Resprouting drives successional pathways and the resilience of Caatinga dry forest in human-modified landscapes

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ABSTRACT

Tropical forest regeneration has gained renewed interest in recent years as secondary forests have being considered biodiversity repositories and a key source for globally relevant ecosystem services as climate regulation and carbon sequestration and storage. Here, we address the regeneration of a Caatinga dry forest in the context of slash-and-burn agriculture and chronic anthropogenic disturbance by examining forest regeneration mechanisms and a comprehensive set of community-level plant diversity measures (i.e., taxonomic, functional, and phylogenetic) in regenerating (4 to 70-yr old) and old-growth forest stands. Resprouting from root suckers was the predominant regeneration mechanism across recently abandoned crop fields. Overall, regenerating forests were similar to old-growth forests in terms of taxonomic and functional composition, and functional and phylogenetic diversity. Moreover, except for the taxonomic diversity, community-level plant diversity measures were not related to forest age or soil properties. Our results suggest that Caatinga dry forest covering sandy soils is particularly resilient due to regeneration driven by resprouting. The same set of plant species dominates the entire regeneration process, including old-growth forest stands. Accordingly, Caatinga dry forest regeneration may follow an initial composition model, rather than following a directional and deterministic trajectory associated with species replacements. This initial composition model probably results from a combination of three factors: (1) early regeneration driven by resprouting rather than seed arrival and seedling recruitment; (2) biomass accumulation mostly due to growth by early colonizers and by those species able to resprout after chronic anthropogenic disturbance and during forest regeneration; and (3) the co-occurrence of functionally distinct plant species. Accordingly, resprouting can guarantee some level of resilience, and hence, the services provided by secondary forests. Nevertheless, forest dynamics in landscapes inhabited by forest-dependent people are affected to a great extent by the nature of the imposed pressures and the ecological profile of the remaining flora.

1. Introduction

Tropical forests represent an irreplaceable ecosystem in terms of biodiversity conservation, provision of globally relevant ecosystem services (e.g., carbon storage, regulation of water flows) and forest products for local human populations (Beer et al., 2010; Houghton et al., 2015; Laurance et al., 2014). However, old-growth forests across the tropics continue to be converted into mixed land-use mosaics, usually consisting of a combination of pasture, crop fields, and forest stands of varying ages, which in many situations result from the practice of letting the fields lie fallow (Chazdon, 2014; Tabarelli et al., 2010; Arroyo-Rodríguez et al., 2017). In this global ecological context, secondary or

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regenerating forest stands often account for much of the remaining forest (Brown and Lugo, 1990; Chazdon, 2003; Chazdon et al., 2009, 2011, 2016; Poorter et al., 2016). Across many regions, the area of secondary or regenerating forests already exceeds that of old-growth forests (FAO, 2018). This is due to the intense land use associated with commercial and subsistence agriculture (Chazdon et al., 2011), cattle ranching, and logging activities, as well as demographic trends promoted by rural migrations to urban areas (Mather and Needle, 1998; FAO, 2018).

Consequently, secondary forests are considered a key component in the context of biodiversity conservation through the provision of ecosystem services which impact the quality of life of rural populations as well as provide a source of forest products for subsistence or commercial purposes (Barlow et al., 2007; Chazdon et al., 2009; Portillo-Quintero et al., 2014). This emerging role in global sustainability and conservation has renewed scientific interest in secondary forest succession and regeneration in human-modified landscapes (see Chazdon et al., 2016; Cueva-Ortiz et al., 2020; Poorter et al., 2016). In this context, it is essential to understand the patterns of secondary forest succession and their resilience, to both anticipate and enhance their potential for providing ecosystem services (Chazdon, 2003; Saatchi et al., 2011; Chazdon et al., 2016; Arroyo-Rodríguez et al., 2017; FAO, 2018; Rozendaal et al., 2019; Souza et al., 2019). This is particularly the case in landscapes and regions dominated by forest-dependent people, such as those in seasonally dry tropical forests (SDTF, *sensu* Pennington et al., 2009), where human populations are exceptionally dependent on firewood, fodder, timber, and slash-and-burn agriculture to support shifting cultivation (Chazdon, 2014; Souza et al., 2019).

Any ecosystem service that secondary forests are expected to offer across human-modified landscapes may be related to two parameters of forest regeneration: recovery rate and successional trajectory (Guariguata and Ostertag, 2001; Feldpausch et al., 2007; Matos et al., 2020). Recovery rate can be likened to the speed at which forest attributes (e.g., biomass, species richness) reach the scores exhibited by old-growth forests and can also be considered a measurement of resilience (Cole et al., 2014). On the other hand, successional trajectories in secondary forests indicate patterns of species and functional group replacements as regeneration proceeds (see Brown and Lugo, 1982; Guariguata and Ostertag, 2001; Chazdon, 2003). However, regeneration in tropical forests following land abandonment occurs at varying rates and can follow diverse successional trajectories due to multiple drivers operating at local to landscape and regional spatial scales (Chazdon et al., 2007; Lohbeck et al., 2013; Arroyo-Rodríguez et al., 2017). Land-use history, proximity to propagules, water and nutrient availability, plant-animal interactions, and stochastic events are just some of the multitude of factors that can influence the recovery rates and successional trajectories (Hammond, 1995; Chazdon, 2003; Holl, 2012). For example, forest regeneration tends to proceed slowly (i.e., low resilience) if the previous land-use resulted in soil degradation or when mechanisms of forest regeneration (e.g., reed rain, soil seed bank, vegetative regeneration) have been eliminated (Vieira et al., 2014). This would result in arrested succession in response to human disturbances (Holl, 2007).

Tropical forest regeneration has been classically thought to follow directional successional trajectories with predictable shifts in structural attributes, plant species and composition of functional groups along the regeneration process; particularly related to light (Bazzaz and Pickett, 1980; Kobe, 1999) and edaphic conditions (Lohbeck et al., 2013; Lohbeck et al., 2014). These abiotic changes can drive alterations at community and ecosystem levels, such as species richness, standing biomass, and forest productivity. Along these directional trajectories, plant species with acquisitive resource-use strategies are gradually replaced by species with stress-tolerant and conservative resource-use strategies (Pianka, 1970; Tilman, 1988; Wright et al., 2004; Kitajima, 1994) or vice-versa in some cases (Lohbeck et al., 2013; Poorter et al., 2019). Such a directional trajectory has been argued to result from a combination of two basic mechanisms or deterministic forces: environmental

filtering and competition leading to limiting similarity (Kraft et al., 2008). Abiotic filters (e.g., environmental conditions) select species that share more characteristics than expected by chance due to the required adaptations for a particular environment (Weiher and Keddy, 2016; Díaz et al., 1999; Cornwell et al., 2006). On the other hand, biotic filters (e.g., processes of competitive exclusion and resource partitioning) are often assumed to restrict coexisting species to functionally distinct species (MacArthur and Levins, 1967; Weiher et al., 2011). Environmental filtering has been proposed as the dominant process in the early stages of regeneration (Cavender-Bares et al., 2009; Lebrija-Trejos et al., 2010), while biotic filtering is expected to become increasingly important as regeneration proceeds (Dinnage, 2009; Letcher, 2010; Letcher et al., 2012; Norden et al., 2012).

