



Nearby mature forest distance and regenerating forest age influence tree species composition in the Atlantic forest of Southern Bahia, Brazil

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Abstract

The recovery of tree species composition after disturbance depends on dispersal either from nearby forests or from surviving individuals within the disturbed area. Understanding the influence of proximity to mature forests on species composition of regenerating secondary forests can help in predicting the trajectory of recovery from anthropogenic disturbances. Using forest inventory data from a chronosequence of regenerating secondary forests in the Atlantic Forest of southern Bahia, whereby transects were arranged from the edge of mature forest 100 m into the regenerating area, we calculated community weighted means (CWMs) for traits and the natural distribution ranges of species. We used Generalized Linear Mixed Models to investigate whether site characteristics such as forest age, distance from mature forest edge, soil chemical and physical properties, and canopy openness influence traits and natural distribution of regenerating secondary forest tree species. Results show that species traits were associated with regenerating forest age while the proportion of endemic and widespread species was associated with distance from mature forest and regenerating forest age. Irrespective of distance from mature forest, regenerating secondary forests recruit species with heavy and recalcitrant seeds, but this increased with regenerating forest age. Our results contribute to understanding the effects of forest fragmentation and in restoring forests after deforestation.

Keywords Secondary forest · Succession · Dispersal limitation · Species' traits · Endemism · Tropical moist forest

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Introduction

The direct influence of nearby mature forest on disturbed areas were first studied in the context of a debate about the influence of clear-cutting on remaining mature forest fragments of western North America (Keenan and Kimmins 1993; Baker et al. 2013). The spatial extent and magnitude of the influence of nearby forests on disturbed areas are related to several aspects such as species' life history traits, height of the surrounding trees, soil condition and type, slope, aspect, latitude and microclimate (Keenan and Kimmins 1993). In addition, resource availability (e.g., light, water, nutrients) and competitive versus facilitative tree species interactions for resources are the major drivers of species' distributions and their geographic ranges (Ries et al. 2004).

In the tropics, studies of edge effects on forest structure and composition in fragmented landscapes are common, but these studies have mostly focused on gradients from the edge into the interior of mature forests. The most comprehensive set of studies that examine the influence of open edge on the interior of intact mature forests were conducted in the Amazon with the Biological Dynamics of the Forest Fragments Project (Laurance and Williamson 2001; Laurance et al. 2002). However, less work has been on understanding reverse effects, i.e., the influence of intact forests on adjacent deforested areas that are regenerating back to forest (Harper et al. 2005; Baker et al. 2013).

Some studies have tested how forest structure in the early stages of regenerating secondary forests within fragmented landscapes of the tropics are influenced by the distance from mature intact forest islands. At the landscape level, research has demonstrated that forest regrowth rates decrease with distance from remnant forests (Thomlinson et al. 1996; Endress and China 2001; Safar et al. 2020). Similarly, Hooper et al. (2004) and Günter et al. (2007) found that proximity to mature forest promotes stand-level variations of structure in regenerating secondary forests. More recently, our ability to study the influence of nearby mature forest on structural recovery in regenerating secondary forests has increased with new technologies such as terrestrial and airborne LiDAR and remote sensing (Palace et al. 2016; Shapiro et al. 2016; Becknell et al. 2018). Studies designed to understand the influence of nearby mature forest on species composition and species functional characteristics that may explain mechanisms of community assembly during regenerating forest development, however, are rare and still rely on intensive fieldwork (Baraloto et al. 2010).

Species composition of regenerating forests after disturbance depends on dispersal either from nearby mature forests or from surviving individuals within the disturbed area. The effectiveness of seed dispersal in disturbed areas depends on species' traits and the availability of suitable habitat. Dispersal limitation can be a constraint to tree species recruitment (Bullock et al. 2002) because distance influences seed dispersal spatially (Reid and Holl 2013; Piotta et al. 2019). This results in distinct floristic assemblages along a distance gradient from remnant forests into open areas. For example, in Belize, Kupfer et al. (2004) found that species composition changed across a 150 m distance of remnant forests, with a higher frequency of legume and liana species establishing within abandoned crop fields farther away from the forest; In Puerto Rico, Myster (2003) found more mid- and late-successional tree species regenerating in old pastures and coffee plantations that were close to remnant mature forest compared to those farther away; and similarly, Ferguson et al. (2003) found that proximity to the forest edge increased the presence of fleshy-fruited regenerating trees and shrubs in old disused agricultural lands in Guatemala.

