contribution (e.g. Lohbeck et al. 2016, Rodrigues et al. 2019). In this way, we can assume that, in addition to the relationship between the two main categorical attributes analysed in this study, also the relationship with structural attributes (i.e. wood density and height) can simultaneously be determinant in carbon stock recover by active forest restoration.

We also observe marked changes in the relative importance of structural attributes when the species of the tree community were classified by functional attributes (syndrome and strategy). These attributes are

also determinants in the AGC because of a direct relationship with growth dynamics and tree biomass storage (Poorter et al. 2015; Rodrigues et al. 2019). Previous studies have indicated that the contribution of each species to the biomass stock depends not only on its abundance (e.g. Fauset et al. 2015), but also on the functional properties (i.e. height and wood density) of each individual of the species, as well as on the attributes that determine how much carbon the species stores and for how long (Paula et al. 2011; Fauset et al. 2015; Poorter et al. 2015).

Most studies with this approach have been developed by analysing a regional scale (e.g. Fauset et al. 2015) and scarcely in a fine scale (e.g. Rodrigues et al. 2019), where restoration activities can be economically and technically viable (Martins 2018). However, a recent study shows that the fine scale could also be important to understand the distribution of ecosystem functions within tree communities, potentially providing a perspective to establish more specific criteria for forests management and conservation, especially regarding forest fragments (Rodrigues et al. 2019). In this sense, we showed that the relative contribution of species to carbon accumulation can vary substantially from one species to another, regardless of their abundance, corroborating a pattern previously observed in the forests of the Atlantic Forest (e.g. Rodrigues et al. at 2019). Therefore, some particularly abundant species may in fact not contribute substantially to ecosystem processes, while rare species may have a higher contribution (Fauset et al. 2015; Lohbeck et al. 2016). In spite of this pattern of species dominance, our results coincide with a recent study in the Atlantic Forest, which showed that the number of stem- and biomass-dominant species increases with increasing richness at the fine scale (Rodrigues et al. 2019).

Based on our results, we assume that species dominance strongly influences the functioning of the restored forest. For example, the highest AGC storage was observed in zoochoric species (23.40 Mg ha^{-1}), followed by anemochoric (19.30 Mg ha^{-1}) and autochoric species (14.80 Mg ha^{-1}). However, there are still no studies with this approach for restored tropical forests, impeding the establishment of a baseline. Although our evaluation was carried out at a fine scale, the results are consistent with those obtained at a regional scale in the Amazonas, where a strong dominance of species has been found in terms of stem density and biomass (ter Steeg et al. 2013; Fauset et al. 2015), and also at the fine scale in the Atlantic Forest (Rodrigues et al. 2019). Similarly, a recent study conducted in the Amazon region has found that only five of the top 20 species contribute to abundance, biomass and productivity, and that approximately one third of the hyperdominant species in terms of biomass and productivity are not even recorded as stem hyperdominant (Fauset et al. 2015). In the Amazon basin, a small number of species contribute disproportionately to the total stem and biomass density, with only 1.4% of the tree species representing half of the regional abundance (species with stem hyperdominance) and only 0.91% of the tree species that represent half of the regional production of AGB (Fauset et al. 2015).

4.3. Implications for forest restoration

Our results present a valuable assessment of how ecosystem functioning is distributed among the tree species of the entire restored forest, identifying the relative contribution of the dominant species to carbon accumulation. The relevance of this study is that it allows us to identify the contribution level of

the species in ecosystem functions, but with the purpose of planning activities of active restoration immediately after the disturbance as well as during the monitoring.

