Forest Ecology and Management 482 (2021) 118854

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Recovering ecosystem functions through the management of regenerating community in agroforestry and plantations with *Khaya* spp. in the Atlantic Forest, Brazil

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A R T I C L E I N F O

Keywords:
Successional agroforestry
Biomass production
Nutrient accumulation
Nutrient cycling
Tropical forest

A B S T R A C T

Our aims were to describe the role of the selective management of regenerating community (RC) on the recovery of ecosystem functions in production areas of African mahoganies under mixed stands and agroforestry systems, established on abandoned farmland. A randomized block experiment was set up with the following treatments: (T1) mixed-plantation of African mahogany under conventional system (including herbicide application); (T2) mixed-plantation of African mahogany with selective conduction of RC; (T3) agroforestry system with African mahogany; (T4) agroforestry system with African mahogany with selective conduction of RC. The parameters of horizontal structure, diversity and ecological attributes of species of the regenerating community were studied. In addition, the production of aboveground biomass and nutrient stocks, soil fertility, and soil microbial activity were assessed. In T1, herbicide application (glyphosate) affected the floristic composition of the regenerating community by reducing the dominance of monocots and *Pteridium arachnoideum*, allowing the regeneration of other taxonomic groups of herbaceous species. In response, there was a reduction in the litter biomass stock comparing to the other treatments. The treatments with selective management of the RC (T2 and T4) produced more biomass and accumulated higher amounts of C and nutrients than the conventional treatments (T1 and T3). These treatments also allowed other shrub and tree species to overcome the ecological filter imposed by grasses and colonize the experimental area. *Baccharis dracunculifolia*, *Vismia guianensis*, *Cecropia pachystachya* and *Inga* sp. were the most important regenerating species that contributed most to the stocks of all nutrients in living aboveground biomass. Pruning and selective management in T4 increased the soil effective cation exchange, while in the T1 treatment there was a lower activity of the β-glucosidase enzyme. The selective management of RC in agroforestry systems through the manipulation of competitive relationships allowed the colonization of native tree and shrubby species that provide several additional ecosystem services, including pollination, fauna attraction, food production, pest control and environmental regulation for the agroecosystem.

1. Introduction

Agroforestry systems allow species diversification which increases the agricultural production, while offering other economic, social and environmental benefits to farmers (Altieri, 2012; Jose, 2009). In addition, they could contribute to the restoration of degraded tropical terrestrial ecosystems (Miccolis et al., 2016; Santos et al., 2019). One important restoration strategy is the use of secondary succession as a catalyst for forest restoration (Chazdon et al., 2017; Chazdon and Guariguata, 2016; Vieira et al., 2009). Agroforestry systems that combine wood and food production along with regenerating community (RC) management are known as successional agroforestry systems, since they attempt to simulate forest environment, in terms of diversity, structure and successional dynamics (Young, 2017)

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https://doi.org/10.1016/j.foreco.2020.118854
Received 7 September 2020; Received in revised form 25 November 2020; Accepted 5 December 2020
Available online 5 January 2021

When successional agroforestry systems are established in abandoned agricultural areas, dominated by invasive grasses and ferns, weeding operations are often needed such as selective mowing to favor the growth of regenerating shrubs and trees. These species may undergo successive regimes of pruning and deposition of its biomass on the soil surface (Vieira et al., 2009). The frequency of these operations is conditioned to site resilience, regulated by duration and intensity of previous soil use and/or by the proximity to forest fragments (Chazdon, 2014; Holl, 2007). Therefore, the organic matter added to the soil through the management of successional agroforestry systems can provide a nutrient-rich substrate for the invertebrate fauna and soil microbiota, improving nutrient cycling and soil fertility levels to sustain agroforestry production (Peneireiro, 1999).

Cezar et al. (2015) report that multi-stratified agroforestry systems (denomination analogous to successional agroforestry systems) at 5 and 10 years of age, under agroecological management (without external inputs), presented diversity of soil fauna and microbial activity similar to an area maintained in natural regeneration for 10 years. These results suggest that multi-stratified agroforestry systems are capable to maintaining edaphic processes vital to the ecosystem functions, as well as producing food and generating income for farmers, when compared to areas under natural regeneration.

Changes over time in floristic structure and composition of regenerating plant communities promote a rapid accumulation of C and nutrients in the above-and belowground biomass (Froufe et al., 2011). As the regenerating community grows the topsoil becomes more enriched with organic matter, the nutrient cycling is intensified and there is an increase in soil fertility and carbon sequestration (Chazdon, 2008; Sang et al., 2013). In addition, regenerating plants may increase the availability of resources for pollinators and dispersers and create favorable microhabitats for the population of natural pest enemies, as well as for species of agroforestry interest that are shade tolerant and/or sensitive to windthrow (Chazdon, 2014; Chazdon and Guariguata, 2016). It demonstrates that hich are some valuable ecosystem functions (supporting and regulating) that could be improved by forest management.

The practice of successional agroforestry systems and the ecological benefits have been widely disseminated in the tropics (Young, 2017). However, the effects of the management of regenerating plants in productive systems has been little explored in field experiments that seek to measure the benefits of successional agroforestry in relation to the conventional managed agroforestry systems. In this context, we put forward the hypothesis that successional agroforestry with selective management of RC increase the provision of ecosystem services when compared to less complex systems managed under conventional practices. More specifically, we compared: (i) the diversity and accumulation rate of aerial biomass, C and nutrients; (ii) the soil fertility levels, intensification of soil microbial activity; and (iii) the availability of resources and habitats, favoring biotic interactions. In order to test our hypothesis, we characterized and described the effects of selective management of RC on the recovery of ecosystem functions in mixed plantations and agroforestry systems with African mahoganies established in abandoned farmland.

2. Material and methods

2.1. Characterization of the study area

The study was carried out at Fazenda Sucupira, a farm located in the municipality of Valença (13°19′55″S, 39°18′41″W), Southeastern of Bahia state, Brazil. The vegetation is characterized by ombrophilous dense submontane forest of the Atlantic Forest. The predominant soil class is the dystrophic Yellow Argisol, with a sandy surface horizon (around 80% of sand), formed by clay eluviation, and a B_t horizon in sub-surface, characterized by more clayey texture.

The climate of the region, according to the Köppen's classification, is humid tropical type (Af) with rainy winters and drier summers (Alvares et al., 2014). The average annual temperature of the region is 23 °C. The highest maximum temperatures are recorded during the summer (ranging from 29 to 32 °C). From April onwards, the temperature decreases progressively until August, when the lowest minimum temperatures are recorded (ranging from 16 to 18 °C). The average annual rainfall is around 2,000 mm, well distributed throughout the year, and the period with the highest rainfall spans from May to September (Santos et al., 2018).

The experiment was conducted in a flat area where swidden agriculture, which makes use of fire, took place for several years and the area was abandoned for almost 10 years. The area presented high dominance of capim-quicuio (*Urochloa humidicola* (Rendle) Morrone & Zuloaga), sapê (*Imperata brasiliensis* Trin.), tiririca (*Cyperus* sp.) and pteridium (*Pteridium arachnoideum* (Kaulf). Maxon). Prior the establishment of the experiment, the soil analyzes indicated low levels of pH, Ca, Mg and high Al contents (personal information provided by the owner).

At the time of planting, 200 g of single superphosphate and 40 g of FTE BR 12 (micronutrient cocktail – B, Cu, Mn, Mo and Zn) were applied to each pit of the *Khaya* sp. trees. Four other fertilizations were made in topdressing, during the first two years after planting, totaling 400 g of NPK (18-27-9) per plant. Two years after *Khaya* spp. planting (summer 2015), 2 Mg ha^{-1} of dolomitic lime and 1 Mg ha^{-1} of gypsum were applied to the soil surface in the total area.

2.2. Experimental design and management description

The experiment was established from a mixed plantation of two African mahoganies species (*Khaya ivorensis* and *Khaya grandifoliola*). The seedlings were produced in the farm and the seeds were obtained from mother trees located in Reserva Natural Vale, Linhares, ES, Brazil. The experiment was installed in January 2016 when *Khaya* spp. trees were 2.2 years old. These species were planted in a 7 × 3 m spacing in alternate rows. At the beginning of the experiment, soil chemical and physical characteristics were analyzed in order to examine changes in soil properties as they could be influenced by the experimental settings (Table 1).

Four randomized blocks were established based on four dominant patterns of plant communities present in the area: capim-sapê (*Imperata brasiliensis*), capim-quicuio (*Urochloa humidicola*), tiririca (*Cyperus* sp.) and pteridium (*Pteridium arachnoideum*). In blocks 1, 2 and 3, the plots were 50 m × 21 m (1,050 m^2), while in block 4, the plots were 30 m × 35 m (1,050 m^2). In each block, four experimental units (plots) were allocated, with the following treatments:

T1: Mixed plantation of African mahogany with elimination of regenerating community (RC) by herbicide application;

T2: Mixed plantation of African mahogany with selective management of RC;

T3: Agroforestry system of African mahogany with elimination of RC, without herbicide application; and

T4: Agroforestry system with African mahogany with selective management of RC.