Even though studies have demonstrated gradients of floristic assemblages with distance from remnant mature forests, the ecological processes driving these changes have not

received much attention (Craven et al. 2015). The influence of nearby mature forest on seed dispersal and on the soil and light resource have been proposed to explain differences in species richness and composition in the regenerating secondary forests (Hooper et al 2004; Günter et al. 2007; Neo et al. 2017). However, initial heterogeneity of both environmental and surviving vegetational patterns at the local and landscape level make the interpretation of spatial variation in species composition in secondary forests difficult. Yarranton and Morrison (1974) noted that spatial variation in secondary forest structure and composition can be confounded with environmental heterogeneity and regenerating forest age. Thus, an integrated understanding of the influence of nearby mature forest on regenerating secondary forests must properly address environmental heterogeneity and successional age.

Here, we studied the influence of nearby mature forest distance and regenerating forest age on tree species composition in the Atlantic Forest hotspot of southern Bahia, which holds a higher level of species endemism and richness than any other part of the Neotropics (Mori et al. 1981; Martini et al. 2007; Thomas and Barbosa 2008; Ostroski et al. 2018). This region is considered to have been a forest refugium during the Pleistocene (Whitmore and Prance 1987) and a potential center of diversity for some major groups of plants (Gentry 1992). The coastal forest of southern Bahia is part of the Brazilian Atlantic forest that encompasses the coastal rain forests up to 300 km inland in its southern portion (Oliveira-Filho and Fontes 2000). The Brazilian Atlantic forest is an important biodiversity hotspot that has been reduced to less than 13% of its original cover (SOS Mata Atlântica 2020). In addition to habitat loss, fragmentation and local extinction of birds and mammals represent an imminent threat to several plant species (Silva and Tabarelli 2000; Galetti et al. 2013) and, as in other tropical forests, local tree species with seed dispersal constraints are probably the most affected by habitat loss and fragmentation (Metzger 2000; Tabarelli and Peres 2002). Consequently, understanding the influence of nearby mature forest on species composition of regenerating secondary forests can help in designing conservation strategies, predicting recovery from anthropogenic disturbances, and mitigating effects of forest fragmentation in tropical landscapes (Matos et al. 2019).

In our study, we tested whether the adjacent mature forest and the age of the regenerating area itself influences the composition of the regenerating forest. Our hypothesis is that tree species trait composition and the proportion of endemic and widespread species are associated with distance from mature forest and the age of the regenerating forest. We also examined whether soil chemical and physical properties and the openness of the regenerating forest canopy also have influence on the regenerating forest trait composition and proportion of endemic and widespread species.

Methods

Study sites

The study was conducted in the Serra do Conduru State Park, southern Bahia, Brazil (14°25' S and 39°05' W). The park encompasses about 10,000 ha and is composed of a mosaic of forest patches in different stages of disturbance and regeneration, including remnants of undisturbed mature forests. The parklands are interspersed with private inholdings. This mosaic facilitated the establishment of a chronosequence of secondary forest stands. The study sites are at an elevation of 120–300 m asl. The average monthly temperature is 24 °C, with annual average precipitation of 2000 mm evenly distributed throughout the

year (Landau 2003). The natural vegetation is classified as tropical moist forest (Thomas and Barbosa 2008), with rolling to undulating topography (10–30% slope). Typical haplorthox soils with low fertility and high iron content prevail in the region (Santana et al. 2002).

Chronosequence classification and sampling design

Sites were selected carefully to minimize variation in environmental conditions arising from past land use history and inherent variation in soils and hydrology in relation to landscape-scale topography. The estimation of stand ages and past land uses was based on a sequence of available aerial photographs and remote sensing data, which provided precise and verifiable estimates of stand age. Changes in forest cover and land use in a 5000-ha area inside Serra do Conduru State Park were estimated from 1965 to 2007. The remote sensing windows were based on aerial photos taken in 1965, 1975, 1986, 1997, 2002, and 2007. Land use maps were generated for every set of aerial photos, and maps of forest age classes were derived using GIS. Information on type and intensity of past land use was gathered by interviewing local farmers.