On the other hand, this study highlights the relative importance of the tree functional attributes associated with carbon storage recovery, through the identification of dominant species by functional groups. This approach can be of relevance for tropical forest restoration activities that are implemented at local and fine scales. First, because there is no single restoration method that can be applied on a large scale; it is important to take advantage of the ecosystem's remaining potential for regeneration, adapting more appropriate techniques for each small-scale situation (Martins 2018). Second, because each restoration context has its unique ecological conditions, it is necessary to evaluate the site condition effects that will be determinant drivers of successional trajectories (Stuble et al. 2017). Third, because the efficiency of most forest restoration actions must be evaluated at the local level through the identification of important species for tree community assemblages and for ecosystem functioning. In this way, the definition of local management criteria is favoured (e.g. Swinfield et al. 2018; Poorter et al. 2019), allowing the establishment of long-term dominant species for the maintenance of ecosystem functions. Therefore, the identification of these key species should be a priority, since it allows us to understand the main ecological and functional differences between tropical forests and to develop more appropriate conservation and restoration strategies.

5. Conclusions

The results of this research show how the forest under active restoration reaches a high carbon accumulation ($\sim 58 \text{ Mg ha}^{-1}$), between two and three times higher than that of second-growth forests with the same or more time of natural regeneration or when compared with other restored Brazilian seasonal semideciduous Atlantic Forest stands. The restored forest presented a marked local carbon dominance, with $\sim 7.5\%$ of the tree species of the community representing 50% of the total AGC. The anemochoric and zoochoric species presented a similar pattern of carbon dominance, while the initial second-growth species presented a higher carbon storage than the pioneer species due to the transitional changes over time. In this sense, we highlight the importance of zoochoric species, which may have a higher carbon storage capacity in the long term, stressing the importance of the conservation of the seed dispersal fauna for the maintenance of ecosystem functioning. Finally, we consider that due to the high variations in the community composition and functional attributes during the succession, because of the initial conditions of restoration and landscape characteristics, there are considerable effects on the recovery and maintenance of ecosystem functions. Our findings provide evidence of the importance of analysing the relative contribution of species classified by functional attributes and by their dominance for ecosystem functioning under fine-scale active restoration.

Abbreviations

CBA: Brazilian Company of Aluminum; CBH: Circumference at breast height; APG: Angiosperm Phylogeny Group; SC: Successional categories; P: Pioneers; ES: Early secondary; LS: Late secondary; DS: Dispersal

syndrome; Zoo: Dispersal by animals; ANE: Dispersal by wind; AUTO: Self-dispersal; AGC: Aboveground carbon; AGB: aboveground biomass; DBH: Diameter at breast height; H: height; NMDS: Non-metric multidimensional scaling; ANOVA: Analysis of variance; ANCOVA: Covariance analysis.

Declarations

Ethical Approval and Consent to participate

(Not applicable)

Consent for publication

(Not applicable)

Availability of supporting data

The datasets used and/or analysed during the current study are available from the corresponding author on reasonable request.

Competing interests

The authors declare that they have no competing interests.

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Authors' contributions

All authors contributed to the design and implementation of analysis. Authors also wrote the manuscript together, and all authors read and approved the final manuscript.

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Tables

Table 1 Carbon dominant species (cumulating up to 50% of total community AGC) for the two functional groups: 1) successional strategies (A), such as early secondary (ES); late secondary (LS); Pioneer (P); and 2) dispersal syndromes (B), such as zoochory (ZOO); anemochory (ANE); autochory (AUTO).

Species	Syndrome	Strategy	AGB (Mg ha ⁻¹)	AGB (Mg ha ⁻¹) Cumulated	% AGB/ species	% AGB cumulated
<i>Inga vera</i>	ZOO	ES	8.325	14.405	8.325	14.405
<i>Anadenanthera peregrina</i>	ANE	ES	8.313	14.385	16.638	28.790
<i>Piptocarpha macropoda</i>	ANE	P	4.486	7.762	21.124	36.552
<i>Croton urucurana</i>	AUTO	P	4.164	7.205	25.288	43.757
<i>Cecropia hololeuca</i>	ZOO	P	4.018	6.952	29.306	50.709
<i>Piptadenia gonoacantha</i>	ANE	ES	3.665	6.341	32.970	57.050
<i>Senna multijuga</i>	AUTO	ES	3.134	5.423	36.104	62.474
<i>Hymenaea courbaril</i>	ZOO	LS	2.201	3.808	38.305	66.281
<i>Schizolobium parahyba</i>	ANE	P	2.106	3.644	40.411	69.925
<i>Cassia grandis</i>	AUTO	ES	2.073	3.587	42.484	73.513
<i>Peltophorum dubium</i>	ANE	ES	1.743	3.016	44.227	76.529