Alternatively, there are models based on random species assembly resulting from stochastic dispersal, colonization, and local extinction (Hubbell, 2001). Under this neutral paradigm, although linear changes in vegetation structure (e.g., plant abundance and biomass) are expected to occur as regeneration proceeds, community-level changes are not linear or predictable, since plant assembly is not governed by either environmental or biotic filtering (Kreyling et al., 2011; Fukami, 2015; Li et al., 2016). Although forest regeneration via directional replacement of functional groups appears to be most common across tropical forests (see Brown and Lugo, 1982; Guariguata and Ostertag, 2001; Arroyo-Rodríguez et al., 2017; Poorter et al., 2019), other less predictable or deterministic regeneration trajectories may emerge, particularly in the case of forest mosaics exposed to chronic anthropogenic disturbances (hereafter chronic disturbance sensu Singh, 1998). We refer to human-modified landscapes, in which remaining forests (both old-growth and secondary forests) are exposed to shifting agriculture as well as firewood collection, timber exploitation, and browsing by livestock (i.e., chronic disturbance). In this context, forest regeneration may be influenced by stumps and resprouts following land abandonment (Ewel, 1977; Murphy and Lugo, 1990; McLaren and McDonald, 2003; McDonald et al., 2010), but also by the resprouting ability of species occurring in regenerating forest patches exposed to chronic disturbance (Kennard et al., 2002; Vieira and Scariot, 2006; McDonald et al., 2010; Pausas et al., 2016). In fact, regeneration from resprouts has led to the *myth* that dry forests have high resilience, that is, rapid recovery rates when compared with other tropical forests (see Figueirôa et al., 2006; Quesada et al., 2009; Sampaio et al., 2010). In synthesis, shifting cultivation and chronic disturbance, by potentially favouring resprouting species, may affect both forest resilience and successional trajectories (McDonald et al., 2010); i.e., classical successional models may not fit properly for this ecological context.

The Brazilian Caatinga dry forest is one of the largest blocks of SDTF globally (Silva et al., 2017). However, Caatinga has been historically converted into successional mosaics due to shifting agriculture and livestock production (Souza et al., 2019). Additionally, remaining forests (both old-growth and secondary forests) represent a key source of several subsistence products such as fodder for free-ranging goats, firewood, timber and medicinal plants; i.e., chronic disturbance (Arnan et al., 2018). Accordingly, many abundant tree species have been reported to resprout in response to human-imposed disturbances, what has been argued to confer resilience to Caatinga dry forest (Figueirôa et al., 2006; Sampaio et al., 2010). This scenario marked by the presence of forest-dependent rural populations is widespread across the tropics, what makes the Caatinga an interesting opportunity to investigate forest regeneration/resilience in the context of forest multiple use.

Here, we examined the regeneration of a Caatinga dry forest in the context of forest stands following slash-and-burn agriculture and facing chronic disturbance (i.e., firewood collection, timber exploitation, and browsing by livestock) to assess both the recovery rate and the successional trajectory. We first examined the relative contribution of resprouting as a mechanism of forest regeneration across the recently abandoned crop fields. We expected resprouting to be the predominant mechanism of forest regeneration in these areas. We also investigated

community-level plant diversity measures (i.e., taxonomic, functional, and phylogenetic) across the regenerating and old-growth forest stands. We expected the Caatinga to exhibit higher forest resilience and a successional trajectory marked by stochastic changes in plant assemblage metrics; i.e., no correlation between community-level measures and time since abandonment, aboveground biomass, or soil properties is expected. Finally, we expected that the chronic disturbance imposed to regenerating forest stands alters plant assemblage composition, reduce species diversity (Ribeiro et al., 2015, 2016), and, consequently, reduce forest resilience and lead to alternative successional trajectories.

2. Material and methods

2.1. Study area

The study was carried out in the Catimbau National Park (8°4′00″ S and 37°09′30″, Fig. 1). This protected area was created in 2002 and covers 607 km². The annual temperature is between 21 °C and 25 °C and annual precipitation ranges between 650 and 1100 mm. Approximately 70% of the park is dominated by litosols and is exposed to two climatic types, with a predominant Bsh semiarid climate and tropical rainy As' found in some areas (according to the Köppen scale, Peel et al., 2007). The prevalent vegetation is a small-statured Caatinga forest dominated by Fabaceae and Euphorbiaceae trees and shrubs throughout the precipitation gradient (Rito et al., 2017; Souza et al., 2019). The Catimbau National Park still supports hundreds of small farmers, which have converted the old-growth forest into a vegetation mosaic consisting of crop fields, regenerating forest stands of varying ages, and old-growth forest stands (Souza et al., 2019). Local farmers depend on the forest for firewood, fodder, and nutrients to support slash-and-burn agriculture (Albuquerque et al., 2017). Thus, the remaining forest in this region is exposed to chronic disturbance (Silva et al., 2017), which is typical for the Caatinga region (Tabarelli et al., 2017).

2.2. Mechanisms of regeneration post-agricultural land use

We selected 32 spatially independent and recently abandoned crop fields (or fallow fields; <5 years abandonment). These fallows resulted from the abandonment of slash-and-burn agricultural fields that had long been devoted to bean, corn, and cassava cultivation, most likely for decades or even centuries (see Tabarelli et al., 2017; Souza et al., 2019; Specht et al., 2019). Traditionally, shifting cultivation in this region is free of frequent/intense fires, biocides and industrial fertilizers as informed by locals, which have been considered key components of land-use history able to affect patterns of forest reliance and successional trajectory (Zermeño-Hernández et al., 2015; Bhaskar et al., 2018). All shrubs and trees ≤ 50 cm tall were surveyed across all the fallows, which did not exceed 100 × 100 m. Plants were classified into two mutually exclusive categories by excavating the soil (up to 30 cm deep) around each plant: (1) seedlings, plants that had emerged from seeds, which exhibited a single apical root without any structure that would indicate resprouting from stumps or subterraneous structures, or (2) resprouts, plants attached to root networks, ground stumps, or large water/carbohydrate storage roots.

2.3. Forest chronosequence

The Catimbau National Park has a network of permanent plots that was installed by the Long-Term Ecological Research Network (www.peldcatimbau.org.br) and exclusively covers stands of Caatinga dry forest (see Rito et al., 2017). We sampled all trees and shrubs with a diameter at soil height ≥ 3 cm and a height ≥ 1 m in the 20 0.1-ha (50 × 20 m) permanent plots. Fifteen of these plots comprised regenerating forest stands of varying ages, from 4 to 70 yrs (for more details, see Table 2 and Table B1), and represented fallows of slash-and-burn agriculture devoted to maize, beans and cassava for a long time; i.e., stands already submitted to several cycles of cultivation-fallow as occurs in the context of slash-and-burn agriculture in the tropics (Ribeiro Filho et al., 2013).

Stand selection was based on semi-structured interviews with the local population, paying special attention to land-use history or pre-regeneration disturbance regime (see also Souza et al., 2019). Chronosequence as a collection of sites/stands with different ages, usually identified by locals or even via satellite imagery, has been the main approach to investigate forest regeneration in the tropics (Chazdon et al., 2007; Dutrieux et al., 2016; Guariguata and Ostertag, 2001; Pinho et al., 2017; Quesada et al., 2009; Wang et al., 2019), although it prevails a detailed description relative to land-use history. Differences in land-use history, particularly in terms of disturbance intensity, are likely to result in differences relative to soil conditions; i.e., a key driver of forest regeneration (Arroyo-Rodríguez et al., 2017; Chazdon and Guariguata, 2016). Thereby, soils across our regeneration and old-growth forest stands were characterized as described further. Here we interpreted similar soil conditions or soil variation associated with the age of
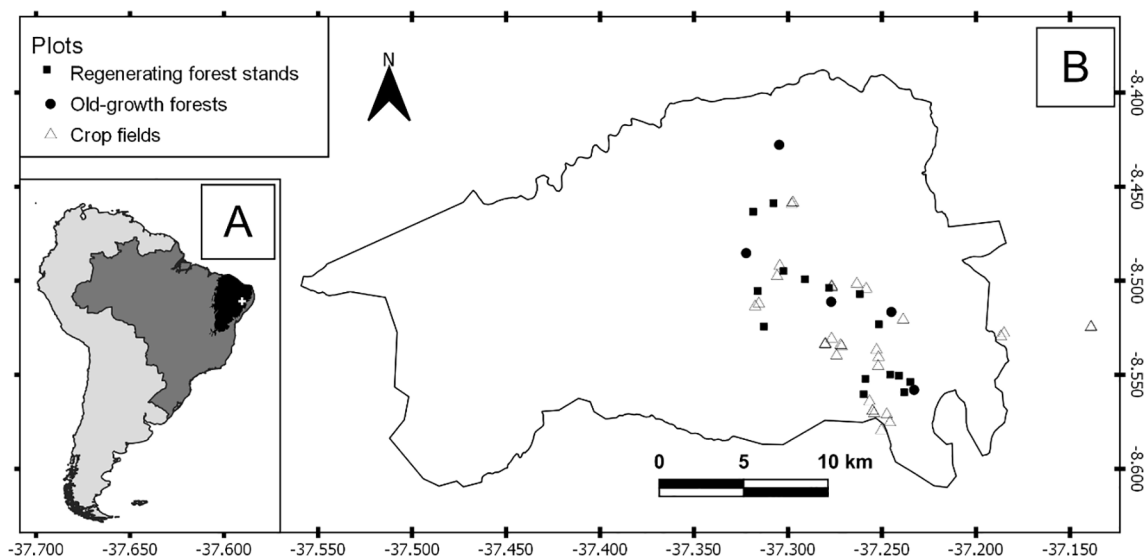