A total of 95 secondary forest stands larger than 3 ha and adjacent to a mature forest were found in the study area. Ages ranged from 10 to 43 years. To study changes in forest structure and composition with forest development, fifteen stands were randomly selected to cover three age classes: 10–12, 22–25, and 37–43 years old, with five replications each. All secondary forest stands selected were established next to a mature forest and had been cleared and burned, followed by 1–2 years of manioc (*Manihot esculenta* Crantz) cultivation, the principal carbohydrate consumed by the people of the region. At each secondary forest, a 100-m-long transect was established from the mature forest edge into the secondary forest.

Vegetation inventory

Forest inventory plots were installed in each secondary forest, comprising five contiguous 20 m × 10 m plots. The plots were continuously distributed along the 100-m transect towards the center of the secondary forest. All tree species with stems ≥ 5 cm diameter at breast height (dbh) were measured (dbh and height) and identified or recorded as a ‘morpho-species.’ A voucher for identification was collected for each morpho-species. Voucher specimens from the vegetation inventory were identified by comparisons with herbarium specimens deposited at the “Centro de Pesquisas do Cacau” (CEPEC) herbarium in Ilhéus, Bahia. All botanical voucher specimens were deposited in the CEPEC herbarium.

Light environments

The light environments of the 15 secondary forests were measured at 75 sample points with a hemispherical canopy photograph. In each secondary forest, five measurements were made at 20-m intervals along the 100-m transect from the mature forest edge into the secondary forest (Fig. 1).

On uniformly cloudy days, photographs were taken at each sample point using an 8-mm hemispherical lens with a Nikon 35 mm camera. The camera was fixed on a tripod and mounted at 1 m above the ground on a leveling device with a compass for image alignment.

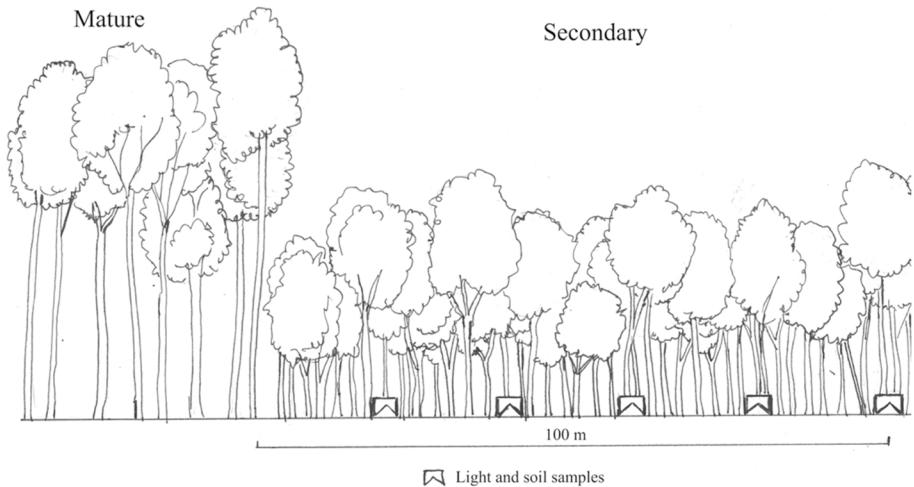


Fig. 1 Illustration of the experimental design of forest inventory plots (five contiguous 20 m × 10 m plots from the mature forest edge) and sample points of soil chemical and physical properties and canopy openness

Photographs were scanned and converted into digital images. Images were analyzed using Gap Light Analyzer 2.0 (Frazer et al. 1999). This software converts images into gray scale and then binary (black and white pixels) using a given gray threshold. The threshold can be manually adjusted to compensate for different sky conditions, but a fixed threshold was used in this study since the photographs were taken under similar sky conditions. Measures of canopy openness were estimated for every image. Canopy openness was the percentage of open sky seen from the forest floor.

Soil sampling

In each secondary forest, five soil samples were taken at 20-m intervals. Measurements were made at 20-m intervals along the 100-m transect from the mature forest edge into the secondary forest (Fig. 1).

Soils were sampled using two methods. The first method (for chemical analysis) was a composite sample of three sub-samples taken at 5-m intervals, encompassing the edges and center of forest inventory plots. Soil sub-samples were collected from 0–10 cm depth immediately below the litter layer using a hammer and a 10 cm stainless steel tube (1 dm³) and pooled together in labeled plastic bags. The soil samples were analyzed for pH (water), Mehlich-1 extractable potassium (K), total nitrogen (N) using the Kjeldahl method, and total carbon (C) and organic matter (OM) using the Tiurin method. All soil analyses were performed at the “Centro de Pesquisas do Cacau” (CEPEC/CEPLAC) soil laboratory.