To avoid the edge effect and the possible influence of neighboring plots, the area occupied by the central *Khaya* spp. trees was defined as a useful plot, excluding a line of plants along the perimeter of each plot (corresponding to an area of 525 m^2).

Treatments T3 and T4 constituted agroforestry systems in which perennial and annual agricultural and fruit species were introduced in the African mahoganies rows and interrows. Three pineapples (*Ananas* spp.) were planted between each African mahogany tree, in the planting rows using 0.5 m spacing. The cassavas (*Manihot esculenta* Crantz) were planted in double rows, at spacing 1 m × 1 m, and at 1 m of the tree rows. In the center of African mahogany interrows, fruit species such as banana (*Musa* spp.), cupuassu (*Theobroma grandiflorum* (Willd. Ex Spreng.) Schum.) and açaí (*Euterpe oleracea* Mart.) were alternately planted, distributed in the 7 × 3 spacing (same density as African

Table 1
Soil chemical characterization at depths of 0–10, 10–20 and 20–40 cm of the experimental area.

Depth (cm)	pH (H_2O)	Al $cmol_c\ dm^{-3}$	H + Al	Ca	Mg	K	P $mg\ L^{-1}$	Total C %	Total N	SB* $cmol_c\ dm^{-3}$	CEC**	m*** %	BS****
0–10	5.73	0.08	4.70	1.83	0.57	0.10	1.19	1.29	0.11	2.50	2.58	3.10	34.72
10–20	5.43	0.20	4.90	1.12	0.33	0.08	1.55	1.09	0.09	1.53	1.73	11.56	23.79
20–40	4.91	0.49	4.67	0.52	0.19	0.04	0.77	0.75	0.07	0.75	1.24	39.51	13.84

* Sum of bases.
** Effective cation exchange capacity.
*** Percent of Al saturation.
**** Percent of base saturation.

mahoganies). Also, in treatments T3 and T4, African mahogany plants with low development or dead were replaced by seedlings of *Plathymenia reticulata* Benth. (vinhático) and *Dalbergia nigra* (Vell.) Fr.All. ex Benth. (jacarandá-da-bahia or Brazilian rosewood), which are N_2-fixing native tree legumes and with timber value. The replaced positions represented 20% (10% of each species) of the initial density of African mahogany plants in each plot.

Fertilization of fruit species was performed with the application of 250 g of natural phosphate (GAFSA) and 40 g of FTE BR 12. Similarly to African mahogany trees, four topdressing fertilizations were also carried out. In total, 400 g of NPK (18-27-9) were applied per plant, parceled between the first two years. Pineapple plants received a single fertilization, equivalent to 30 g NPK (10-10-30) per plant.

Until January 2016, at the beginning of the experiment, the management of RC and invasive plants was done through periodic selective cuttings, in order to release native regenerating tree species. It is worth pointing out that the existence and capacity of RC of shrubby and arboreal species in the studied sites were favored by the presence of large fragments of secondary forests surrounding the experimental area, in addition to the soil seed bank and resprouting from previously cut tree shoots.

In treatments T1 and T3, all regenerating plants were eliminated at the beginning of the experiment; after this stage, in T3, the control was performed by mowing all the regenerating vegetation (in a non-selective manner), with the same frequency of selective mowing in treatments T2 and T4. In T1, the management was similar to T3 up to 39 months. From the fortieth month after the African mahogany planting, regeneration was eliminated by an herbicide application (glyphosate).

In treatments T2 and T4, RC and invasive plants were controlled by periodic selective mowings, which prioritized the cutting of dominant exotic plants (grasses and pteridium) in order to release shrubby and arboreal native plants to accelerate the progress of the secondary succession. In these treatments, RC was conducted in such a way that the growth of African mahoganies or other species introduced into the agroforestry system were not impaired.

2.3. Vegetation inventory of the regenerating community

The horizontal structure and floristic diversity of the RC were evaluated at 58 months after planting. The community was compartmentalized at two levels, as follows:

- Level I: included herbs, shrubs and young trees, up to 50 cm height. Three subplots were allocated within the plots. The allocation was made by successive random launches of a 1 m^2 PVC quadrant in the useful area of each experimental unit, corresponding to the area occupied by the most centralized plants (525 m^2). Cover estimation was performed according to the Braun-Blanquet (1979), as described on Table 2.
- Level II: included shrubs and trees with >50 cm of height. For the characterization of this stratum, a census was performed inside the useful plots. Height measurements were taken and the crown area (projection on the soil surface) of each individual was assumed as a cover measure.

Table 2
Braun-Blanquet (1964) scale adopted during community cover evaluation.

Scale	Cover-rate	Mean cover (%)
5	>3/4 of sampling area	87.5
4	Ranging from 1/2 to 3/4 of sampling area	62.5
3	Ranging from 1/4 to 1/2 of sampling area	37.5
2	Ranging from 1/10 to 1/4 of sampling area	15
1	Numerous or sparse individuals with <5% of sampling area	2.5
+	Few individuals with low cover	0.1
R	Rare plant with low cover	0.01

For the taxonomic identification of regenerating species, botanical material collections and photographic records were made for species not identified in the field, for further consultation to experts and/or searches for voucher materials available on the website of the Virtual Herbarium Reflora (Reflora, 2019). Besides the taxonomic identification, the information of endemism and natural distribution range of the species was also obtained in the Virtual Herbarium Reflora. When identification was not possible, individuals were classified into morphospecies, and the nomenclature “undetermined” was attributed, followed by a sequential numbering.

2.3.1. Horizontal structure of the regenerating community

The horizontal structure was evaluated based on density, dominance, cover, and frequency. Density was not evaluated at level I, due to the difficulty of individualizing some groups of plants such as grasses and rhizomatous or stoloniferous plants. As a measure of dominance, the average cover was used, according to the cover-scale of Braun-Blanquet (1979) (Table 2) for level I. On the other hand, the canopy projection was used to represent the dominance of the level II (Mueller-Dombois and Ellenberg, 1974). Frequency was determined for both levels. The Importance Value Index (IVI) and Coverage Value Index (CVI) were calculated (Mueller-Dombois and Ellenberg, 1974).

2.3.2. Diversity of the regenerating community

Diversity and equability at level I were not performed due to the methodology used, which did not account for the number of individuals, as explained above. Thus, the species richness analysis was the way to measure diversity at this level. On the other hand, at level II, the following indices were calculated: Richness (R), Jentsch mixture quotient (MQ), Shannon index (H’), Simpson index (S’) and Pielou equability index (J’) (Mueller-Dombois and Ellenberg, 1974).

2.4. Biomass and nutrient contents in the regenerating community

The biomass of regenerating individuals was also estimated at two levels. At level I, exactly where the quadrant was placed for floristic and phytosociological sampling, the aboveground biomass was collected with pruning shears, cutting at the soil surface. The material was placed in paper bags and weighed in analytical balance (±0.01 g), before being taken to a forced-air oven at 65 °C, until constant weight. Subsequently, the samples were weighed again to determine moisture content.

To represent level II, the 10 species with the highest IVI were selected (five shrubs and five trees species). Three individuals of each species were selected and felled. The aboveground biomass fractions (leaves, branches and stem) were then separated and weighed in the field to obtain fresh matter with a suspended digital balance (±0.1 kg). Subsamples of the components were collected and placed in paper bags to determine the moisture content and correction of the fresh mass.

After drying, all biomass samples from levels I and II were grounded in a knife mill and then directed to the laboratory to determine the macronutrients contents (EMBRAPA, 2009).

2.5. Stock and nutrient contents in the litter

After floristic and aboveground biomass quantification (level I), all litter accumulated on the soil within the quadrant limits were collected using a rake. All organic material collected was placed in paper bags. Subsequently, the samples were taken to a forced-air oven at 65 °C for 48 h and then weighed to obtain the dry mass. Contamination of the mineral fraction (from the soil) in the litter samples was corrected by passing the samples on a set of sieves, followed by manual separation. The mass of the mineral fraction was discounted from the total mass of the wet and dry samples.

The samples were grounded in a knife mill and taken to the laboratory for chemical characterization. Macronutrient contents were analyzed according to methodologies proposed by EMBRAPA (2009). The nutrient content stored in the litter was estimated by the product between the content of each nutrient by dry biomass. The values of nutrient contents were expressed in kg ha^{-1}.

2.6. Soil sampling

Soil samples were taken at 29 and 58 months after planting. Soil samples were collected at 0–10 cm depth in six random points within the plots using a Dutch auger, with three samples collected in the planting rows, and three in the interrows. These samples were mixed to produce one compound sample per plot. Samples were placed in plastic bags and kept in ice-filled thermal boxes until arrival in the laboratory. The samples were sieved (2 mm) and subsamples were stored in a refrigerator (±5C) until the microbial analyzes (carried out in 15 days) or air-dried for chemical analyzes.