Fig. 1. Location of the study area in the Caatinga dry forest, northeast region of Brazil (A), with emphasis on the Catimbau National Park in the state of Pernambuco (B), and details of the 52 plots studied, 32 crop fields, 15 regenerating forest stands and five old-growth forests.

forest stands as an evidence that our focal regenerating stands were exposed to a relatively similar historical land use as informed by local; i. e., a sort of true forest chronosequence. The other five stands were composed of old-growth forest stands with no recent record of agriculture (Souza et al., 2019) and were incorporated by using data from Rito et al., (2017). The 20 forest stands had a total of 4885 woody plants (shrubs and trees) belonging to 154 species, with Fabaceae and Euphorbiaceae being the most abundant and species-rich families (Appendix A: Table A.1).

All collected individuals (i.e., from crop fields and regenerating forest stands) were identified to the lowest possible taxonomic level with the aid of local parataxonomists, taxonomists, and by checking specimens at the UFP Herbarium. Vouchers are available in the UFP Herbarium and the Laboratory of Applied Plant Ecology, both at the *Universidade Federal de Pernambuco*, Brazil. For each plot, we also obtained the total aboveground biomass (data from Souza et al. (2019)) and soil fertility (*sensu* Lu et al., 2002). Biomass has been used as a proxy for regeneration time in tropical forests (Chazdon, 2008; Lohbeck et al., 2015) and was adopted in this study as a complementary variable to our chronosequence approach.

2.4. Soil sampling

To estimate the soil properties in our 20 forest plots, we collected nine samples of topsoil (up to 20 cm deep) per plot and then pooled them into a single sample per forest stand. Soil samples were then sent to private companies (Agrolab *Análises Ambientais* and *Instituto Agronômico de Pernambuco*) to be analysed following the Brazilian protocol for soil analysis (Claessen, 1997). Soil attributes were combined to create a single soil fertility index (*sensu* Lu et al., 2002): SF = [Ca + Mg + K – log (1 + Al)] * OM + 5, where SF = Soil Fertility, Ca = Calcium (cmolc dm^{-3}), Mg = Magnesium (cmolc dm^{-3}), K = Potassium (cmolc dm^{-3}), Al = Aluminium (cmolc dm^{-3}), and MO = Organic Matter (g kg^{-1}). This approach has been adopted elsewhere (Sfair et al., 2018; Souza et al., 2019; Pinho et al., 2019); see Appendix B for detailed information on soil attributes across forest stands.

2.5. Chronic disturbance

We obtained information on chronic disturbance for each forest stand from Arnan et al. (2018). The approach integrates measures from three categories: (1) spatial context — measurements of the geographic context of each stand, such as distance to human settlements; (2) socio-ecological context, assessed with semi-structured interviews examining the use of forest products in smallholdings; and (3) direct measures of disturbance in each plot, such as goat trail length, number of goat dung deposits, amount of cattle dung, and dead/fallen wood. Using these measures, three indices of anthropogenic disturbances were calculated: (1) Livestock pressure; (2) Wood extraction; and (3) People pressure. Finally, these three indices were integrated into a Global multi-metric chronic anthropogenic disturbance index scaled from 0 (least disturbed) to 100 (most disturbed) as proposed by Arnan et al. (2018). For further details, see Arnan et al. (2018). In summary, regenerating forest stands varied between 3.61 (37 age of fallow period) and 48.11 (70 age of fallow period) and between old growth forest stands, 2.74 and 58.07. This chronic disturbance CAD index has been previously adopted in our focal landscape (Sfair et al., 2018; Pinho et al., 2019; Zorger et al., 2019; Silva et al., 2019; Trindade et al., 2020).

2.6. Plant trait data

Woody species recorded across the 20 forest stands were scored for seven functional traits. Four of these traits were related mainly to the species' competitive ability, growth rate, and ability to respond to disturbance: (1) maximum canopy height (m); (2) leaf area (LA; cm^2); (3) specific leaf area (area of a fresh leaf divided by its dry mass (SLA;

cm^2/g); and (4) leaf dry matter content (leaf dry mass divided by its water-saturated fresh mass; LDMC; mg g^{-1}). The remaining three traits were related to hydraulic characteristics and represent the ability of the species to withstand water stress: (1) leaf thickness (LT; mm); (2) succulence (water content per unit area of a leaf; SUC; g/cm^2); and (3) wood density (dry mass per volume; WD; g/cm^3). These traits are associated with plant responses to environmental conditions and resource use (Pérez-Harguindeguy et al., 2013). To measure species traits, 1–6 individuals of each species were sampled in each forest stand, with a total of 5–30 leaves and 1–6 wood samples being collected per species; in total 107 species were measured. We collected leaf and wood samples from the sunlit crown of mature individuals, following established sampling protocols for plant functional traits (Cornelissen et al., 2003; Pérez-Harguindeguy et al., 2013). Leaves were hydrated among layers of moist paper towels and kept in a refrigerated environment (~4 °C) for 24 h (Ryser et al., 2008). We removed the petiole of each leaf before measuring the functional attributes.

The maximum height corresponded to the highest plant found for the species (Cornelissen et al., 2003). Leaf area of water-saturated leaves was measured from photos using the ImageJ software (Abràmoff et al., 2004). The leaves were dried at 70 °C and weighed (balance precision of ±0.0001 g) to determine the specific leaf area. Leaf thickness was measured with the aid of a digital caliper (accuracy of ±0.01 mm), avoiding the central vein. In some cases, secondary veins were also avoided, if they protruded above the surface, to reduce the chances of overestimating the thickness of the leaf. The wood samples were dried at 70 °C to obtain the dry mass, and the volume was obtained after immersing the sample in water (Pérez-Harguindeguy et al., 2013). We averaged the trait values for each site to obtain a single representative value for each species.

2.7. Taxonomic, phylogenetic, and functional diversity measures

We adopted equivalent numbers (Hill Numbers) to calculate traditional metrics of taxonomic diversity (species richness, Shannon's diversity, and Simpson's diversity); where q = 0 refers to the species richness of the communities, q = 1 refers to Shannon's diversity — which balances species exactly by their frequencies, without favouring common or rare species — and q = 2 refers to Simpson's diversity, which attributes greater weight to the most common species (Chao and Jost, 2012).

To build the phylogenetic tree, we used the GenBank (http://www.ncbi.nlm.nih.gov/genbank/) database. We searched the database for four gene sequences that are widely adopted in published phylogenies for angiosperms: ribulose-bisphosphate carboxylase gene (rbcL), maturase K (matK), 5.8S ribosomal RNA, and trnL-trnF intergenic spacer. When gene information was not available for a species, we used an alternative, congeneric gene. Following Burns and Strauss (2011) and Ribeiro et al. (2015), *Amborella trichocarpa* (Amborellaceae) and *Magnolia virginiana* (Magnoliaceae) were adopted as basal lineages of angiosperms to increase the root depth of the phylogenetic tree. Gene sequences were aligned to each region independently using MUSCLE (Edgar, 2004) and combined into a single super array using Geneious, version 7.1.4 (http://www.geneious.com, Kearse et al., 2012). For more information, see Appendix C.