The second method (for physical analysis) was a composite sample of two sub-samples taken 5 m apart with a Kopecky’s ring. This ring is made of stainless steel (5 cm diameter, 2.5 cm depth, and volume of ≈50 cm³) and was driven into the soil with a hammer. The surface litter was removed before sampling. Samples were carefully extracted from the ring and stored in metal containers. Containers were labeled and sealed immediately after the samples were taken to preserve soil moisture. At the soil laboratory, soil samples were weighed, dried at 105 °C for 48 h, and weighed again to determine soil moisture content

(difference between wet and oven dried weight). Bulk density was determined by the ratio between soil oven-dried weight and the ring volume.

Natural distribution range and species' traits

The natural distribution range and the traits characterizing dispersal mode, seed dormancy, weight of 1000 seeds, ability to persist in the soil seed bank, and N-fixation were compiled from the literature for every species. The natural distribution ranges were compiled from Forzza et al. (2010) and categorized as: widespread South America (WSA), endemic of the Atlantic forest of eastern Brazil (EEB), and endemic of the Atlantic forest of southern Bahia and northern Espírito Santo (EBA), following Thomas et al. (1998).

Species with reports of root-nodules were classified as nitrogen-fixing species. Information on nodulation of tree species was compiled from Sprent (2009). The dispersal mode was categorized as biotic (animal-dispersed) or abiotic (wind and explosive dispersal). The categorization of dispersal modes included an extensive literature review and examination of herbarium specimens. The information on seed dormancy and weight of 1000 seeds was obtained from the Seed Information Database (Royal Botanic Gardens Kew 2017) and the Compendium of Information on Seed Storage Behavior (Hong et al. 2000). For some species for which information was not available, seed viability and/or seed weight was estimated using information of congeneric species, species descriptions in the literature, and herbarium specimen verification. Because not all orthodox seeds are dormant (Murdoch 2014), the ability of each species to persist in the soil seed bank was also included as a trait. Persistence in the soil seed bank was determined after a literature search of soil seed bank studies performed in the Neotropics (Young et al. 1987; Nepstad et al. 1996; Dalling et al. 1997; Dupuy and Chazdon 1998; Wijdeven and Kuzee 2000; Araujo et al. 2001; Baider et al. 2001; Grombone-Guaratini and Rodrigues 2002; Sautu et al. 2006; Costalonga et al. 2006; Gasparino et al. 2006; Baraloto and Forget 2007; Mamede and Araújo 2008; Braga et al. 2008).

Data analyses

We calculated community weighted means (CWM) for each functional attribute and natural distribution range. For the categorical variables, CWM represents the proportion of individuals for each functional attribute and natural distribution range (Ricotta and Moretti 2011). Then, we investigated how functional attributes and natural distribution range (CWM) responded to mature forest distance (mature.forest.distance) and regenerating forest age as fixed or explanatory variables using a Generalized Linear Mixed-effects Models (GLMM). The secondary forest fragment (site) was the random effect. This statistical approach of random intercept allows the model to control possible variance in the intercept values of each site (Zuur et al. 2009), although we were only interested in the population model. We also added the 20×10 m inventory plots (plot) as another random effect to account for plot-level variability (Bates et al. 2014; Harrison 2015). We used binomial distribution family for all variables except the weight of 1000 seeds, where we applied a Gamma distribution. All models were validated using the relationship between standardized residuals with standardized normal quantiles and, for the weight of 1000 seeds, the residuals were tested for deviation from the normal distribution using the Shapiro test. To compare the effect size, all explanatory variables were standardized, centering on the mean and rescaling to unit variance. To account for possible confounding effects promoted

by environmental gradients in the models, we also included co-variables that could also influence the response variable. However, to avoid problems with variance inflation we included into the models only variables with Spearman correlations values lower than 0.6 (Fig. S1), i.e., canopy openness (CO), pH, potassium (K), nitrogen (N) and bulk density (BD) were included while total carbon (C) and organic matter (OM) were not included. Thus, we defined our global model as follows:

$$\text{CWM} \sim \text{age} + \text{mature.forest.distance} + \text{CO} + \text{pH} + \text{K} + \text{N} + \text{BD} + (\text{random} = \text{site})$$

We selected our models using the corrected Akaike Information Criterion (AICc). All models with $\Delta\text{AICc} \leq 4$ were considered as plausible models (Burnham and Anderson 2002). Then, we used the approach of Multimodel Inference to obtain the effect size and the relative importance of each fixed variable, which allowed us to account for model selection uncertainty or precision (Burnham and Anderson 2002). When the 95% confidence interval of an explanatory variable did not include zero, the effect was considered to have substantial evidence in support of it. (Burnham and Anderson 2002; Grueber et al. 2011; Symonds and Moussalli 2011).