2.7. Soil analyses

2.7.1. Chemical soil analyses

Subsamples of air-dried fine soil (<2 mm) were analyzed according to EMBRAPA (2017). Available P, soil pH, exchangeable acidity (H + Al), Al^{+3} and base cations K^{+}, Ca^{2+}, and Mg^{2+} concentrations were evaluated (EMBRAPA, 2017). Also, the effective and potential cation exchange capacity, and the percent of base saturation (%BS) were also calculated. The total organic carbon content was analyzed according to Yeomans and Bremner (1988) and results converted to organic matter content.

2.7.2. Soil microbial analyses

For the evaluation of soil microbial biomass carbon (MBC), the fumigation-extraction method was used (Brookes et al., 1985; Vance et al., 1987). The C extracted in fumigated and non-fumigated samples were analyzed by colorimetry (Bartlett and Ross, 1988), and the values of MBC were obtained by applying a constant (Kc) equal to 0.35 on the C concentrations (Anderson et al., 2008).

The soil basal respiration rate (SBR) was measured by the soil incubation method using NaOH as a trap, according to Silva et al. (2007). Also, the microbial quotient was obtained by the ratio of MBC to the total organic carbon. Soil microbial activity was measured by determination of hydrolysis of fluorescein diacetate (FDA) (Schnurer and Rosswall, 1982). Additionally, the activities of phosphatase, β-glycosidase and arylsulfatase enzymes were evaluated spectrophotometrically, according to Tabatabai (1994) and Eivazi and Tabatabai (1988).

2.8. Data analysis

For the data obtained with the sampling of level I, a rarefaction curve was constructed, based on the number of samples collected, using the software EstimateS version 9.1.0 with 100 randomizations (Colwell, 2006).

To deal with the low sample intensity related to destructive sampling of biomass of the regenerating species (level II), we used the methodology proposed by Akindele and LeMay (2006). For this purpose, a cluster analysis was performed using the *k-means* method based on structural variables (height and crown area) and dry matter values of leaf, branch and stem of the sampled species. After defining the groups, the observed data of the species were pulled to form a more robust data set for each group. Then, the adjustment of allometric models was performed to estimate the biomass of each fraction (leaf, branch and stem), using regression analyzes. The crown height and area or combination of both were used as predictive variables. This procedure allowed indirectly to estimate the biomass of individuals that were not quantified by the destructive method. It should be highlighted that rare or low IVI species were not included in the aboveground biomass estimation of the RC and, therefore, we recognized that the values of this study are underestimated.

After checking normality and heteroscedasticity, the data on soil fertility, soil microbial activity, aboveground biomass and nutritional contents were submitted to analysis of variance (ANOVA) considering the completely randomized block design. Data with non-normality and heteroscedasticity underwent logarithmic transformations. Thereafter, the means of all variables were discriminated by F test ($p < 0.05$) and compared by Tukey test ($p < 0.05$). The nutritional contents in the aboveground biomass fractions of the shrub and tree species (level II) of treatments T2 and T4 were analyzed using the t-student test. The R software was used for the parametric analyzes, through the *ExpDes* package (Ferreira et al., 2013). Then, a principal component analysis was performed to better understand the patterns associated with soil quality in the different experimental treatments, and the groups were compared by PerMANOVA. For this, we used the *vegan* package (Oksanen et al., 2017), also available for R (R Development Core Team, 2018).

3. Results

3.1. Floristic and phytosociological description

At level I of the RC, 32 species were found, distributed in at least 13 different botanical families. At this same level, the families with the greatest species richness were Asteraceae and Poaceae (both with 7 species) (Supplementary data 1A). Whereas in level II of the RC, 33 species were found, nine of which also had individuals sampled at level I. Thus, a total richness of 56 regenerating species was found at both

Table 3
Regenerating community level II diversity parameters.

Parameter	Value
Total number of individuals	258
Total number of species	32
Jentsch's mixture quotient (QM)	0.12
Simpson's index (S')	0.91
Shannon's index (H')	2.74
Pielou's equability index (J')	0.79

levels. From such species, four are endemic to the region, five are naturalized and 37 are native. Nine species were identified only up to the family level and five others could not be identified at any taxonomic level (Supplementary data 1A).

The rarefaction curve did not reach an asymptote, but the tangent calculated on the largest sample size was approximately 0.2. In addition, the model used estimates that the proportion of species found was about 98%, which can be considered a good sample effort. Such values suggest that there would be a slight increase in species diversity (level I) with the increase in sample effort, showing that the sampling used was sufficient to characterize species richness in the experimental area (Fig. 1) (Jiménez-Valverde and Hortal, 2003).

In general, the species with the largest CVIs were: *Urochloa humidicola*, *Hydrocotyle bonariensis*, *Imperata brasiliensis*, *Cyperus* sp., *Sphagneticola trilobata* and indeterminate 1 (Asteraceae). However, the importance of the species varied according to the type of management. In the T1 treatment, for example, it was observed that the species *S. trilobata*, *H. bonariensis* and indeterminate 1 (Asteraceae) were the ones that presented the highest CVIs (Fig. 2). On the other hand, in T2, T3 and T4, the species *U. humidicola*, *I. brasiliensis*, *H. bonariensis* and *Cyperus* sp. were always among the most important in level I (Fig. 2).

The level II of the RC was evaluated only in treatments with selective management of the RC (T2 and T4). Jaccard's similarity between the two treatments was 0.64, indicating that the plots of these treatments presented high floristic similarity. In addition, the species with the highest IVI occurred in the plots of T2 and T4 in similar proportions (data not presented).

The parameters of the horizontal structure of level II of the community are described in Supplementary data 3A. The species with the largest IVIs were: *Baccharis dracunculifolia*, *Vismia guianensis*, *Cecropia pachystachya*, *Inga* sp., *Pleroma heteromallum*, *Mikania* sp., *Bactris ferruginea*, *Solanum crinitum*, *Cyrtocymura scorpioides* and *Lantana camara*. *B. dracunculifolia* and *V. guianensis* were the two species with the highest density, frequency and dominance rates. *P. heteromallum*, in turn, stood out for presenting high relative density values, suggesting that individuals of this species occurred in clumps within the plots. On the other hand, *Inga* sp. and *C. pachystachya* were relevant because they presented higher dominance, due to the large size in relation to the individuals of the other species. Other important species were *Mikania* sp., *L. camara*, *B. ferruginea*, *C. scorpioides* and *S. crinitum,* which presented intermediate values of frequency, density and dominance in relation to the previously mentioned species.

3.2. Aboveground biomass estimates

At level II of the RC, 258 individuals (about 566 individuals/ha) were distributed among 32 different species (Table 3). The clustering analysis of the ten species with higher IVIs (level II) showed that the data set with dry matter information of biomass fractions (leaves, branches and stem) and structural information (crown area and height) of the sampled individuals could be organized into three groups (1, 2 and 3), especially along the first principal component (PCA1), as shown in Fig. 3. Thus, information of all individuals measured in the vegetation inventory was pulled according to the group referring to each species. The combination of these data allowed the adjustment of allometric equations for estimating the dry matter of leaves, branches and stem for each group of species (Supplementary data 1B).

The biomass estimation equations for group 1 were reasonably adjusted to the data set, especially for leaves and stem (values of R^2 equal to 0.40 to 0.24, respectively), and their coefficients were significant (Supplementary data 1B). In addition, the equation for estimating the biomass of branches for group 1 was considered to be well adjusted (R^2 equal to 0.72 and Syx of 1.7 kg individual^{-1}) (Table 7). For groups 2 and 3, the equations for all fractions were well adjusted (R^2 ranging from 0.68 to 0.96) and with high significance ($p < 0{,}001$) of the coefficients β_1 and β_2, except for the stem equation of group 3, which presented significant coefficients at 10% (Supplementary data 1B).

The litter stock in the T1 (1599.1 kg ha^{-1}) was significantly lower than the other treatments (T2, T3 and T4), which presented values between 3942.6 kg ha^{-1} and 4941.7 kg ha^{-1}. There were no significant differences ($p > 0.05$) regarding biomass stock at level I (Table 4). Regarding level II of the community, aboveground biomass stocks for leaves, branches and stems fractions of arboreal and shrubby species also did not show significant differences ($p > 0.05$). However, the total biomass stock (sum of litter and regenerating plants biomass) was higher in T2 and T4 (10.462.2 and 12.411.0 kg ha^{-1}, respectively) in relation to T1 and T3 (4.182.7 and 6.979.4 kg ha^{-1}, respectively) (Table 4).