Two measures of phylogenetic diversity were calculated for each forest stand: standardized effect size (SES) for mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD). MPD is defined as the average phylogenetic distance between all combinations of species pairs, while NTMD represents the mean phylogenetic distance for the nearest relative for all species in a sample (Webb et al., 2011). These two measurements of phylogenetic diversity capture different information, with MPD providing an overall value for the phylogenetic structure of the community, and NTMD being equivalent to species' rates by genus (Webb, 2000).

For all forest stands, were calculated community weighted mean

(CWM; that was estimated for each functional attribute) and the Rao's Q diversity index (Rao, 1982). Rao's Q diversity index was adopted using Euclidean distance to describe patterns of functional convergence and divergence.

2.8. Data analysis

First, we assessed the collinearity of our explanatory variables (i.e., forest age, forest aboveground biomass, soil fertility, and chronic disturbance) using the Variance Inflation Factor (VIF) from the *car* package in R. Overall, correlations were weak (all VIF values < 2; VIF values: age = 1.43, biomass = 1.96, soil fertility = 1.08, and chronic disturbance = 1.40). Consequently, all variables were included in further analyses (Jou et al., 2014). Moreover, we tested whether the abundance and taxonomic (q = 0, q = 1, and q = 2), functional (CWM H_{Max}, CWM LA, CWM SLA, CWM LDMC, CWM LT, CWM Suc, CWM WD, and RaoQ) and phylogenetic (MPD and NMTD) diversity measurements differed between regeneration and old-growth forest stands with t-tests using the SigmaPlot 12.0 software. The relative effect of each predictor on each response variable (i.e., abundance and taxonomic, functional, and phylogenetic measurements) was examined via generalized linear models by using the *sjstats* R package, adopting negative binomial distribution for discrete data (abundance and q = 0 data) and Gaussian distribution for continuous data (q = 1, q = 2; taxonomic, functional and phylogenetic data) (Crawley, 2014). We tested the homoscedasticity of the residuals using the Shapiro-Wilk test and no overdispersion of the data was detected.

We also examined species-level responses to chronic disturbance to examine the extent to which this process might affect forest regeneration, particularly the successional trajectory. The chronic anthropogenic disturbance index was correlated with relative species abundance using the *vegan* R package.

To verify the existence of plant groups related to forest age, we applied a non-metric multidimensional scaling (NMDS) and permutational multivariate analysis of variance (PERMANOVA) based on Bray-Curtis dissimilarity matrices using the *vegan* R package. Finally, we tested whether our model errors presented spatial autocorrelation using a Mantel test (Legendre and Fortin, 1989). Spatial autocorrelation was not observed in the errors of any of our models, confirming that our plots can be considered independent replicates (r = 0.73, p = 0.36).

3. Results

3.1. Soil conditions across forest stands

Soils across forest stands proved to be sandy, acid and impoverished in terms of nutrients (Table 1). Furthermore, regenerating and old-growth forest stands exhibited similar soil conditions, with relatively low variation across regenerating forest stands.

3.2. Mechanisms of forest regeneration across abandoned crop fields

We recorded a total of 471 individuals from 34 plant species across the 32 crop fields (Appendix A: Table A.2). The crop fields varied in terms of plant abundance (0 to 53), but the majority of plants (298; 63.27%) were resprouts, either from remaining tree stumps (7.72%) or roots (92.28%). Twenty-four species were considered capable of resprouting, with a predominance of the tree species *Pityrocarpa moniliformis* (Benth.) Luckow & R.W.Jobson (Fabaceae). Of the 298 resprouters found, 50 were identified as *P. moniliformis*; 46 were connected to root networks and only 4 *P. moniliformis* were from seedlings.

3.3. Community-level changes during regeneration and forest resilience

A total of 4885 stems from 154 woody plant species were recorded across the 20 forest stands. The number of sampled individuals varied

Table 1

Soil physicochemical properties (mean ± standard deviation (SD); and coefficient of variation (CV (%))) exhibited by 15 regenerating forest stands (RGS) and 5 old-growth forest stands (OGF) in the Catimbau National Park. OM = Organic matter, CEC = Cation exchange capacity.

Soil atributes	RFS	OGF	P	Test
pH (H$_2$O)	5.05 ± 0.55; 10.84	4.6 ± 0.27; 5.99	0.11	*t* test
P (mg/dm^3)	7.27 ± 3.64; 50.12	6 ± 2.44; 40.82	0.50	*t* test
K (cmolc/dm^3)	0.07 ± 0.04; 48.17	0.06 ± 0.02; 18.22	0.56	Mann-Whitney
Ca (cmolc/dm^3)	0.9 ± 0.54; 59.11	0.95 ± 0.71; 75.17	1.00	Mann-Whitney
Mg (cmolc/dm^3)	0.55 ± 0.14; 27.03	0.56 ± 0.16; 29.01	0.87	*t* test
OM (g/kg)	18.47 ± 13.81; 74.78	18.89 ± 6.52; 34.48	0.60	Mann-Whitney
CEC (cmolc/dm^3)	4.59 ± 1.63; 35.35	5.46 ± 1.77; 32.29	0.35	*t* test
Residual moisture (%)	1.43 ± 0.39; 27.47	1.34 ± 0.23; 17.87	1.00	Mann-Whitney
Fine sand (%)	23.4 ± 7.29; 31.13	22 ± 7.61; 34.61	0.73	*t* test
True density (g/cm^3)	2.61 ± 0.02; 0.63	2.63 ± 0.01; 0.24	0.08	Mann-Whitney

Table 2

Phylogenetic diversity indexes calculated for all studied forest stands in the Catimbau National Park, Pernambuco, Brazil. Standardized effect size (SES) for mean phylogenetic distance (MPD) and mean nearest taxon distance (MNTD). RFS = regeneration forest stands plus the age of the fallow period and OGF = old-growth forest stands. Bold values are indicating phylogenetic grouping (<-1.96) or phylogenetic dispersion (>1.96; Vamosi et al., 2009).

Plot	SES.MPD	SES.MNTD
RFS4	0.25	0.78
RFS6	−0.30	−1.80
RFS7	**−2.59**	−0.47
RFS10	1.53	0.75
RFS12	0.43	−0.30
RFS17	−0.14	1.70
RFS18	0.83	−0.26
RFS20	0.48	0.25
RFS23	−0.87	−0.94
RFS30	0.28	0.96
RFS37	1.44	1.92
RFS40	1.11	1.01
RFS45	−0.28	−0.44
RFS50	0.32	1.58
RFS70	0.30	−0.08
OGF	−0.76	−0.02
OGF	1.50	0.83
OGF	−0.43	**2.32**
OGF	−0.23	0.04
OGF	1.23	0.23

across regenerating forests (101 to 389) and old-growth forests (232 to 393). However, on average, regenerating forests had a lower abundance (220.67 ± 100.96; mean ± SD) when compared to old-growth forests (315.00 ± 61.45; t = −1.95; df = 18; p = 0.03). In terms of species richness (q = 0), regenerating forests (20.73 ± 8.08), had fewer species than old-growth forests (30.37 ± 11.40; t = −2.09; df = 18; p = 0.02). Similarly, typical species (q = 1) across regenerating forests (7.67 ± 3.78) were lower when compared to old-growth forest stands (12.60 ± 5.10; t = −2.32, df = 18, p = 0.01). Although q = 0 and q = 1 presented lower numbers, some regenerating forest stands had the same degree of variation presented by old-growth forest stands (Fig. 2). In relation to dominant species (q = 2), regenerating (4.99 ± 2.55) and old-growth (7.86 ± 3.49) forest stands differed (q = 2; t = −1.99, df = 18; p = 0.04). Additionally, age was negatively related to q = 1 (X^2 = 4.39; p =