To calculate CWM we used the function “functcomp” from the “FD” package, which follows the calculation proposed by Lavorel et al. (2008). For variables standardization we used the function “decostand” and applied the standardization method “sta” (Oksanen et al. 2020) from the “Vegan” package. The GLMM models were built using the function “lmer” from the package “lme4”. For model selection and multimodel inference we used the function “dredge” from the “MuMIn” package. Analyses were performed in the R statistical computing language, version 3.6.0 (R Core Team 2019).

Results

We recorded a total of 3405 individuals of 307 tree species. Traits and natural distribution range of recorded species are shown in Table 1. While measures of soil properties and canopy openness were correlated with regenerating forest age, they did not correlate with distance from mature forest edge (Fig. S1). All soil measures and canopy openness in regenerating forest plots immediately adjacent to mature forest edges were similar to plots at 100 m into the regenerating forests.

Table 1 Traits by natural distribution range of 307 inventoried tree species found in a chronosequence of secondary forests in the coastal forests of southern Bahia, Brazil

Natural range	N-Fixer		Zoochoric dispersal		Recalcitrant		Persist in seedbank		Average and standard error of weight/1000 seeds (g)
	No	Yes	No	Yes	No	Yes	No	Yes	
EBA	60	7	8	59	22	45	59	8	2320.0 (633.2)
EEB	118	7	19	106	56	69	95	30	568.4 (102.2)
WSA	108	7	10	105	51	64	82	33	759.1 (123.7)

WSA (widespread South America), EEB (endemic of the Atlantic forest of eastern Brazil), and EBA (endemic of the Atlantic forest of southern Bahia and northern Espírito Santo) are species' natural distribution range

The multi-model inference approach showed substantial evidence of associations between all species’ traits and regenerating forest age, except the proportion of zoochoric dispersal. While the proportion of nitrogen-fixing species and the proportion of species that persist in the soil seed bank were negatively associated with regeneration age, the proportion of recalcitrant species and weight of 1000 seeds were positively associated (Fig. 2). Additionally, regeneration age showed substantial evidence of association with species natural distribution range. The proportion of EBA species was positively associated with regeneration age, while the proportion of WSA species was negatively associated (Fig. 2).

Among the species’ traits, the only trait associated to distance from mature forest was the proportion of nitrogen-fixing species, which showed evidence of a positive association,