3.3. Nutrient stocks

In general, the T1 presented the lowest macronutrient contents of the litter stored on the soil, in relation to the other treatments (Supplementary data 1E). There were no differences in litter nutrient stocks in T2, T3 and T4, except for Ca that was accumulated in a higher amount in the T2 (Supplementary data 1E). Regarding the nutrient stocks in the

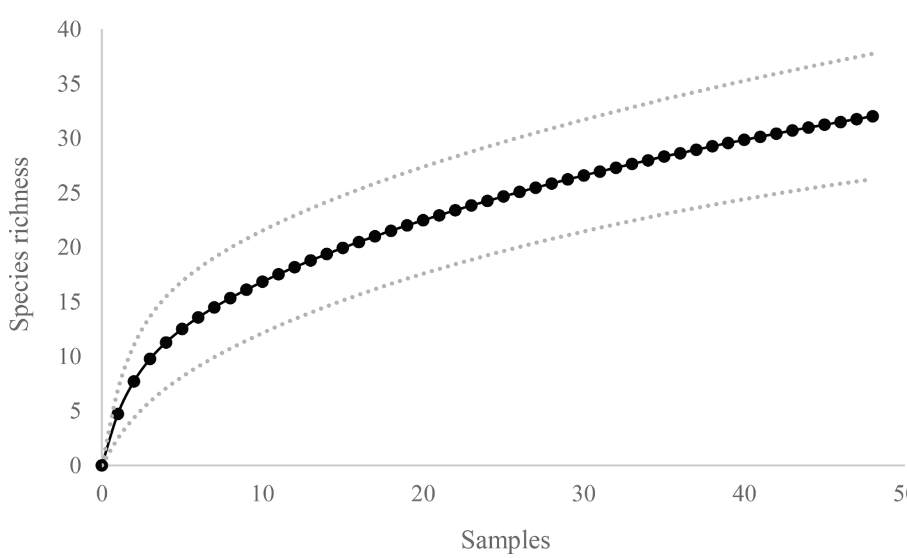

Fig. 1. Rarefaction curve for the 48 samples of the regenerating community (level I). Dotted lines indicate the upper and lower limit of the confidence interval at 95% of probability. Parameters found: a = 2.2828; b = 0.0740.

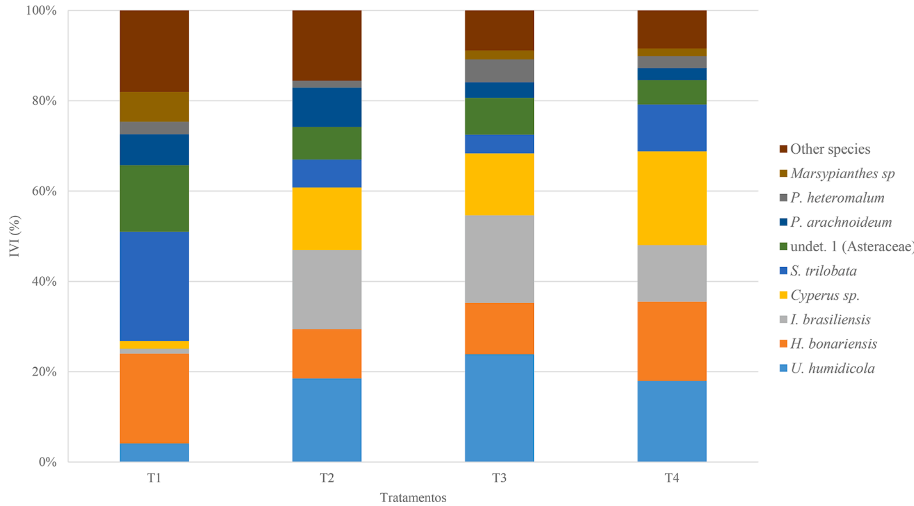

Fig. 2. Main species of the regenerating community (level I) among the treatments, based on the importance value in percentage.

Table 4
Aboveground biomass estimation within each regenerating community level and litter stocks (kg ha^{-1}).

Treatments	Litter stocks	Level I	Level II						Total
			Shrubby			Arboreal			
			Leaves	Branches	Stems	Leaves	Branches	Stems	
T1	1599.1 (±380.5) b	2583.7 (±335.0) a	–	–	–	–	–	–	4182.7 (±833.4) b
T2	4941.7 (±873.3) a	2613.1 (±361.1) a	194.2 (±60.71) a	523.5 (±177.85) a	400.8 (±163.55) a	309.0 (±141.47) a	509.8 (±303.41) a	970.1 (±462.57) a	10462.2 (±525.1) a
T3	3942.6 (±562.4) a	3036.8 (±393.9) a	–	–	–	–	–	–	6979.4 (±344.1) b
T4	4823.0 (±651.9) a	2768.9 (±311.7) a	200.3 (±112.41) a	554.8 (±315.09) a	460.1 (±283.12) a	732.5 (±309.21) a	795.2 (±320.34) a	2076.2 (±894.14) a	12411.0 (±1468.3) a

Same letters in each column indicate absence of statistical differences between treatments, according to the Tukey test ($p < 0.05$). Values in parentheses represent the mean standard error.

biomass of the regenerating species at level I, no significant differences were found among the treatments ($p > 0.05$) for all macronutrients (Supplementary data 2E). For the level II, no differences were found in the nutrient stocks in the aboveground fraction of the shrubby species in T2 and T4 (both managed with selective cutting of RC) (Supplementary data 3E). However, for the tree species found in T4, the stocks of all nutrients in the aboveground fractions were significantly higher than T2 (Supplementary data 4E). When considering the total stock of all nutrients, T2 and T4 showed significantly higher stocks compared to T1 and T3 (Table 5). In comparative terms, regenerative management provided a greater total accumulation of all nutrients above the soil (taking into account the sum of the litter stocks and the aboveground biomass of regenerating vegetation), in relation to conventional management (Table 5).

3.4. Soil atributtes

There were no differences in pH values and in H + Al, Mg, K and soil organic matter among the treatments (Table 6). In treatment T3, P content was significantly higher ($p < 0.05$) than in T1 and T2, while T4 presented intermediate levels of this element (Table 6). On the other hand, Ca contents, effective cation exchange capacity (t) and base saturation (V) presented higher values in T4 treatment compared to T1 and T2 (Table 6). Potential cation exchange capacity (T) in T4 was higher than T2, with intermediate values for T1 and T3 treatments (Table 6).

There were no differences among treatments in relation to MBC, qMic, FDA, arylsulfatase and phosphatase ($P > 0.05$) (Table 7). The T1 treatment presented significantly lower values of SBR and β-glucosidases activity ($P < 0.05$), as compared to the other treatments (Table 7).

The treatments were arranged through the principal component analysis based on the matrix of data of soil microbiological variables. The groups were ordered along the two principal components that explained about 60% of the total variance of the data (Fig. 4). The permutational multivariate variance analysis (PerMANOVA) indicated that at least one group was significantly different from the others ($p = 0.201$). Therefore, it is noted that the T1 treatment was specially separated over the first principal component (PC1). The β-glycosidases activity and the soil basal respiration were the variables that most correlated with PC1 and contributed to the separation of T1 treatment from the others.

4. Discussion

4.1. Management effects on the structure and compostion of the regenerating community

In the T1 treatment, there was a change in floristic composition, especially in the groundstore (level I). It happened due to glyphosate application, a post-emergent, non-selective, and systemic action herbicide, widely employed in chemical weed controls in reforestation and agricultural crops (Leles and Resende, 2017). This product has a wide spectrum of action against weed plants, including monocots and annual or perennial eudicots species (Ruas et al., 2012; Toledo et al., 2003). Desiccation with glyphosate caused a reduction in the dominance of grasses (Poaceae) that colonized our experimental area, such as *Imperata*