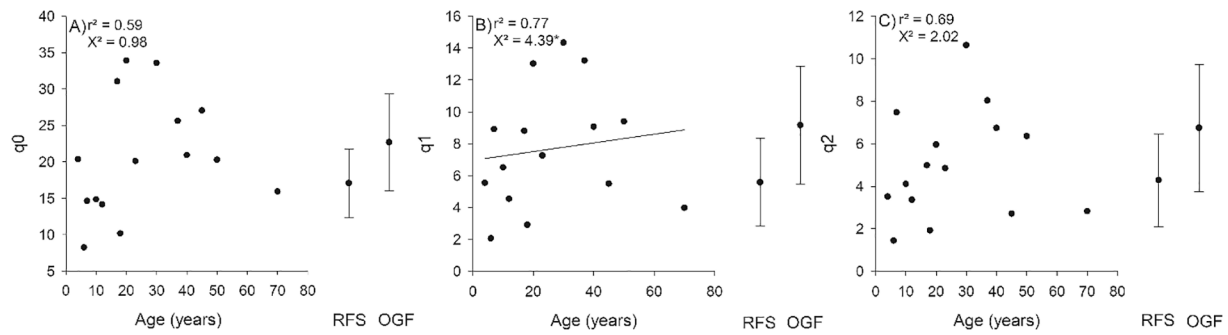**Fig. 2.** Relationship between age and Hill's numbers for observed richness (A; q = 0), typical species (B; q = 1), and dominant species (C; q = 2) of woody plant communities in the Catimbau National Park, Brazil. RFS = Regeneration forest stands plus the age of fallow period and OGF = Old-growth forest stands. Coefficients of determination (r^2) and Chi-square (χ^2) value are given. *$P < 0.05$.

0.03), whereas aboveground biomass was positively related to abundance ($X^2 = 46.88$; $p = <0.01$; q = 0 ($X^2 = 18.87$; $p = <0.01$), q = 1 ($X^2 = 23.01$; $p = <0.01$), and q = 2 ($X^2 = 10.63$; $p = <0.01$), soil fertility and chronic disturbance were positively correlated to abundance ($X^2 = 4.77$; $p = 0.03$ and $X^2 = 33.66$; $p = <0.01$, respectively), and soil fertility only was positively correlated to q = 0 ($X^2 = 3.97$; $p = 0.04$) (Appendix D: Table D.1).

Considering the phylogenetic measurements, only the 7-yr old stand was phylogenetically clustered, while an old-growth forest stand was phylogenetically dispersed (Table 2). It is worth mentioning that, among the most abundant and richest families (e.g., Fabaceae and Euphorbiaceae), there were numerous genera (e.g., *Senegalia*, *Mimosa* and *Croton*) with species spread across the whole set of environments, regardless of the regeneration time or level of chronic anthropogenic disturbance. This implied a certain degree of phylogenetic homogenization of plant assemblages through the regeneration process. Standardized effect size (SES) for Mean Phylogenetic Distance (MPD) was similar between forest regeneration (0.19 ± 1.01) and old-growth forest stands (0.26 ± 1.03; t = -0.14; df = 18, $p = 0.44$), as was Mean Nearest Taxon Distance (MNTD; 0.31 ± 1.05 vs. 0.69 ± 0.98; t = -0.69; df = 18, $p = 0.25$). Both were not correlated with age, aboveground biomass, soil fertility, or chronic disturbance (Fig. 3, Appendix D: Table D.4).

Community-level functional attributes also exhibited a wide variation across regenerating forests (Table 3), but only the leaf dry matter content ($p = 0.02$) and maximum hight ($p = 0.02$) showed difference between regenerating (LDMC = 393.21 ± 55.81; $H_{Max} = 4.09 \pm 1.10$) and old-growth forest stands (LDMC = 444.88 ± 38.60; $H_{Max} = 5.66 \pm 1.80$) (Fig. 4, Appendix D: Table D.2). Moreover, CWM values of leaf area (25.17 ± 14.27), specific leaf area (154.44 ± 24.81), leaf thickness (0.14 ± 0.05), leaf succulence (0.48 ± 0.21), leaf dry matter content (393.21 ± 55.81), wood density (0.67 ± 0.07), and maximum height (4.09 ± 1.10) were not related to age and soil fertility (Appendix D: Table D.3). Only aboveground biomass and chronic disturbance were correlated with some functional traits. Aboveground biomass was positively correlated with leaf dry matter content ($X^2 = 4.71$; $p = 0.03$), and chronic disturbance was negatively correlated with leaf area ($X^2 =$

4.76; $p = 0.02$) and specific leaf area ($X^2 = 6.74$; $p = 0.01$). In relation to Rao's Q diversity index, it was positively correlated only with aboveground biomass ($X^2 = 4.01$; $p = 0.05$) (Appendix D: Table D.3).

The community-level weighted means (CWM) of plant traits revealed: (1) little correspondence between functional composition and forest regeneration status (regenerating vs. old-growth forests); and (2) the co-occurrence of species with different functional attributes regardless of the time since abandonment and soil fertility (Table 3; Appendix D: Table D.3). As an example, *Waltheria brachypetala* Turks. co-occurred with the *Jatropha mutabilis* (Pohl) Baill. with distinct values for wood density (0.66 vs. 0.21 mg/cm³), specific leaf area (99.23 vs.178.91 cm²/g), and leaf dry mass content (436.65 vs. 182.73 mg g⁻¹) in the 12-yr old regenerating; i.e., co-occurrence of species with distinct ecological strategies. This also implied the co-occurrence of both conservative and acquisitive resource-use strategies.

The functional composition of the community was strongly influenced by the dominant species. The highest values found for leaf area and specific leaf area in the forest with a fallow age of 40 yrs resulted from the dominance of *Manihot carthagenensis* (Jacq.) Müll.Arg. (Euphorbiaceae). On the other hand, the low wood density in the 12-year-old forest stand was dominated by *Jatropha mutabilis* (Euphorbiaceae); all measured individuals presented values lower than 0.30 g/cm³.

Finally, the plot ordination based on the taxonomic composition did not show any pattern of organization according to the age of forest stands or their successional status (PERMANOVA = Pseudo-$F = 1$; $R^2 = 0.05$; $p = 1$; Fig. 5). Although the organization of the plant assemblages exhibited few responses to environmental variables across forest regeneration (i.e., from early to old-growth forest stands), some species-level responses were observed relative to chronic disturbance. For example, *Balfourodendron molle* (Miq.) Pirani occurred only in the plot with the lowest level of chronic disturbance. A similar pattern occurred with, *Aeschynomene marginata* Benth., *Melochia* sp., and *Libidibia ferrea* (Mart. ex Tul) L.P.Queiroz, while *Zanthoxylum stelligerum* Turcz. and *Jatropha mutabilis* (Pohl) Baill. was dominant in disturbed areas (Appendix E: Fig. E.1).
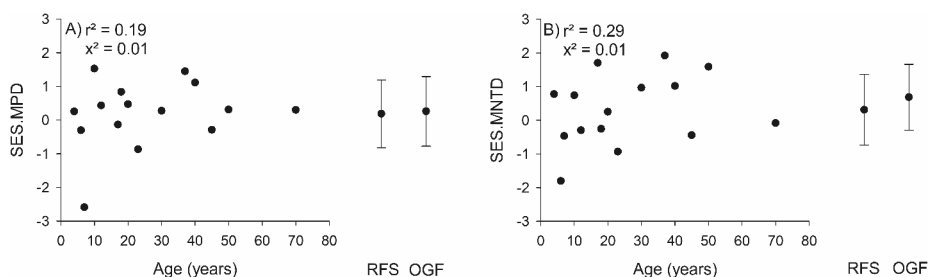

Fig. 3. Relationship between age and standardized effect size for mean phylogenetic distance (SES.MPD) and mean nearest taxon distance (SES.MNTD) for woody plant species in the Catimbau National Park, Brazil.