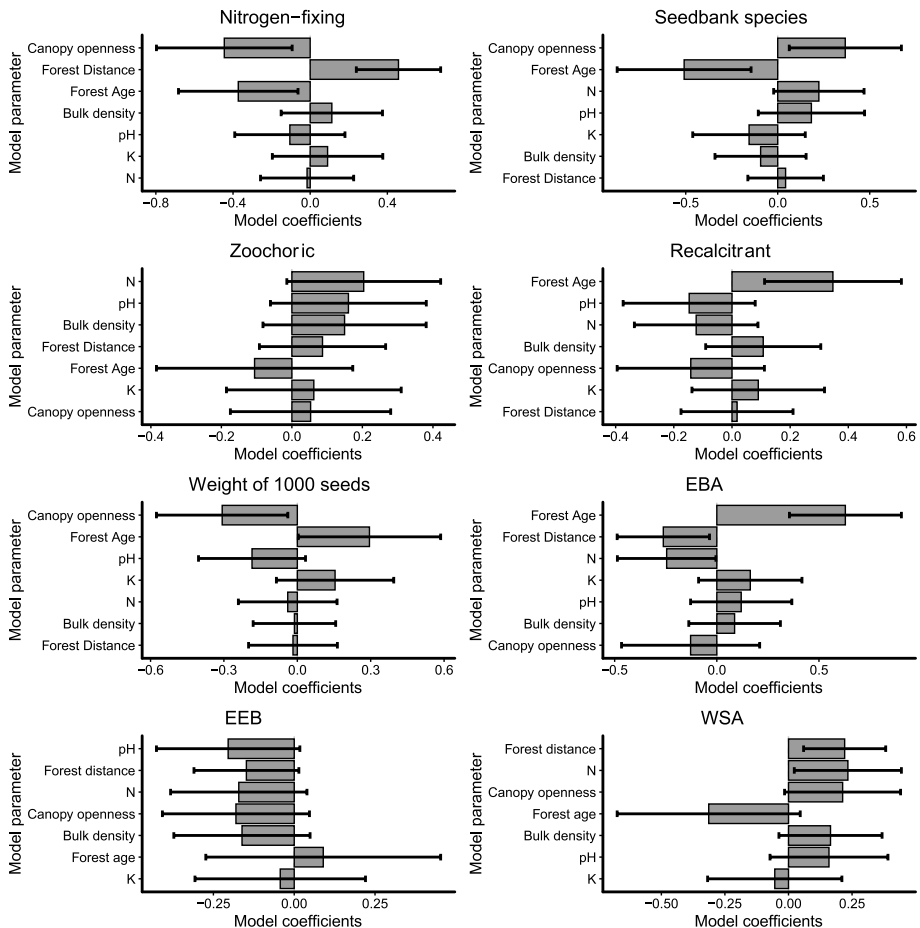


Fig. 2 Results of the multimodel inference (model averaging) with all candidate models ($\Delta AIC_c \leq 4$). All averaged coefficients (95% confidence intervals). All explanatory variables were standardized, but the original units were: Forest distance (m); Forest age (years); Canopy openness (%); Soil bulk density (g/cm^3); K = Potassium ($cmol\ c/cm^3$); pH = pH in H_2O ; N = Total nitrogen ($cmol\ c/cm^3$). Nitrogen-fixing, Seedbank species, Zoochoric, Recalcitrant, and Weight of 1000 seeds are species’ traits. WSA (widespread South America), EEB (endemic of the Atlantic forest of eastern Brazil), and EBA (endemic of the Atlantic forest of southern Bahia and northern Espirito Santo) are species’ natural distribution range

i.e., nitrogen-fixing species proportion increased with distance from mature forest. In addition, distance from mature forest showed substantial evidence of associations with species natural distribution range. There was evidence to support an association between distance from mature forest with the proportion of WSA species (positive association) and EBA species (negative association).

Environmental variables also showed high explanatory importance in our models (Fig. 3). For species' traits, there was evidence to support a negative association of canopy openness with the proportion of nitrogen-fixing species and a positive association of canopy openness with the proportion of species that persist in the soil seed bank. For species'