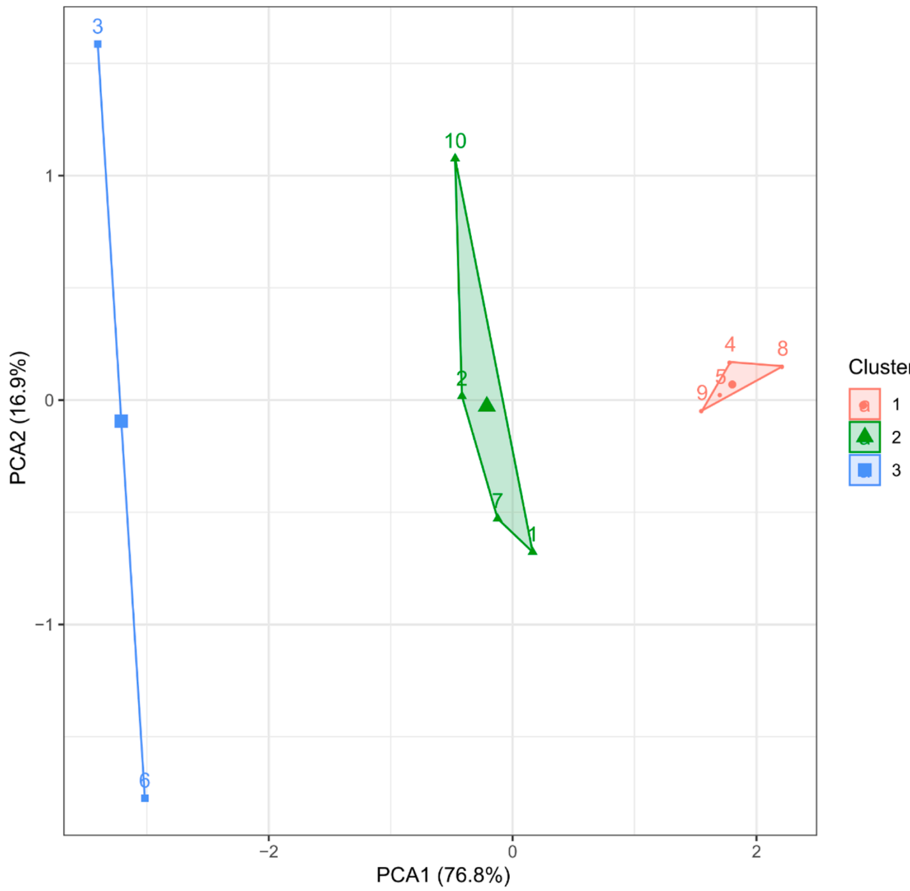

Fig. 3. Cluster analysis by the K-means method graphically represented by the sorting of species according to the principal components of structural variables (height and crown area) and biomass fractions (leaves, branches and stem) of species with higher IIV. Species: 1 – *B. dracunculifolia*; 2 – *V. guianensis*; 3 – *C. pachystachya*; 4 – *C. scorpioides*; 5 – *P. heteromallum*; 6 – *Inga* sp.; 7 – *S. crinitum*; 8 – *L. camara*; 9 – *Mikania* sp.; 10 – *B. ferruginea*.

Table 5
Total nutrient content in the aboveground compartments (litter and living biomass) of the regenerating community (levels I and II).

Treatments	N kg ha^{-1}	P	K	Ca	Mg	S
T1	45,54 (±8,70) b	2,68 (±0,60) b	43,81 (±9,98) b	31,46 (±8,29) b	7,96 (±1,67) b	4,47 (±0,94) b
T2	87,25 (±8,03) a	5,20 (±0,74) a	61,99 (±5,24) a	84,82 (±9,42) a	16,16 (±1,40) a	8,65 (±0,57) a
T3	60,53 (±6,83) b	3,71 (±0,33) b	49,04 (±8,99) b	39,29 (±9,82) b	11,75 (±1,30) b	6,02 (±0,85) b
T4	89,93 (±16,36) a	5,97 (±0,60) a	63,48 (±10,94) a	66,66 (±24,54) a	17,76 (±3,40) a	8,50 (±0,68) a
Differences between groups (%)*	67	85	35	114	72	64

Same letters in each column indicate absence of statistical differences between treatments, according to the Tukey test ($p < 0.05$). Values in parentheses represent the mean standard error. * Mean difference between T2 and T4 *versus* T1 and T3, in terms of percentage.

brasiliensis, *Urochloa humidicola*, as well as *Cyperus* (Cyperaceae) and *Pteridium arachnoideum* (Dennstaedtiaceae). As weed dominance decreased, other taxonomic groups began to spontaneously regenerate from the soil seed bank and seed rain, including: *S. trilobata*, undetermined 1 (Asteraceae), *H. bonariensis*, *B. dracunculifolia*, *Marsypianthes* sp. and *C. scorpioides*.

In herbicide-free treatments, the dominance of *P. arachnoideum* and Poales (Poaceae and Cyperaceae) remained elevated. Many of these species have high resilience to mowing compared to eudicots. This is because they have rhizomes and runners that give them competitive advantages, such as accumulation of nutritional reserves and vegetative propagation for exploitation of surrounding areas, even if they are often mowed or grazed (Brighenti and Oliveira, 2011; Hempson et al., 2015). In addition, grasses are adapted to intense light and temperature conditions (plants with C4 metabolism) and are highly efficient in water and nutrient use (Linder et al., 2018). After mowing, these plants regrow quickly and produce a lot of biomass in a short period of time, physically inhibiting the regeneration of other species, even with active dispersal of propagules from nearby forests. Therefore, the breakdown of grasses dominance becomes difficult when only mowing is carried out in areas with high infestation of these species.

This situation has particularly occurred in treatment T3, where mowing operations have been carried out indiscriminately, suppressing the aboveground biomass of all regenerating plants. In this treatment, infestation of *P. arachnoideum* and grasses reached high levels and may extend for several years until they get shaded out by trees. Consequently, the agroforestry production can suffer severe negative impacts because of competition for water and nutrients or the production system may become very costly because of the need for frequent mowing and weeding.

The productive systems managed with selective cuttings of the RC (T2 and T4) also exhibited a set of species very similar to T3 (level I). However, the selective mowing allowed that other shrubs and tree species (level II) to compete with weeds and colonize the area. Thus, the

Table 6
Soil chemical variables at 58 months after planting.

Variable (unit)	Treatments							
	T1		T2		T3		T4	
pH (H_2O)	6.2 (±0.2)	a	6.6 (±0.2)	a	6.4 (±0.1)	a	6.5 (±0.1)	a
P (mg dm^{-3})	0.6 (±0.1)	b	0.6 (±0.2)	b	3.9 (±1.8)	a	1.3 (±0.5)	ab
K^+ (mg dm^{-3})	27.8 (±3.1)	a	45.5 (±3.6)	a	48.3 (±3.8)	a	59 (±17.7)	a
Ca^{2+} ($cmol_c$ dm^{-3})	2.2 (±0.2)	b	2.2 (±0.2)	b	2.7 (±0.3)	ab	3.1 (±0.3)	a
Mg^{2+} ($cmol_c$ dm^{-3})	0.9 (±0.1)	a	0.9 (±0.1)	a	1.0 (±0.1)	a	1.0 (±0.1)	a
H + Al ($cmol_c$ dm^{-3})	2.4 (±0.3)	a	1.5 (±0.3)	a	1.9 (±0.5)	a	1.7 (±0.1)	a
Effective CEC ($cmol_c$ dm^{-3})	3.2 (±0.3)	b	3.3 (±0.2)	b	3.9 (±0.4)	ab	4.3 (±0.4)	a
Potential CEC ($cmol_c$ dm^{-3})	5.5 (±0.3)	ab	4.7 (±0.2)	b	5.8 (±0.8)	ab	6.0 (±0.4)	a
Base saturation (%)	57.6 (±4.7)	b	69.6 (±4.6)	a	68.0 (±4.7)	ab	71.7 (±2.6)	a
Organic matter (dag kg^{-1})	4.7 (±1.3)	a	5.3 (±0.8)	a	5.7 (±1.6)	a	5.4 (±1.2)	a

Same letters in each row indicate absence of statistical differences between treatments, according to the Tukey test ($p < 0.05$). Values in parentheses represent the mean standard error.

management has changed the structure and floristic composition of these treatments through the manipulation of competitive relationships that favored some species over others. In addition, some of regenerating species had already colonized the site and were saved from mowing or resprouted from stumps – internal ecological memory (Chazdon, 2014) – inside the experimental plots. Hence, as shrubs and trees began to gain dominance in level II (the intermediary and upper strata), they provide shade that inhibited the growth of weeds, which are typically light demanding and highly water- and nutrient competitive species (Hooper et al., 2002; Vieira et al., 2009).

The diversity indices were coherent with those obtained in other studies with natural regeneration in abandoned farmland of Atlantic Forest. Although we adopted a sampling method that differs from the other studies performed in regenerating forests in the same biome, especially regarding the size of plots and minimum inclusion diameter, which not allow direct comparisons with them, our results shows similar trends (Table 3). Piotto et al. (2009) studied a cronosequence of abandoned areas by swidden agriculture surrounded by remaining mature forests in northeastern Brazil and found values of H' close to 3.0 nats/individual (dbh > 5 cm) in areas with 10 years of regeneration after abandonment. In other regions within the Atlantic Forest, Siminski et al. (2011) found values of 3.0 nats/individual, 0.7 and 0.93 for the indices H', S and J', respectively, during initial stages of succession (0–8 years), in plots of 10 m × 10 m, where all the individuals (>1.5 m height) were identified and measured. Similar values were also found in the Amazon. Uhl et al. (1988), for example, assessed through transects all the trees (>2 m height) and found H' and S' equal to 2,86 nats/individual and 0.73, respectively, after 5 years of abandonment of slash-and-burn agriculture. It suggests that the diversity found in the successional agroforestry systems of the current study is comparable to young secondary forests in the region.

The successional trajectories of abandoned farmlands are strongly influenced by abiotic factors, the surrounding landscape, in addition to the intensity and duration of prior land use (Holl, 2007; Martínez-Ramos and García-Orth, 2007). The successional trajectory of the RC in T2 and T4 seems to follow trajectories already described for secondary forests in the region (Piotto et al., 2009; Salomão et al., 2012) with dominance of few pioneer tree species belonging to the genera *Vismia*, *Cecropia* and *Solanum*. The successional trajectories of abandoned farmland with high predominance of the genera *Vismia* and *Cecropia* have been associated to the intensity and duration of prior land use (Williamson et al., 2014). In Central Amazon, studies have already demonstrated that in the areas where the agricultural or livestock were more intense (including with fire use) and long-lasting, the resulting secondary forests were dominated by species of *Vismia* (Mesquita et al., 2001). Many species of that genus also have capacity of resprout from root buds, after the fire passage (Wieland et al., 2011). On the other hand, *Cecropia* has been associated to less intense and lasting practices after the deforestation (Wieland et al., 2011; Williamson et al., 2014). Such findings corroborate our results as the experimental areas had records of different prior land uses, including: abandoned pastures, anthropic uses, and shifting cultivation with fire-clearing techniques. Thus, it is plausible that both genera were included among those with higher importance in the RC.