note

Figures

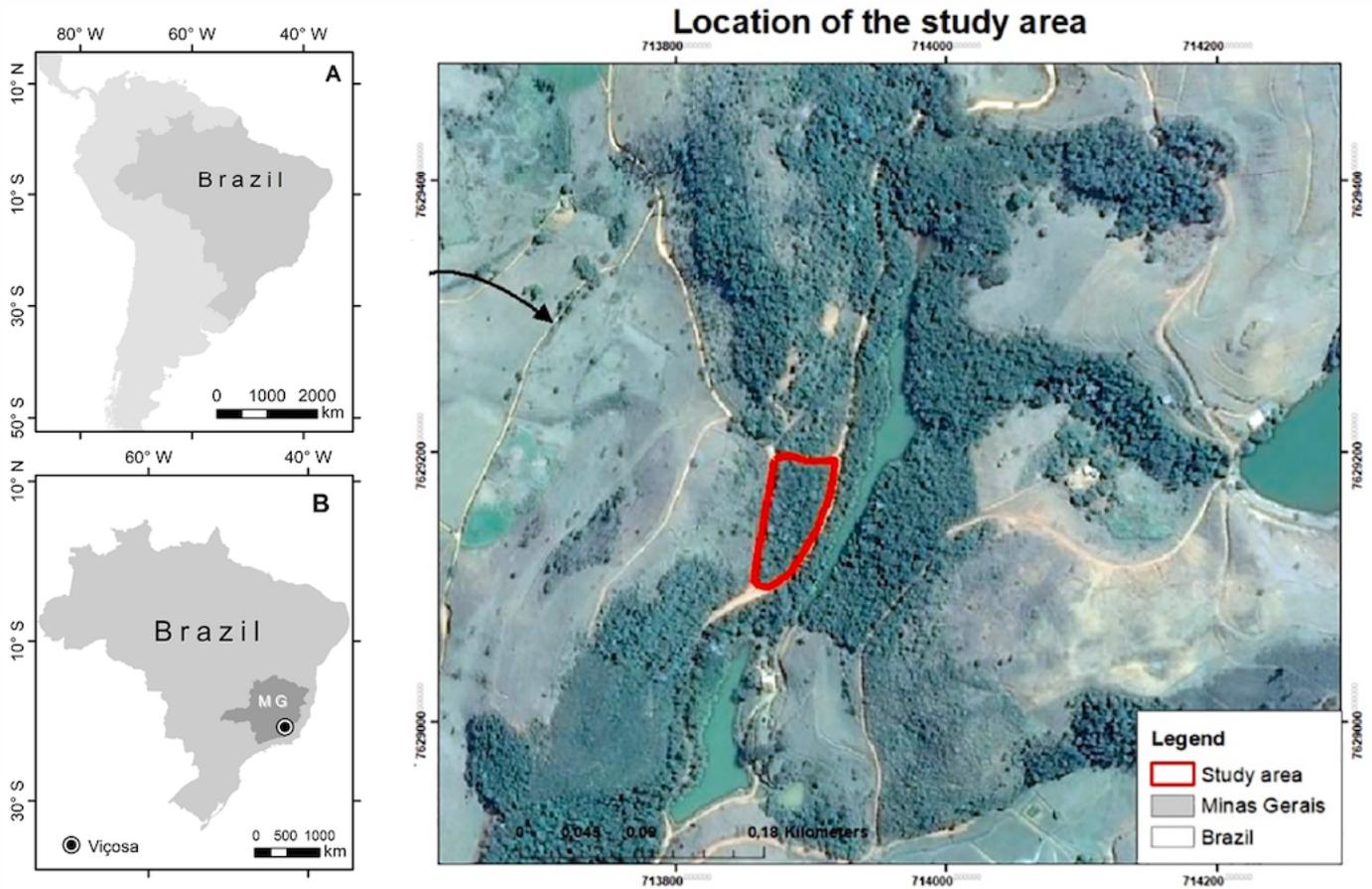


Figure 1

Localisation of the study area in relation to South America (A), the state of Minas Gerais, Brazil (B), and the forest fragment, Descoberto municipality, Minas Gerais state, southeastern Brazil (C).