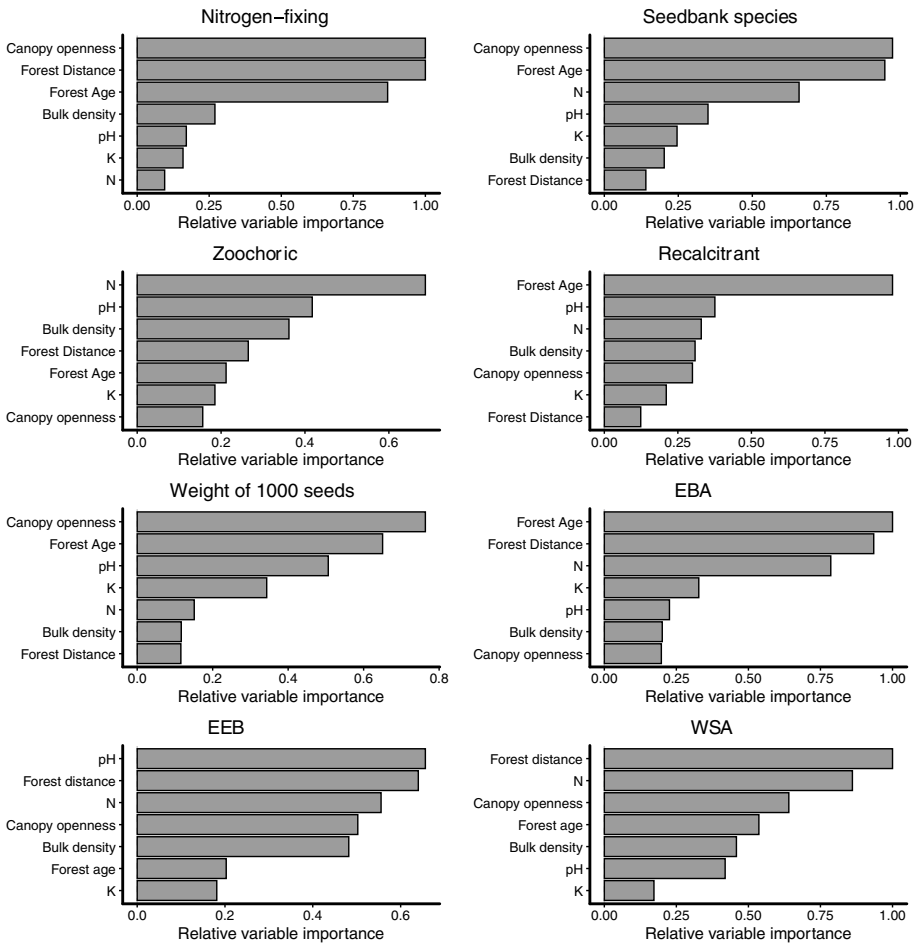


Fig. 3 Results of relative importance values of each explanatory variable (sum of the weights of all models that the variable appears $\Delta AICc \leq 4$). All explanatory variables were standardized, but the original units were: Forest distance (m); Forest age (years); Canopy openness (%); Soil bulk density (g/cm^3); K=Potassium ($cmol\ c/cm^3$); pH=pH in H_2O ; N=Total nitrogen ($cmol\ c/cm^3$). Nitrogen-fixing, Seedbank species, Zoochoric, Recalcitrant, and Weight of 1000 seeds are species' traits. WSA (widespread South America), EEB (endemic of the Atlantic forest of eastern Brazil), and EBA (endemic of the Atlantic forest of southern Bahia and northern Espírito Santo) are species' natural distribution range

natural distribution range, there was evidence to support a positive association of soil nitrogen (N) with the proportion of WSA species and a negative association of soil nitrogen with the proportion of EBA species.

Discussion

Influence of regeneration age and distance from mature forest on species' traits

Our results show that successional changes in forest structure leads to lower light availability but higher soil nutrient contents (C, N, and K) in regenerating secondary forests. Changes in environmental factors directly prevent the establishment or persistence of tree species during forest regeneration through environmental filtering (Uriarte et al. 2010; Lebrija-Trejos et al. 2010; Kraft et al. 2015). In general, studies have used functional and reproductive traits to assess the effects of environmental filtering in community assembly based on the main assumption that particular combinations of traits are expected under different environments (Walker and Chapin 1987; Uriarte et al. 2010). As found in our study, traits related to the establishment and persistence of tree species change in importance with forest development (Lasky et al. 2014; Craven et al. 2015). This is because in early stages of stand development, regenerating secondary forests are commonly dominated by pioneer tree species, with life history traits that favor establishment and fast growth in disturbed sites (Finegan 1996). Typical traits of pioneer tree species are small seed size, abundant seed production and dispersal, seed dormancy, photoblastic seeds, high light saturation intensity and compensation point, and high rates of photosynthesis, respiration, and transpiration (Bazzaz 1979; Wright et al. 2004).

With forest development, changes in the life history traits of trees are mainly caused by the replacement of dominance from pioneer species to long-lived late successional species (Opler et al. 1980; Ibarra-Manríquez and Martínez-Ramos 2001; Chazdon et al. 2003; Kang and Bawa 2003; Lebrija-Trejos et al. 2010; Craven et al. 2015). For instance, Opler et al. (1980) found that flower and pollinator sizes became larger and mean seed weight and associations with animal dispersal increased with forest development, while inbreeding, the number of seeds per fruit, and seed dormancy decreased. Our results show similar associations. The weight of 1000 seeds increased with regenerating forest age, as did the proportion of trees with recalcitrant seeds, whereas the proportion of nitrogen-fixing species and species that persist in the soil seed bank decreased with the age of regenerating forest. These changes in dominant life history traits across the chronosequence of regenerating secondary forests can be mostly attributed to the correlation found between forest age and environmental variables (soil properties, canopy openness), indicating that community assembly in these secondary forests may be influenced by environmental filtering. However, we found no associations of soil characteristics or stand canopy openness with distance from mature forest edge into the regenerating forest. This suggests that the spatial variation in tree species composition found with distance from mature forest edge is unrelated to soil conditions or the degree of canopy openness.