The presence of woody taxa, in T2 and T4, such as *X. sericea*, *B. sericea*, *Inga* sp., *A. pedicellaris*, *C. pachystachya* and *V. guianensis* suggests that there was no stagnation of the secondary succession. Besides, the management is allowing floristic turnover and favoring the emergence of native tree species. It is appropriate to highlight that naturally regenerated trees are currently forming the canopy of the experimental plots and very likely, these species will be replaced by more shade tolerant species with successional age. It could be inferred by the little abundance or non-occurrence of such taxa (*V. guianensis*, *C. pachystachya*, *Inga* sp.) at the level I of the RC.

In addition to the natural regeneration from seed rain and soil seed bank, it is appropriate to highlight the role of some species which are

Table 7
Soil microbial and biochemistry variables at 58 months after planting.

Variable* (unit)	Treatments							
	T1		T2		T3		T4	
MBC (mg kg^{-1})	47.70 (±0.64)	a	53.78 (±1.15)	a	50.35 (±1.07)	a	50.79 (±3.06)	a
SBR (mg C-CO_2 kg^{-1} d^{-1})	3.65 (±0.32)	b	5.99 (±0.68)	a	6.26 (±0.65)	a	6.21 (±0.88)	a
qMic (%)	0.24 (±0.07)	a	0.19 (±0.04)	a	0.19 (±0.05)	a	0.19 (±0.05)	a
FDA (μg fluorescein g^{-1} h^{-1})	63.89 (±3.31)	a	70.55 (±1.87)	a	99.67 (±30.09)	a	100.48 (±35.24)	a
β-glicosidase (μg *p*-nitrophenol g^{-1} h^{-1})	34.57 (±2.81)	c	40.74 (±1.73)	b	53.64 (±8.58)	a	45.35 (±1.01)	ab
Fosfatase (μg *p*-nitrophenol g^{-1} h^{-1})	873.70 (±50.54)	a	803.77 (±38.47)	a	872.7 (±140.3)	a	754.04 (±85.63)	a
Arilsulfatase (μg *p*-nitrophenol g^{-1} h^{-1})	147.87 (±6.31)	a	150.95 (±9.18)	a	163.68 (±21.96)	a	169.77 (±11.77)	a

*MBC: microbial biomass carbon; SBR: soil basal respiration; qMIC: microbial quotient (MBM / SOC); FDA: hydrolysis of fluorescein diacetate.
Same letters in each row indicate absence of statistical differences between treatments, according to the Tukey test ($p < 0.05$). Values in parentheses represent the mean standard error.

remnants from the forest formation previous to agricultural/anthropic use of the experimental area, such as *B. ferruginea* and species of Lecythidaceae (*Lecythis lurida* and *Couratari* sp.) which were found in T2 and T4, all of them resprouting from stumps (with multiple stems). This represents the ecological memory, since they hardly establish in open and abandoned farmlands. Many species of Lecythidaceae are dispersed by bats, birds, rodents, and primates (Faria et al., 2006). In addition, they may act as natural perches and play a relevant role for in restoring abandoned farmlands (Chazdon, 2014; Nepstad et al., 1991; Piotto et al., 2009; Vilela et al., 2012).

4.2. Management effects on biomass, C, and nutrients accumulation by the regenerating community

The litter stocks were influenced by the type of management of RC. The application of glyphosate reduced the living soil cover for at least 4 to 6 months and caused a reduction in the litter stocks in T1 treatment, compared to the other treatments. Consequently, the contents of all litter macronutrients in T1 were significantly reduced, with exception of K. Due to the fact of the elimination of the RC in treatment T1, the litter layer was composed by non-woody, little lignified and easily decomposable material, coming predominantly from herbaceous species. The results suggest that part of such nutrients was quickly mineralized and uptaken by African mahogany trees. This fact can be evidenced by the high growth index of both species in treatment T1, right after the regenerating plants desiccation (Santos et al., 2020). However, the absence of statistical differences in the stocks of all macronutrients in the biomass of regenerating plants (level I) also indicates that another part of these nutrients may be reuptaken by the regenerating plants that colonized the areas of this treatment. If new herbicide applications are not performed, it is possible that litter biomass and litter nutrient stocks recover in the short term.

On the other hand, upon allowing secondary succession to be expressed in the sites, there was a greater accumulation of aboveground biomass in treatments T2 and T4 (ranging from 10 to 12 Mg ha^{-1} of dry matter). It is worth noting that there were two events of pruning and thinning of mature shrubs and trees in these treatments, whose the last event was approximately 12 months before biomass stock assessments. This fact suggests a rate of aboveground biomass between 3 and 5 Mg ha^{-1} $year^{-1}$, considering only the biomass of plants at level II (trees and

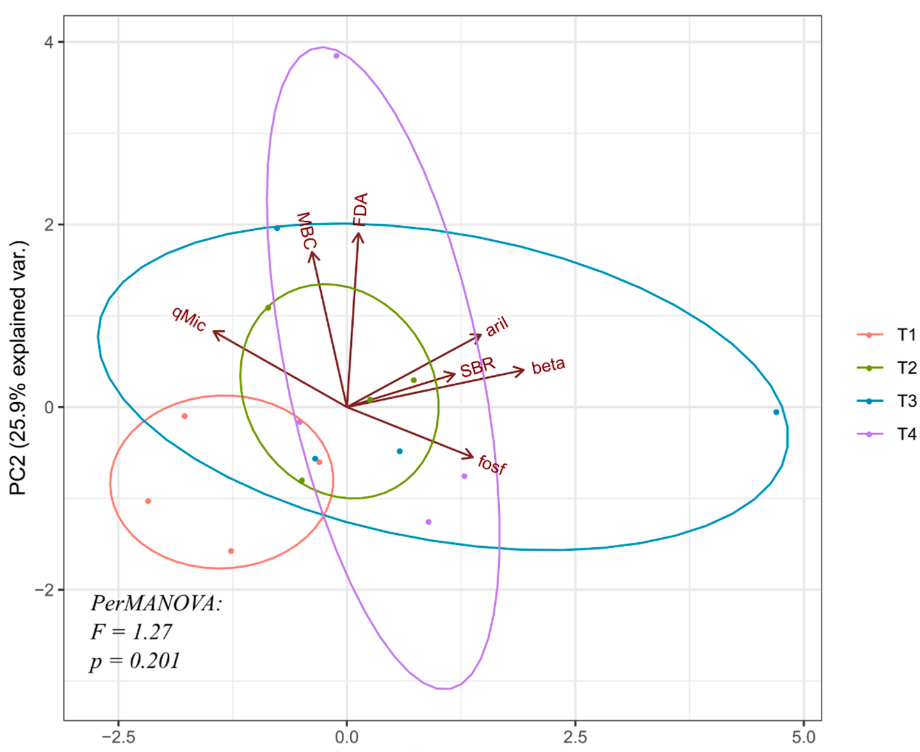

Fig. 4. Principal component analysis (PCA) of the variables associated with microbial activity in the experimental treatments.

shrubs). Taking into account a half-life of 12 months for the litter and that regenerating plants at level I quickly reestablish themselves (<6 months), the biomass production rates after intervention (mowing, pruning and thinning) reached values between 8 and 10 Mg ha^{-1} year^{-1}.

In the humid tropics, Szott et al. (1999) reported that the biomass accumulation rate in fallow areas may vary from 4 to 15 Mg ha^{-1} year^{-1} during the first ten years after abandonment. According to Poorter et al. (2016), the secondary forests in the Neotropical region have the potential to accumulate approximately 120 Mg ha^{-1} of aboveground biomass, up to 20 years of age, which represents a rate of 6 Mg ha^{-1} year^{-1}. In southern Bahia, Becknell et al. (2018) estimated through airborne LiDAR that biomass accumulation rate can reach approximately 15 Mg ha^{-1} year^{-1} in the first 10 years of age but with a wide variation of biomass accumulation rates. Despite methodological differences to assess biomass accumulation rates, our results show that the estimates obtained in the successional agroforestry systems are similar to the rates found for secondary forests in the region.

The highest biomass production and the greatest enrichment of N, P, K, Ca and Mg in the aboveground biomass of the natural regeneration of T4, in relation to those of T2, suggest that they may be benefiting from the residual nutrients applied to the agroforestry species through fertilization, as it was observed for African mahogany trees (mainly for *K. ivorensis* – (Santos et al., 2020)). This fact allows greater efficiency in the conservation of nutrients in organic structures of regenerating species, especially for those nutrients with higher mobility in the soil (N and K, for example) and more subject to leaching losses. In practice, it means that the inorganic nutrients once not uptaken by the cultivated agroforestry species are then returned in organic form through the pruning and deposition of fresh biomass around the agroforestry species.