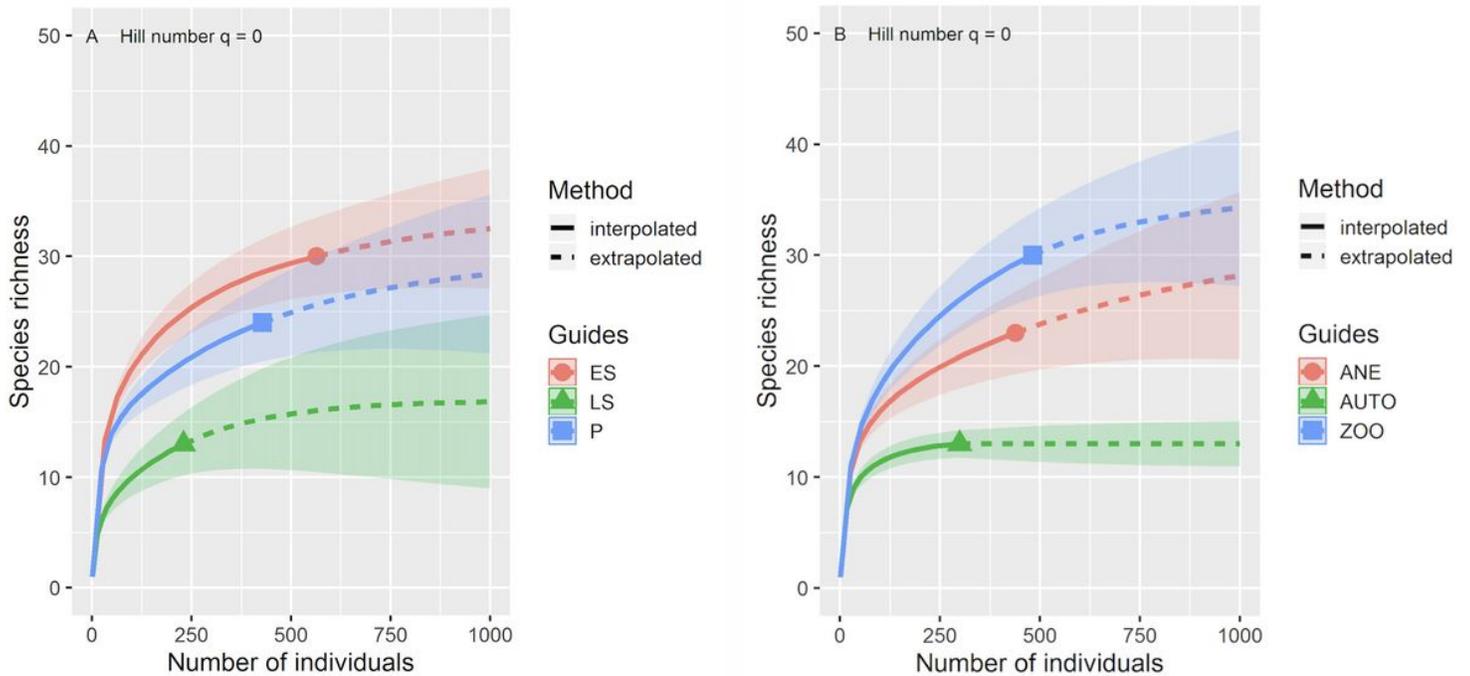


Figure 2

Individual-based rarefaction (solid line) and extrapolation curves (dashed lines) of woody species richness for the two functional groups: 1) successional strategies (A), such as early secondary (ES); late secondary (LS); pioneer (P); and 2) dispersal syndromes (B), such as zoochory (ZOO); anemochory (ANE); autochory (AUTO). Rarefaction and extrapolation curves present the lines that represent the mean values and the bands the standard deviation with 95% confidence intervals.