Table 3

Functional signature (minimum (Min), maximum (Max), mean ± standard deviation (SD)) of regenerating and old-growth forest stands reflected by composition functional (CWM) means of seven plant functional attributes in the Catimbau National Park, Brazil. RFS = Regeneration forest stands plus the age fallow period and OGF = Old-growth forest stands. LA = Leaf area, SLA = Specific leaf area, LT = Leaf thickness, LDMC = Leaf dry matter content, WD = Wood density and, H_{Max} = Maximum height.

Plot		LA	SLA	LT	Succulence	LDMC	WD	H_{Max}
RFS4	Min – Max	1.02–54.35	70.38–286.14	0.02–0.30	<0.01–1.39	146.96–668.45	0.25–1.17	1.50–3.50
	Mean ± SD	26.30 ± 32.12	155.55 ± 73.65	0.15 ± 0.08	0.49 ± 0.51	415.61 ± 121.31	0.69 ± 0.14	3.71 ± 1.82
RFS6	Min–Max	6.38–123.36	137.21–280.19	0.01–0.18	0.07–2.77	155.57–561.45	0.20–0.76	1.50–2.40
	Mean ± SD	25.94 ± 33.93	152.20 ± 70.47	0.14 ± 0.08	0.49 ± 0.54	419.74 ± 125.46	0.67 ± 0.12	3.88 ± 1.87
RFS7	Min–Max	1.95–142.14	70.14–289.32	0.09–0.27	0.02–2.30	162.72–491.93	0.26–0.81	1.50–6.00
	Mean ± SD	27.02 ± 33.04	156.02 ± 71.06	0.15 ± 0.09	0.50 ± 0.52	414.22 ± 121.41	0.67 ± 0.12	3.80 ± 1.86
RFS10	Min–Max	4.03–54.89	43.31–233.24	0.04–0.54	0.07–1.13	266.68–519.30	0.53–0.71	1.00–4.20
	Mean ± SD	24.55 ± 33.88	146.72 ± 70.63	0.15 ± 0.09	0.48 ± 0.52	425.02 ± 124.60	0.67 ± 0.11	3.83 ± 0.79
RFS12	Min–Max	1.93–56.04	11.71–215.12	0.11–0.29	0.07–0.88	182.73–548.84	0.21–0.76	1.50–6.10
	Mean ± SD	26.46 ± 31.97	151.43 ± 74.39	0.14 ± 0.09	0.51 ± 0.50	420.37 ± 121.47	0.68 ± 0.14	3.79 ± 1.82
RFS17	Min–Max	4.14–153.82	42.53–407.74	0.04–0.15	0.06–2.21	146.29–510.74	0.27–1.47	1.50–5.00
	Mean ± SD	27.88 ± 33.64	154.02 ± 74.70	0.14 ± 0.09	0.52 ± 0.54	415.87 ± 122.74	0.68 ± 0.14	3.47 ± 1.81
RFS18	Min–Max	4.16–47.91	59.47–213.85	0.11–0.32	0.06–0.99	343.13–539.10	0.65–0.83	1.70–3.50
	Mean ± SD	26.62 ± 32.61	155.91 ± 70.47	0.15 ± 0.09	0.49 ± 0.52	414.16 ± 122.55	0.67 ± 0.14	3.78 ± 1.85
RFS20	Min–Max	1.30–170.74	63.15–348.36	0.03–0.19	0.02–2.64	148.95–638.07	0.26–0.76	1.65–5.50
	Mean ± SD	27.20 ± 32.97	154.69 ± 73.42	0.15 ± 0.08	0.51 ± 0.54	415.49 ± 121.65	0.68 ± 0.13	3.47 ± 1.83
RFS23	Min–Max	7.72–38.94	27.22–305.92	0.03–0.23	0.16–0.99	255.03–513.62	0.59–0.77	2.00–6.00
	Mean ± SD	27.12 ± 33.04	154.84 ± 73.33	0.14 ± 0.08	0.51 ± 0.53	415.52 ± 121.85	0.68 ± 0.14	3.72 ± 1.82
RFS30	Min–Max	4.28–45.22	45.52–585.13	0.03–0.38	0.02–0.99	302.39–772.52	0.67–0.90	1.70–6.00
	Mean ± SD	26.90 ± 36.66	156.88 ± 74.46	0.14 ± 0.08	0.51 ± 0.53	413.88 ± 122.19	0.68 ± 0.14	3.71 ± 1.85
RFS37	Min–Max	0.87–94.25	68.26–316.04	0.02–0.36	<0.01–1.86	241.15–652.47	0.38–0.92	1.00–8.00
	Mean ± SD	26.28 ± 31.64	156.72 ± 74.33	0.15 ± 0.09	0.49 ± 0.51	413.08 ± 123.10	0.68 ± 0.14	3.72 ± 1.84
RFS40	Min–Max	4.98–306.28	98.79–438.52	0.09–0.36	0.06–3.25	177.17–472.68	0.34–0.82	2.50–7.00
	Mean ± SD	26.80 ± 32.97	155.39 ± 73.13	0.14 ± 0.09	0.50 ± 0.54	415.12 ± 122.83	0.69 ± 0.14	3.72 ± 1.83
RFS45	Min–Max	8.06–73.02	36.84–297.60	0.02–0.33	0.09–1.88	194.71 – 559.12	0.42–0.74	1.60–7.50
	Mean ± SD	25.52 ± 31.78	158.09 ± 75.49	0.14 ± 0.09	0.48 ± 0.51	412.45 ± 124.43	0.68 ± 0.13	3.69 ± 1.84
RFS50	Min–Max	2.48–166.99	55.26–260.26	0.03–0.26	0.04–1.66	213.78–256.35	0.47–0.83	1.60–6.00
	Mean ± SD	26.96 ± 32.66	156.40 ± 74.71	0.14 ± 0.09	0.50 ± 0.53	414.93 ± 124.18	0.67 ± 0.13	3.76 ± 1.85
RFS70	Min–Max	0.64–77.63	59.32–174.84	0.07–0.23	<0.01–1.77	194.64–580.96	0.53–0.80	1.50–5.00
	Mean ± SD	26.71 ± 32.51	155.92 ± 73.77	0.15 ± 0.09	0.50 ± 0.53	414.03 ± 121.93	0.68 ± 0.13	3.69 ± 1.83
OGF	Min–Max	8.82–88.20	104.56–278.47	0.08–0.30	0.10–1.42	195.36–552.28	0.43–0.78	2.20–8.00
	Mean ± SD	26.91 ± 32.78	155.57 ± 74.19	0.15 ± 0.08	0.50 ± 0.53	415.18 ± 121.62	0.68 ± 0.14	3.72 ± 1.83
OGF	Min–Max	1.23–131.60	54.69–315.70	0.07–0.36	0.02–2.46	200.49–656.99	0.41–0.82	1.50–11.50
	Mean ± SD	26.17 ± 31.85	157.65 ± 75.29	0.15 ± 0.08	0.49 ± 0.51	413.46 ± 123.85	0.67 ± 0.14	3.66 ± 1.80
OGF	Min–Max	0.69–81.87	57.62–330.38	0.02–0.40	<0.01–1.15	207.59–756.86	0.32–0.85	1.30–6.25
	Mean ± SD	27.09 ± 32.98	157.15 ± 74.19	0.15 ± 0.09	0.50 ± 0.53	414.44 ± 122.44	0.69 ± 0.14	3.73 ± 1.82
OGF	Min–Max	7.45–52.95	28.91–277.25	0.03–0.29	0.12–1.15	161.68–519.30	0.38–0.83	2.00–10.00
	Mean ± SD	26.91 ± 32.50	155.48 ± 73.26	0.14 ± 0.08	0.51 ± 0.53	413.38 ± 120.67	0.69 ± 0.14	3.71 ± 1.82
OGF	Min–Max	0.45–149.02	40.22–285.08	0.03–0.29	<0.01–2.39	176.77–947.26	0.29–0.88	1.25–8.00
	Mean ± SD	27.28 ± 33.11	155.41 ± 74.35	0.14 ± 0.08	0.52 ± 0.54	414.72 ± 120.94	0.68 ± 0.14	3.79 ± 1.78