The diversity of species with different nutrient contents, besides to the exploitation of differentiated soil layers, can contribute to enhance nutrient conservation (Chazdon, 2014). Among the regenerating taxonomic groups (level II) and with high dominance in the natural regeneration, there are key species that may be recommended to be tended in agroforestry systems. These species have a high capacity to accumulate certain nutrients in their tissues (Supplementary data 1A to 3A), which can often be added to the system via fresh biomass deposition, originated from prunings. These pruning residuals have distinct and complementary chemical qualities. These characteristics are desirable for a suitable biogeochemical cycling mediated by decomposing microorganisms, mainly in soils degraded by agricultural activity (Cezar et al., 2015; Vieira et al., 2009).

The species *S. crinitum* had, on average, high levels of N, P, Ca and Mg in its aboveground tissues. On the other hand, it presented lower levels of K and S, which were found in higher concentration in tissues of other species such as *Mikania* sp., *B. ferruginea* and *C. scorpioides* (Supplementary data 1A to 3A). However, the greatest contribution to the nutrient accumulation was provided by the dominant species in terms of cover. *B. dracunculifolia* accumulated the highest quantities of all nutrients among the shrubs, although the nutrient contents in its tissues were not so high as the other shrub species (Supplementary data 1C to 6C). *V. guianensis*, *C. pachystachya* and *Inga* sp stand out as the main nutrient accumulators. *V. guianensis* and *C. pachystachya* played an important role in nutrient accumulation, contributing to >60% of the total of all nutrients accumulated in live aboveground biomass (Supplementary data 1C to 6C).

The case of *Inga* sp. is particularly interesting as its tissues are usually more N-enriched because of symbiotic nitrogen fixation. In a hypothetical situation, upon performing a drastic pruning of a single tree of *Inga* sp. with medium size (crown area of 30 m^2, 13 kg of dry matter of leaves, 18 kg of branches and 20 kg of trunk – real proportions obtained in a field sample), a total of 0.54 kg of N (organic) could be generated to be deposited on the soil surface. However, the stoichiometric ratios of N:P of *Inga* sp. tissues were the highest among the regenerating species of this study, suggesting that the decomposition may be slower due to the low availability of P for the decomposing organisms (Hättenschwiler et al., 2005; Hättenschwiler and Jørgensen, 2010; Santos et al., 2017). However, if they are mixed with other regenerating species residues that accumulate larger amounts of P (*C. pachystachya*, for example), the decomposition and release of nutrients for agroforestry species of interest may be accelerated.

The management of the RC also allowed a greater accumulation of C in the aboveground biomass. Hughes et al. (1999) observed that C contents in different aboveground compartments (including litter) in the regenerating forests in Mexico, varied from 41% to 48%. For the purpose of calculation, an average C content equivalent to 45% was considered in this study. Based on the aboveground biomass values (including the biomass of the regenerating plants and litter stocks), T2 and T4 accumulated 3.6 and 4.5 Mg of C ha^{-1} year^{-1}, respectively. On the other hand, for T1 and T3 the values ranging from 1.5 Mg of C ha^{-1} year^{-1} to 2.25 Mg of C ha^{-1} year^{-1}, respectively. According to Chazdon (2014), the C accumulation rate can range from 2 to 3.5 Mg of C ha^{-1} year^{-1} in secondary forests under 20 years of age. Becknell et al. (2018) found values close to 7 Mg of C ha^{-1} year^{-1} in secondary forests in the southern region of Bahia (up to 10 years old). Edaphoclimatic factors, duration and type of prior land use may influence the carbon and biomass accumulation rates in the regenerating tropical forests (Uhl et al., 1988). It is worth pointing out that in this calculation, biomass of rare and less important species was not considered. However, the estimates of this study have shown that the selective management of natural regeneration allowed to double C accumulation rate of the aboveground biomass in the first five years.

4.3. Management effects on soil quality

Because of the time elapsed from the implantation of the experiment to the evaluation period of this study, no conclusive evidences have been found yet regarding improvements in the soil nutrient concentrations between treatments with or without selective management of natural regeneration. The highest levels of P and soil bases (Ca, Mg and K) in agroforestry systems treatments (T3 and T4) were possibly due to fertilization operations of fruit species cultivated in the inter-rows and among the African mahogany trees. However, the species diversity, structural complexity and pruning management in treatments T2 and T4 can bring possible benefits to soil fertility in the medium and long term (Markewitz et al., 2004). Over the years, the regenerating species can explore the deeper layers of the soil and can recycle part of the nutrients lost by leaching, which can return to the soil surface through litter deposition and/or pruning and thinning management. In addition, early successional plants contribute to the local agroecosystem and facilitate the establishment of subsequent species along the successional trajectory. These plants accumulate C and nutrients in their biomass, and return them through the litter (above-and belowground) deposition, contributing to the increase of organic matter and other chemical soil attributes (Chazdon, 2014). One of the first indications of these changes concerns the highest effective cation exchange capacity values presented by T4 treatment, especially in relation to T1 (Table 6). These results suggest that the soil has increased its capacity to exchange bases with the soil solution, due to the increased loads provided by the organic matter enrichment in the system (Canellas et al., 2008).

The management of successional agroforestry systems has been described previously as a promising alternative for the soils recovery exhausted by farming activity. Peneireiro (1999) carried out a comparative analysis between a 12-year area of successional agroforestry systems and a fallow area in the northeastern Brazil. Both were established in abandoned areas of successive cycles of cassava crops (*Manihot esculenta* Crantz.) with typically dystrophic soils. It was found that the management of pruning and selective weeding contributed to increase soil fertility levels, in relation to the areas of fallow (control), especially for P content, and sum and saturation by bases. In addition, it is noteworthy that the effective cation exchange capacity of the soil in successional agroforestry area was 2.5 times higher than the control

Table 8
Ecosystem functions and services of some main regenerating species.

Species	Ecosystem functions and services	References
Baccharis dracunculifolia	Medicinal use and source of resin for the production of green propolis	(Almeida et al., 2003; Santos et al., 2010; Sforcin et al., 2012)
Bactris ferrugínea	Food source (heart of palm and fruits)	(Lorenzi et al., 2004; Medeiros-Costa, 2002)
Cecropia pachystachya	Animal feed source (birds and mammals)	(Marcondes-Machado and Oliveira, 1987; Sato et al., 2008)
Cyrtocimura scorpioides	Bee plant and medicinal use	(Almeida et al., 2003; Mouga and Krug, 2010; Rauh, 2008)
Inga sp.	Animal feed source and N_2-fixing tree	(Canosa and Moraes, 2016)
Lantana camara	Pollinated by bees and other insects; medicinal use	(Ribeiro et al., 2010)
Miconia albicans.	Source of food for birds and medicinal use	(Allenspach and Dias, 2012)
Pleroma heteromallum	Pollinated by bees and other insects, source of food for birds	(Campos, 2010; Santos, 2018)
Solanum crinitum.	Mammalian food source	(Dias-Filho, 1998; Canosa and Moraes, 2016)
Vismia guianensis	Mg and P accumulators, bee plant, source of food for bats (open areas)	(Boehm et al., 2000; Dias-Filho, 1998; Santos and Machado, 1998)

area.

Unlike soil chemical attributes, some indicators associated to microbial activity were more sensitive to changes caused by the management of natural regeneration. Such indicators are often used to evaluate impacts on soil quality due to land use and management (Acosta-Martínez et al., 2007; Silva et al., 2012). The analysis of principal components, which was used here to evaluate the biochemical profile of the soil, showed that the T1 treatment was significantly discriminated from the other treatments along the first principal component (PC1) (Fig. 4). The β-glucosidase activity and the soil basal respiration were the variables that most correlated with PC1 and contributed to the biochemical differentiation of the soil between T1 and the other treatments.

According to Turner et al. (2002), β-glucosidases act at the ending phase of cellulose transformation, producing substrates more easily usable by the soil microbial community in later phases of decomposition. Organic matter has a direct influence on the activity of β-glucosidase, since it provides substrate for the action of these enzymes and also protects them through the formation of humic-enzyme compounds (Deng and Tabatabai, 1997). Thus, the results of the present study suggest that the decrease in β-glucosidase activity was associated with the reduction of living soil cover and litter stocks promoted by the herbicide application. On the other hand, greater β-glucosidases activities were detected in treatments where management activities did not impact litter stocks and at the same time contributed to a greater deposition of fresh organic matter through mowing (selective or not) and/or pruning, which indicate benefits to the soil C cycling.