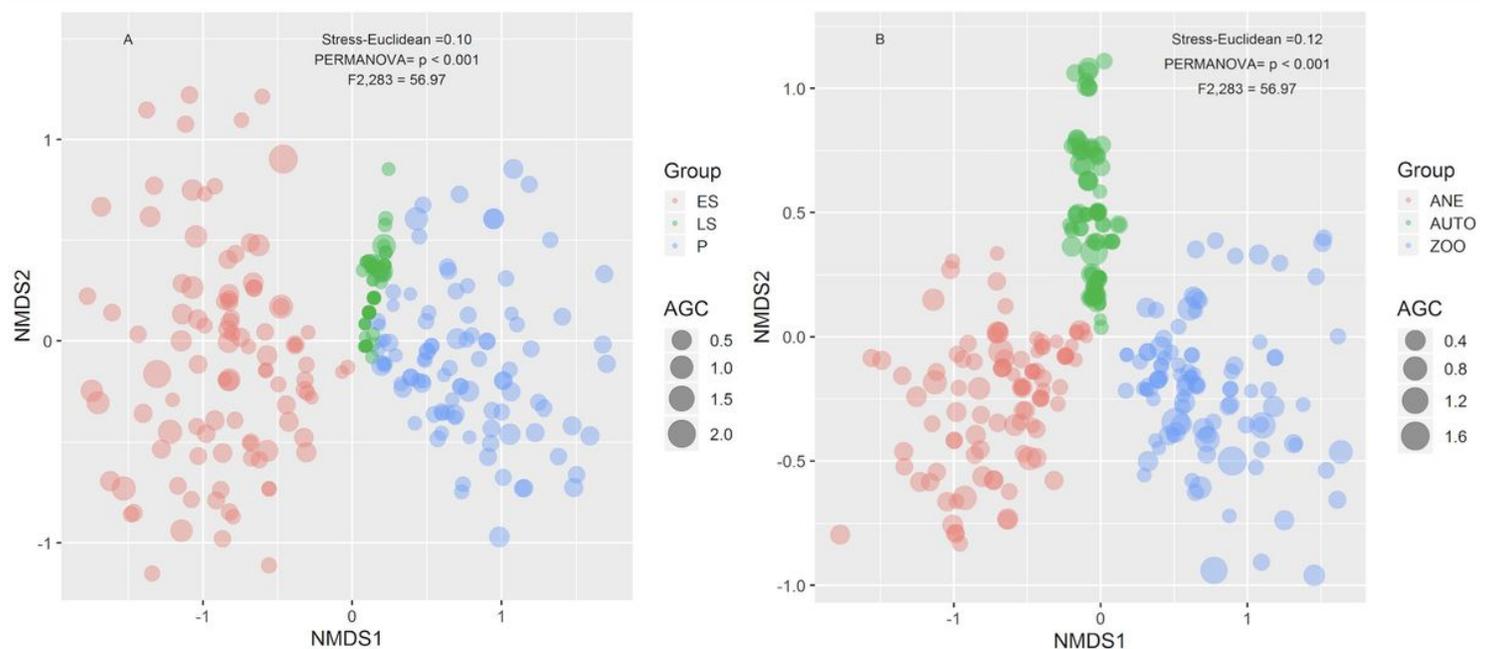


Figure 3

Non-metric multidimensional scaling based on species composition according to aboveground carbon gradient (circles sizes) and the two functional groups: 1) successional strategies (A), such as early secondary (ES); late secondary (LS); Pioneer (P); and 2) dispersal syndromes (B), such as zoochory (ZOO); anemochory (ANE); autochory (AUTO), within 1-ha permanent plots in the Atlantic Forest, Minas Gerais, Brazil.