4. Discussion

Our results suggest that the early stages of Caatinga dry forest regeneration following slash-and-burn agriculture are driven by the resprouting of remaining roots and stumps of shrub and tree species. Overall, woody plant assemblages along natural regeneration exhibited elevated, but nonlinear cross-site variation. Accordingly, regenerating forests were taxonomically, functionally, and phylogenetically similar to old-growth forests. This pattern implies: (1) high forest resilience, at least at some sites, while others apparently experience arrested succession, and (2) a regeneration process not marked by directional changes in community-level plant diversity measures. Moreover, soil fertility and chronic disturbance do not seem to be important forces in the structuring of plant assemblages, although some woody plant species are either positively or negatively affected by chronic disturbance. In synthesis, the regeneration of the Caatinga dry forest covering sandy soils and exposed to chronic disturbances apparently consists of plant collections not assembled by abiotic or biotic filtering, what supports the emerge of seral/functional stages; i.e., directional trends as proposed by classical successional models.

It is true that sites of different ages (i.e., chronosequence) may differ more than a single site monitored through the same age range (i.e., long-term monitoring or dynamic approach sensu Maza-Villalobos et al., 2011), particularly in terms of species composition. This has been argued to result from differences in terms of disturbance history and

landscape-level variables such as forest cover (Chazdon et al., 2007; Norden et al., 2015; Zermeño-Hernández et al., 2015). However, the chronosequence approach has been able to document the major "successional trends" through both humid and dry tropical forests (see Quesada et al., 2009; Lohbeck et al., 2013). Here we assume that our uncovered patterns are unlikely to result from cross-site differences relative to pre-regeneration disturbances causing soil degradation since: (1) even aboveground biomass, a proxy for successional trends and a less sensitive attribute to pre-regeneration disturbances (Zermeño-Hernández et al., 2015), was neither correlated with forest age (Souza et al., 2019) nor with other community-level attributes we measured in our focal landscape, (2) soils were not degraded during cultivation cycles, and (3) fire, biocides and industrial fertilizers (three important sources of disturbance associated with land-use history) are not observed or documented in the Caatinga dry forest.

Our findings reinforce the notion that resprouting is a frequent regeneration mechanism in SDTFs following human disturbances such as slash-and-burn agriculture (Kennard et al., 2002). However, we offer evidence suggesting that root suckers (i.e., resprouting from roots) are more frequent than both stump sprouts and true seedlings in the early stages of forest regeneration across fallows. Although we did not find evidence of a major role by true seedlings (i.e., seedlings from seeds), it is worth inform that they have been reported to play in other Caatinga sites (Lopes et al., 2012; Souza et al., 2014). Ongoing research in our focal landscape has already identified several woody plant species with
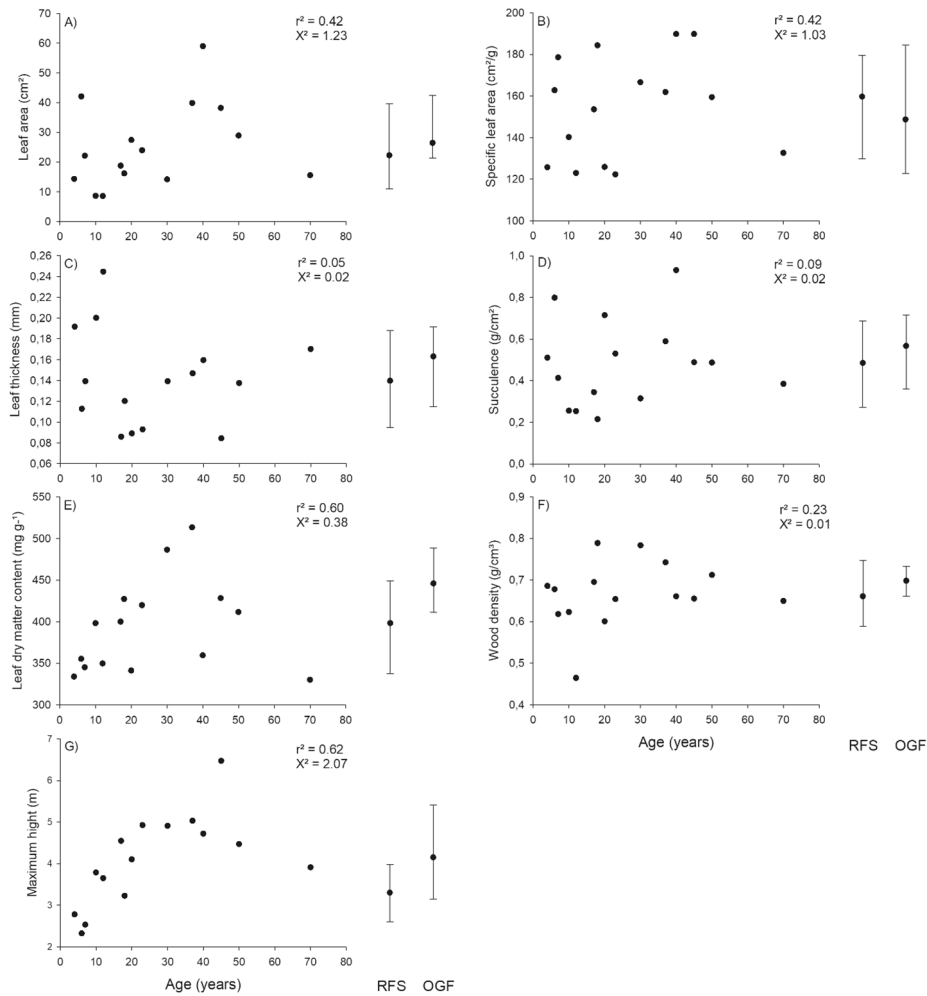
Fig. 4. Relationship between age and functional composition (community weighted mean) reflected by seven functional traits for woody plant species in the Catimbau National Park, Brazil. RFS = Regeneration forest stands plus the age of fallow period and OGF = Old-growth forest stands. Coefficients of determination (r^2) and Chi-square (χ^2) value are given.
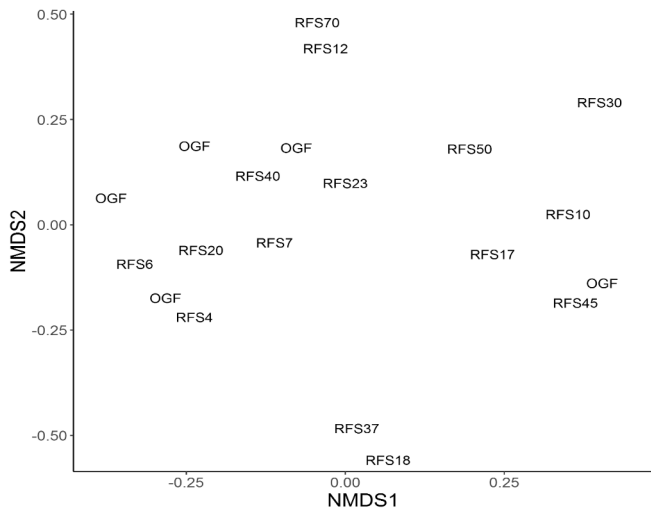

Fig. 5. Non-metric multidimensional scaling ordination based on the taxonomic composition of woody species in the Catimbau National Park, Brazil. RFS = Regeneration forest stands plus the age of fallow period and OGF = Old-growth forest stands. Stress = 0.19.