Assuming that dispersal limitation associated with the distance from mature forest edge influences the contribution of seed rain to tree regeneration, we expected to find spatial variation in tree species traits. However, we only found that the proportion of nitrogen-fixing species was positively influenced by distance from mature forest. None of the other traits used in this study were influenced by distance from mature forest. Perhaps distances

longer than 100 m from the mature forest edge or a greater selection of life history traits are necessary to detect the influence of nearby forests on regenerating tree species' traits. Our study supports many other studies that show higher numbers of N-fixing species in younger regenerating forests, and this declines with forest regeneration age (Gehring et al. 2005; Davidson et al. 2007; Batterman et al. 2013; Winbourne et al. 2018). In addition, the positive influence of distance of mature forest edge on the proportion of N-fixing species suggest differential seed dispersal of N-fixing species as compared to other species. As in our study, Kupfer et al. (2004) found a higher frequency of legumes establishing within abandoned crop fields farther away from the forest and no evidence of differences in soil characteristics between crop fields closer or farther from the forest. Other studies in temperate forest ecosystems suggest that N-fixing species have higher water use efficiencies, which might be a reason why such plants are more abundant in the open, desiccating environment of younger forests farther from mature forest patches (Wright et al. 2003). Further studies need to examine the relationships of N-fixing species dispersal and establishment in more detail.

Influence of secondary forest age and distance from mature forest on species natural distribution range

Research on the recovery of widespread and endemic tree species during regenerating secondary forest development has been controversial. Liebsch et al. (2008) estimated that about 2000 years are necessary for young secondary forests to reach the proportions of endemic species that occur in mature forests in the Brazilian Atlantic forest. Our results suggest they might have underestimated the potential of regenerating secondary forests to recover populations of endemic tree species. In fact, a significant body of research elsewhere found trends similar to the ones of our research, with potentially rapid recovery of endemic tree species with secondary forest development (Greig-Smith 1952; Kessler 2001; Endress 2002; Gemerden et al. 2003; Piotta et al. 2009; Chai and Tanner 2010).

The results of our study show a positive relationship between the proportion of individuals of endemic species with regenerating secondary forest age, indicating a shift in species characteristics from widespread to endemic species in the first 40 years of forest development. Endemic species recovery during secondary forest development has been traditionally measured in two ways: changes in the proportion of endemic species, and changes in the proportion of individuals of endemic species. Part of the debate about recovery of endemic tree species in secondary forests may be explained by differences in the rates of recovery of species and individuals. While recovery of the proportion of endemic species in secondary forests approaches mature forest levels very early in development (Greig-Smith 1952; Endress 2002; Chai and Tanner 2010), recovery of the proportion of individuals of endemic species takes much longer to reach those found in the mature forest (Greig-Smith 1952; Piotta et al. 2009; Chai and Tanner 2010; Matos et al. 2019; Safar et al. 2020).

Endemic species occur more commonly on relatively infertile substrates (Cowling and Holmes 1992); and are known to be more restricted to stressful habitats and unable to compete with more widespread species for resources in more productive habitats (Lavergne et al. 2004). In addition, endemic plant species have lower colonization ability than widespread species (Byers and Meagher 1997), i.e., local persistence is a key feature of populations of these species. Consequently, local endemic trees should exhibit a suite of life history traits reflecting stress-tolerance as well as traits related to low frequency and short distance dispersal abilities. In this study, local endemic trees exhibit, in general, heavy and

recalcitrant seeds that germinate immediately after dispersal, factors which limit dispersal frequency and distance (Greene and Johnson 1993). The only trait that reflects stress tolerance used in this study was symbiotic nitrogen fixation, which was positively correlated with the proportion of local endemic species (EBA) and may reflect their tolerance to relatively infertile substrates.

Our results show that distance from mature forest, mediated by regenerating secondary forest age, influenced the recovery of local endemic and widespread tree species. Thus, medium to large-sized anthropogenic disturbances may result in biotic homogenization by potentially restricting the ability of local endemic species to recolonize secondary forests, while favoring widespread species establishment in fragmented tropical landscapes (Lôbo et al. 2011; Solar et al. 2015).

Implications for forest conservation in the region

The results of this research showed that secondary forests are successfully recruiting trees common to mature forest stands, including several endemic and threatened tree species. Furthermore, the results indicate that endemic species recovery is more rapid in areas immediately around forest remnants. These findings strongly suggest that secondary forests can serve as refuges and reservoirs of biodiversity for native trees in the region. Thus, policies that guarantee the protection of the last remnants of the Atlantic forest and promote restoration strategies building around these forests can be fruitful for tree species conservation in the region.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10531-021-02192-w>.

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