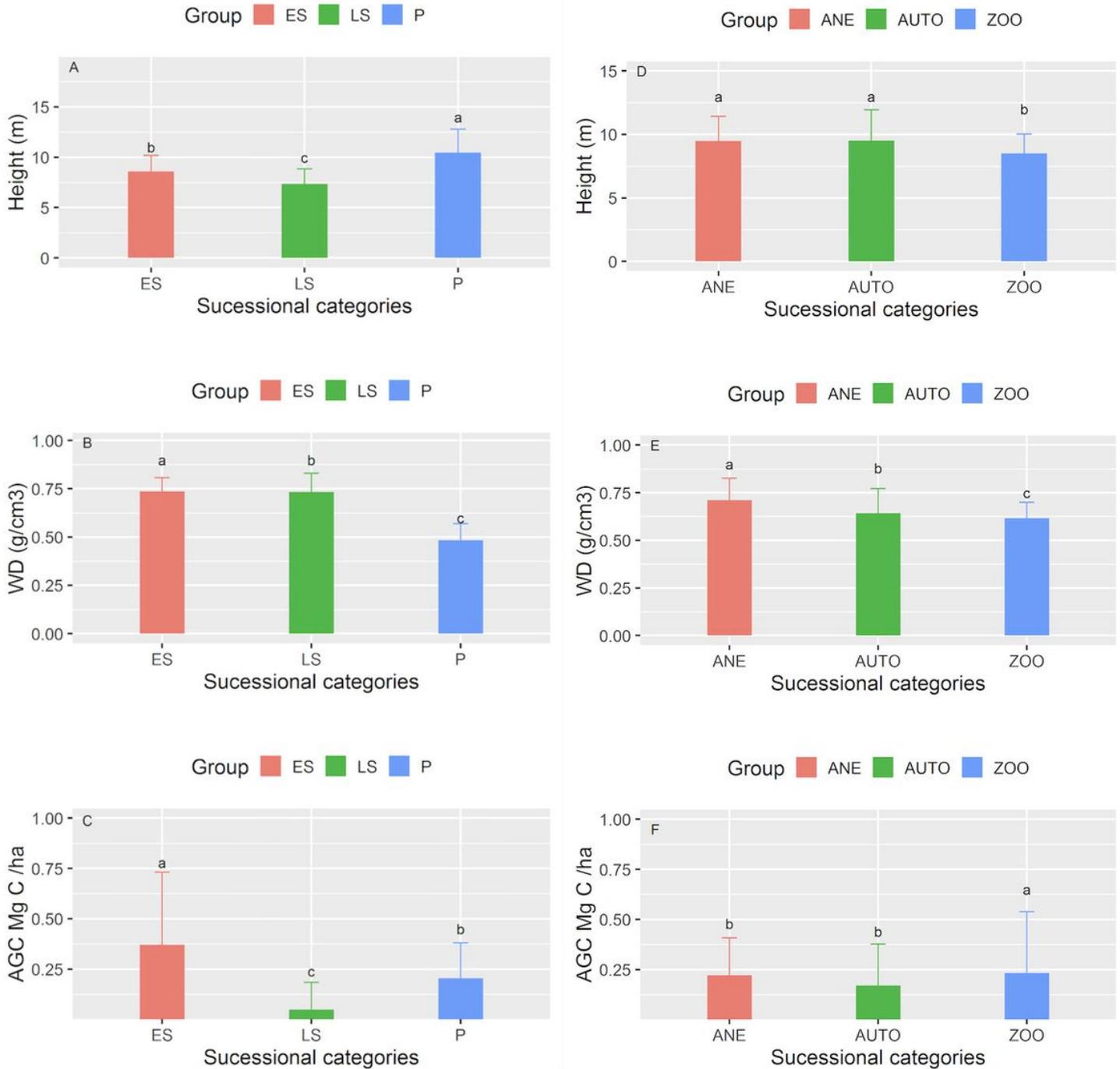


Figure 4

Differences in tree height, wood density and aboveground carbon for the two functional groups: 1) successional strategies, such as early secondary (ES); late secondary (LS); Pioneer (P); and 2) dispersal syndromes, such as zoochory (ZOO); anemochory (ANE); autochory (AUTO). Different letters indicate significant differences (Dunn's test, $P < 0.05$) among the sampled plots.