root suckers as a reproduction strategy, including *Pityrocarpa*

moniliformis, Cenostigma pyramidale (Tul.) E. Gagnon & G.P. Lewis (Fabaceae), and *Croton tricolor* (Euphorbiaceae), which are the most abundant plant species throughout the Caatinga dry forest – both at regenerating and old-growth forest stands - in our study landscape (Rito et al., 2017; Souza et al., 2019). While we believe that fire and other cultivation practices, such as regular weeding, likely eliminate most stumps, leaving roots untouched, further studies will be needed to assess this hypothesis. A high abundance of resprouts or resprouting sources (i. e., stumps and roots) at the time of land abandonment probably explains why some regenerating forest stands have similar plant assemblages to those supported by old-growth forest stands. On the other hand, regenerating forests lacking these sources may experience arrested succession, as we found in our focal landscape (see Souza et al., 2019). Resprouting capacity has been identified as a key process to vegetation resilience, particularly in biotas that have been exposed to fire during their evolutionary history, such as the Mediterranean shrublands, Californian chaparral and, the Brazilian Cerrado (Rizzini and Heringer, 1962; Schwilk and Ackerly, 2005; Pausas et al., 2016). Although the Caatinga dry forest is not considered a fire-prone biota (Silva et al., 2017), its resilience has been directly associated with the fast biomass recovery through stump resprouting (Figueirôa et al., 2006; Gariglio et al., 2010). Although our findings support this pattern (i.e., regenerating forests with scores similar to old-growth forests), higher resilience is probably restricted to sites with high abundance of resprouter from stumps and/or rootstocks (Chazdon and Guariguata, 2016).

Regarding the succession trajectory, our findings do not corroborate the historical and predominant view describing forest regeneration or secondary succession following land abandonment as a directional community-level process driven by a combination of environmental filtering and species competition as key resources alter (Connell and Slatyer, 1977; Leibold et al., 2004; Lohbeck et al., 2013). There are countless studies documenting directional changes in all attributes of plant assemblages along the regeneration process, whether fallow age and/or forest structural measurements (i.e., aboveground biomass or basal area), which accumulate with time (Brown and Lugo, 1982; Becknell et al., 2012; Guariguata and Ostertag, 2001; Arroyo-Rodríguez et al., 2017) and are considered metrics for regeneration. In such a directional regeneration process, only the taxonomic composition shows lower predictability due to several factors such as dispersal limitation, predation, desiccation, and seedling survival (Holl, 1999). Directional changes in the functional composition of assemblages commonly indicate changes in the resource-saving spectrum throughout the forest regeneration, whether from acquisitive to conservative species and strategies or vice versa (see Lebrija-Trejos et al., 2008; Lohbeck et al., 2013; Pinho et al., 2017).

Our findings suggest the occurrence of successional models controlled by random and/or stochastic factors, such as initial floristic composition models or priority effects (Clements, 1916; Egler, 1954); in which neither environmental filtering nor competition govern the organization of assemblages in time or space. In our focal landscape, only abundance, taxonomic diversity measures, LDMC, and RaoQ index increased as biomass accumulates (i.e., a proxy of forest regeneration) and both regenerating forest and old-growth forest stands were taxonomically, functionally, and phylogenetically indistinguishable. We refer to a forest regeneration or successional process marked by: (1) a persistence of the same dominant species across the chronosequence, and (2) a lack of directional, community-level changes due to species replacement in response to changes in the physical environment. In other words, a regeneration process predominantly based on the development of species and individuals that are resilient to land cultivation (by stump and root resprouting) and able to persist during forest regeneration via resprouting. It also includes those species reaching secondary forest stands through seed dispersal but are able to resprout in response to chronic disturbance imposed to forest stands; e.g., firewood and fodder collection. It is important to remember that plant regeneration by regrowth can eliminates/reduces the environmental filtering imposed on seeds and seedlings, such as water and nutrient shortages in the soil surface layers (Kammesheidt, 1999; Stoner and Sánchez-Azofeifa, 2009). That is, regrowth may represent an escape mechanism for factors considered as organizers of plant assemblages in the Caatinga dry forest and other dry forests and savannas, such as water stress or nutrient scarcity (Sousa et al., 2012; Costa et al., 2014; Barros et al., 2017; Sfair et al., 2018). Regrowth/resprouting is one of the reasons why species exhibiting contrasting functional profiles or strategies related to resource use coexist through the entire process of forest regeneration, such as the low-wood density *Jatropha* species coexisting with the high-wood density *Croton* species. It has previously been noticed that Caatinga dry forest regeneration benefits from resprouting (Figueirôa et al., 2006; Schacht et al., 1988; Sampaio et al., 2010). However, we propose that resprouting in response to human disturbances, in fact, governs the Caatinga dry forest dynamics in human-modified landscapes covering sandy soils. In other words, the Caatinga dry forest regeneration is limited or determined by the extensive agricultural practices and/or forest exploitation (both old-growth and secondary forests) that favour resprouting woody plant species, although seedling recruitment from seeds can a play a major role across certain contexts (Lopes et al., 2012). This scenario has been described elsewhere, particularly in the Caribbean and Mexican dry forests (see Murphy and Lugo, 1986; McLaren and McDonald, 2003; Ordonez et al., 2014).

In synthesis, the Caatinga dry forest has been exposed to slash-and-burn agriculture since Europeans arrived in the 16th century, initiating a process of converting old-growth forest into human-modified landscapes consisting of successional mosaics (Tabarelli et al., 2017; Souza et al., 2019). Under this human-dominated ecological scenario, regeneration in the Caatinga is driven by resprouting in some ecological contexts, whereas deterministic species replacements play a subordinate role. This initial composition model probably results from a combination of three factors: (1) early regeneration driven by resprouting, rather than seed arrival and seedling recruitment as documented here; (2) stem/biomass/species accumulation mostly resulting from the growth by early colonizers and by those species able to resprout as regeneration progresses and chronic disturbance occurs; and (3) the co-occurrence of functionally distinct plant species. While it is unclear whether regeneration driven by resprouting represents the regeneration that would have taken place in undisturbed Caatinga dry forest prior to the settlement of human populations in this region (given that resprouting can occur in response to natural drought (Bond and Midgley, 2001)). It is likely that slash-and-burn agriculture and the use of forest products probably favor resprouting species, while eliminates or largely reduces the population size of those completely dependent on seeds for successful establishment. Although resprouting can confer some level of resilience to secondary forests and the services they provide, forest dynamics in landscapes inhabited by forest-dependent people rely to a great extent on the nature of the imposed pressures and, consequently, on the ecological profile of the remaining flora. Given the theoretical and practical implications for biodiversity conservation, the provision of ecosystem services, and the well-being of populations that are dependent on the resilience of these forests, further studies are needed to improve our understanding of secondary succession in human-modified landscapes and the role that resprouting plays, and to assess the generality of the patterns found here.

CRediT authorship contribution statement

Maria Fabíola Barros: Conceptualization, Methodology, Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Elâine M.S. Ribeiro:** Formal analysis, Investigation, Writing - review & editing. **Renato Soares Vanderlei:** Formal analysis, Investigation, Writing - review & editing. **Alexandre Souza de Paula:** Methodology, Investigation, Writing - review & editing. **Ana Beatriz Silva:** Methodology, Investigation, Writing - review & editing. **Rainer Wirth:** Conceptualization, Investigation, Writing - review & editing. **Marcus V. Cianciaruso:** Conceptualization, Methodology, Investigation, Writing - review & editing. **Marcelo Tabarelli:** Conceptualization, Funding acquisition, Methodology, Validation, Supervision, Writing - review & editing.

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Authors contributions

MFB, MT, RW and MVC conceived the ideas and designed methodology; MFB, ASP and, ABS collected the data; MFB, EMSR and RSV analyzed the data; MFB and MT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for

publication.

Declaration of Competing Interest

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

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118881.

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