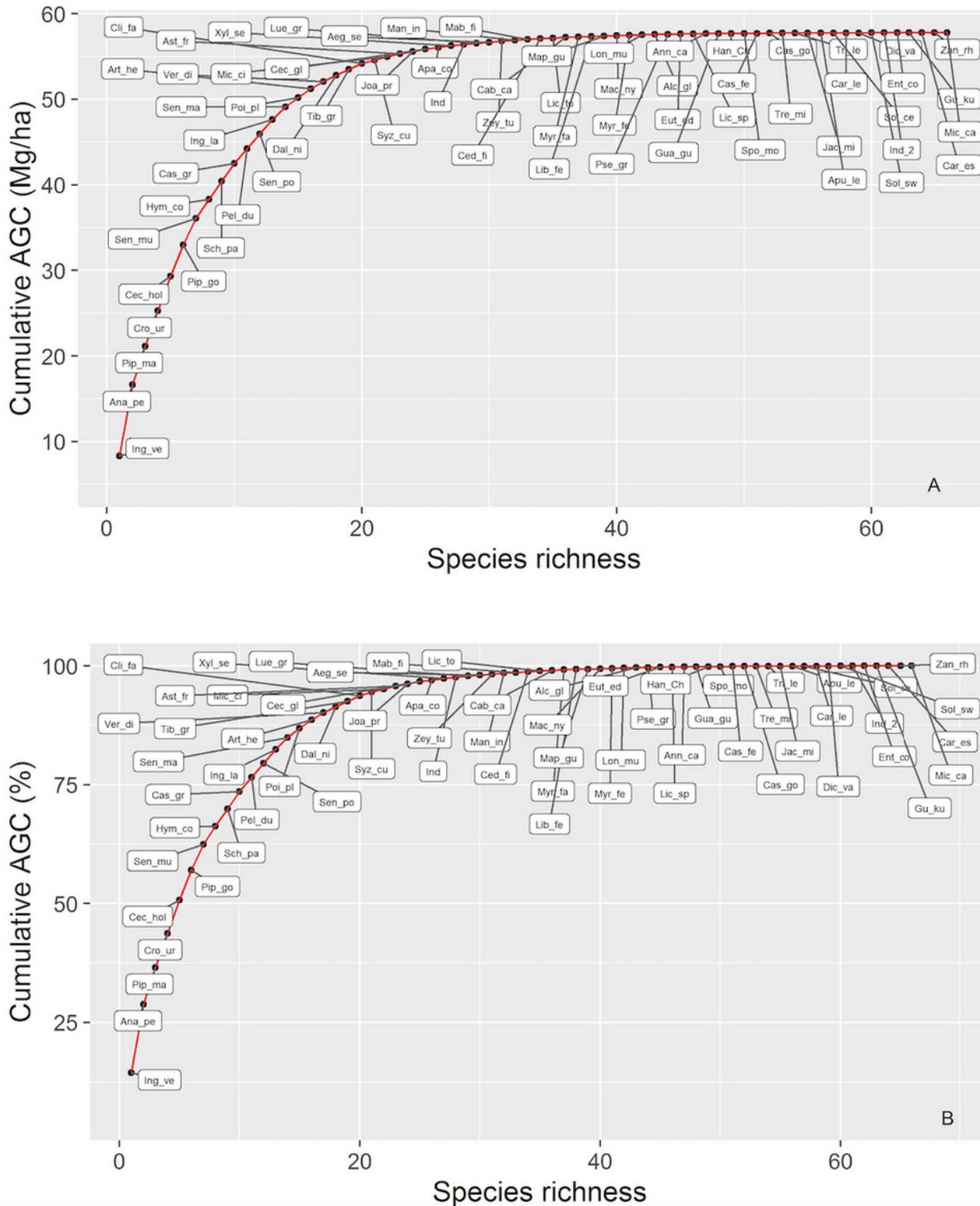


Figure 5

Cumulative aboveground carbon species within 1-ha permanent plots in the Atlantic Forest, Minas Gerais, Brazil. There is a cumulative absolute (A) and proportional carbon (B). See full names of the species in Table A1 from ESM.

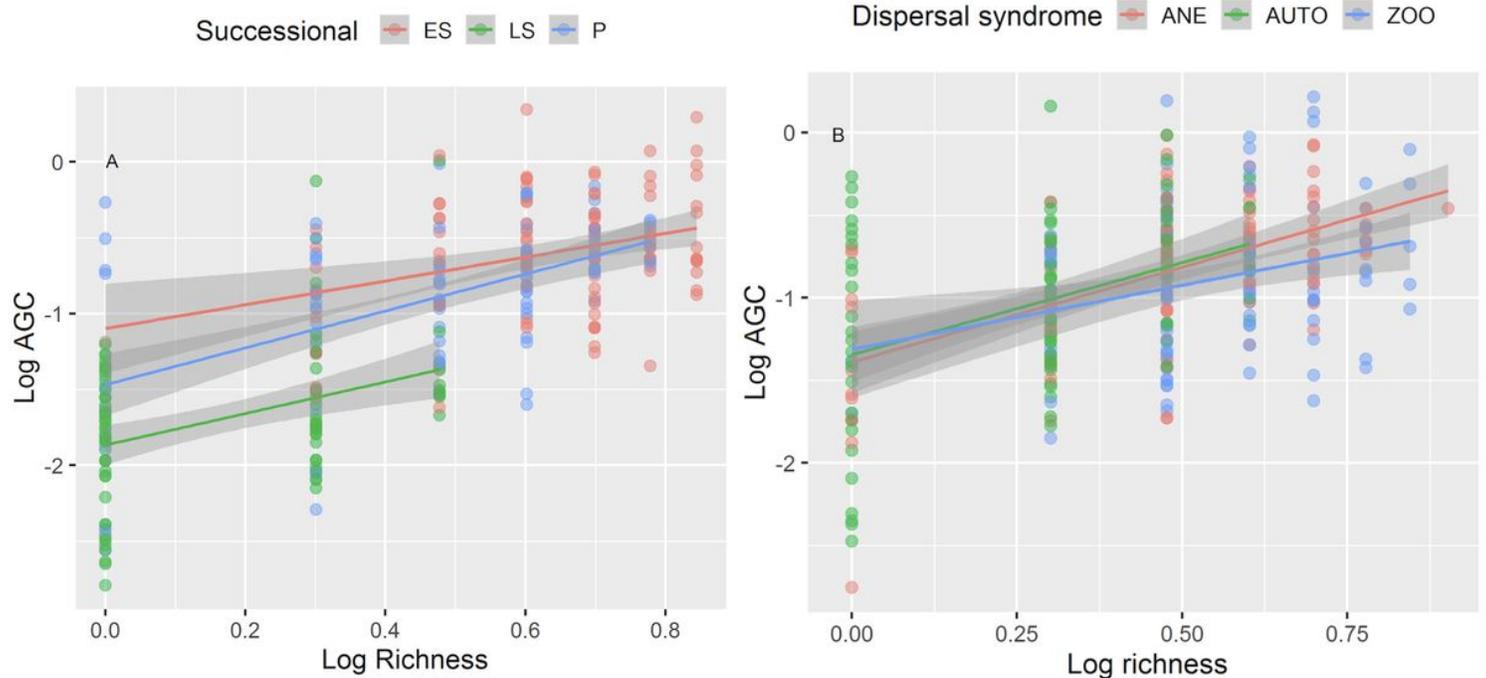


Figure 6

Relationship between aboveground carbon (AGC) and species richness for the two functional groups. Regression lines are shown for each functional group, 1) successional strategies, such as early secondary (ES); late secondary (LS); Pioneer (P); and 2) dispersal syndromes, such as zoochory (ZOO); anemochory (ANE); autochory (AUTO). Dots indicate the observed values, and solid lines represent fit (predicted) values of the LM; the shaded polygons represent the 95% associated with the modelled predictions.

Supplementary Files

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