4.4. Management effects on other ecosystem functions

The greater diversity and abundance of regenerating species could attract and maintain pollinating populations (Menz et al., 2011). Among the trees and regenerating shrubs of this study, there were several taxonomic groups pollinated by bees and/or other insects (Table 8). The flowers of *V. guianensis*, *Mikania* sp., *C. scorpioides* are constantly visited by several species of bees (Table 8). Whereas, *B. dracunculifolia* is a plant frequently visited by bees seeking resins present in the leaf primordia to manufacture green propolis, a raw material used in the hives covering (Table 8). The presence of *B. dracunculifolia* and other bee plants in the landscape may provide basic resources for increasing bee abundance and diversity within the agroecosystem. Collectively, these insects also play a fundamental role in pollination of fruit species cultivated in the agroforestry systems of this study.

Besides to serve as natural perches, some species also produce fruits that are dispersed by wildlife, mainly by birds and mammals, such as *Inga* sp., *S. crinitum* and *C. pachystachya* (Table 8). The constant presence of these animals contributes to the increase of seed rain, favoring the propagation of these species and the recruitment of new species in the agroforestry system (Chazdon, 2008).

More complex productive systems, such as successional agroforestry systems, provide a greater number of habitats and niches that favor the presence of natural enemies of pests (Young, 2017). In addition, structural diversity and complexity make attacks of pests more difficult. For example, one of the main pests of African mahogany is *Hypsyphylla grandella*, a microlepidoptera that attacks mainly the apical buds and causes bends and economic losses, especially during the initial phase of growth, when the plants are monopodial and have not formed its crown yet. In theory, the most diverse systems with several strata make it difficult to locate the host plants of African mahogany, either by creating physical obstacles or by interfering in the perception of the chemical signs that guide the moth (Opuni-Frimpong et al., 2014).

The selective management of the RC also allowed the establishment and growth of pioneering species that contribute to environmental regulation and at the same time favor the advance of secondary succession. Many of the species found at level II of the RC create microhabitats for the planting of enrichment of other shade-tolerant species (*Euterpe edulis*, for example) in the future phase, or even for those introduced by the seed rain. In addition, some regenerating species provide medicinal products, as well as alternative fibers and foods that can be domesticated and commercially exploited. *B. ferruginea*, for example, is a palm tree native species in the southern region of Bahia, Brazil (Lorenzi et al., 2004) and may provide edible fruits and palm hearts (Table 8). Thus, the management of the RC contributes to the formation of high diversity agroforestry systems, which provide greater food security and productive seasonality for farmers, and several environmental services.

5. Conclusions

The single application of the herbicide (glyphosate) caused a transformation in the floristic composition and richness of the regenerating community (RC) of T1, previously dominated by a small group of grasses and fern species. After desiccation with glyphosate, reductions in litter and soil cover were observed in this treatment. On the other hand, in addition to the greater diversity, it is observed that the regenerative management of T2 and T4 promoted a greater accumulation of biomass and C, in relation to the treatments with conventional management. The incorporation of fresh biomass from pruning and mowing contribute to a higher activity of enzymes associated to the C cycle, with positive effects on soil fertility in the medium and long term, especially in relation to T1.

The selective management of RC also promoted the increase of the diversity of taxonomic groups (in addition to those of agroforestry interest) and enhanced the provisioning of other ecosystem goods and services within the agroecosystem, with the supply of other types of food and fibers, pest control, pollinators' attraction and environmental regulation, among the most relevant ones. The management descripted in our study could be a grateful tool to forest restoration in the tropical abandoned farmland.

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.

Acknowledgments

This study was financed in part by the Coordenação de

Aperfeiçoamento de Pessoal de Nível Superior (CAPES) – Finance Code 001. The work was also supported by Embrapa [project number 03.13.14.011.00.00] and CNPq [grant number 420467/2016-5].

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118854.

References

Acosta-Martínez, V., Cruz, L., Sotomayor-Ramírez, D., Pérez-Alegría, L., 2007. Enzyme activities as affected by soil properties and land use in a tropical watershed. Appl. Soil Ecol. 35, 35–45. https://doi.org/10.1016/j.apsoil.2006.05.012.

Akindele, S.O., LeMay, V.M., 2006. Development of tree volume equations for common timber species in the tropical rain forest area of Nigeria. For. Ecol. Manage. 226, 41–48. https://doi.org/10.1016/j.foreco.2006.01.022.

Allenspach, N., Dias, M.M., 2012. Frugivoria por aves em *Miconia albicans* (Melastomataceae), em um fragmento de Cerrado em São Carlos, sudeste do Brasil. Brazilian J. Biol. 72, 407–413. https://doi.org/10.1590/S1519-69842012000200024.

Almeida, D., Marchini, L.C., Sodré, G.S., et al., 2003. Plantas visitadas por abelhas e polinização. ESALQ - Divisão de Biblioteca e Documentação, Piracicaba.

Altieri, M., 2012. Agroecologia: bases científicas para uma agricultura sustentável, 3rd ed. Expressão Popular, Rio de Janeiro.

Alvares, C.A., Stape, J.L., Sentelhas, P.C., Leonardo, J., Gonçalves, M., Sparovek, G., 2014. Köppen's climate classification map for Brazil. Meteorol. Zeitschrift 22, 711–728. https://doi.org/10.1127/0941-2948/2013/0507.

Anderson, J.D., Ingram, L.J., Stahl, P.D., 2008. Influence of reclamation management practices on microbial biomass carbon and soil organic carbon accumulation in semiarid mined lands of Wyoming. Appl. Soil Ecol. 40, 387–397. https://doi.org/10.1016/j.apsoil.2008.06.008.

Bartlett, R.J., Ross, S.D., 1988. Colorimetric determination of oxidizable carbon in acid soil solutions. Soil Sci. Soc. Am. J. 52, 1191–1192.

Becknell, J.M., Keller, M., Piotto, D., Longo, M., Nara dos-Santos, M., Scaranello, M.A., de Oliveira, Bruno, Cavalcante, R., Porder, S., 2018. Landscape-scale lidar analysis of aboveground biomass distribution in secondary Brazilian Atlantic Forest. Biotropica 50, 520–530. https://doi.org/10.1111/btp.12538.

Boehm, V., Sschimdt, P., Skatulla, M., et al., 2000. *Vismia guianensis* (Aubl.) Choisy, Clusiaceae: management factors in early stages of agroforestry systems. - Portal Embrapa. In: German-Brazilian Workshop on Neotropical Ecosystems. Achievments and Prospects of Cooperative Research. Vulnerability of Ecosystems and Sociity in the Northeast of Brazil (WAVES) Arbeitsstelle. für. Wissenschaftliche Weiterbildung, University of Hamburg, Hamburg, p. 299.

Braun-Blanquet, J., 1979. Fitosociología: bases para el estudio de las comunidades vegetales. Blume.

Brighenti, A.M., Oliveira, M.F., 2011. Biologia de plantas daninhas. In: Oliveira, R.S., Constantin, J., Inoue, M.H. (Eds.), Biologia e Manejo de Plantas Daninhas. Omnipax, Curitiba, pp. 1–36.

Brookes, P.C., Landman, A., Pruden, G., Jenkinson, D.S., 1985. Chloroform fumigation and the release of soil nitrogen: a rapid direct extraction method to measure microbial biomass nitrogen in soil. Soil Biol. Biochem. 17, 837–842. https://doi.org/10.1016/0038-0717(85)90144-0.

Canellas, L.P., Mendonça, E.S., Dobbs, L.B., Baldotto, M.A., Velloso, A.C.X., Santos, G.A., Amaral Sobrinho, N.M.B., 2008. Reações da matéria orgânica. In: Santos, G.A., Silva, L.S., Canellas, L.P., Camargo, F.A.O. (Eds.), Fundamentos Da Matéria Orgânica Do Solo: Ecossistemas Tropicais e Subtropicais. Metrópole, Porto Alegre, pp. 7–18.

Campos, C.C.F., 2010. Biologia reprodutiva de *Tibouchina heteromalla* Cogn. (Melastomataceae) e *Ocimum selloi* Benth (Lamiaceae). UFLA.

Canosa, G.A., Moraes, L.F.D., 2016. Atributos funcionais de espécies da Mata Atlântica: ferramentas para o planejamento ambiental e econômico - Portal Embrapa. Seropédica.

Cezar, R.M., Vezzani, F.M., Schwiderke, D.K., Gaiad, S., Brown, G.G., Seoane, C.E.S., Froufe, L.C.M., 2015. Soil biological properties in multistrata successional agroforestry systems and in natural regeneration. Agrofor. Syst. 89, 1035–1047. https://doi.org/10.1007/s10457-015-9833-7.

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

Chazdon, R.L., 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. Science (80-.) 320, 1458–1460. https://doi.org/10.1126/science.1155365.

Chazdon, R.L., Bodin, B., Guariguata, M.R., Lamb, D., Walder, B., Chokkalingam, U., Shono, K., 2017. Partnering with Nature: The Case for Natural Regeneration in Forest and Landscape Restoration. Forest Ecosystem Restoration Initiative.

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

Colwell, R.K., 2006. EstimateS: Statistical estimation of species richness and shared species from samples.

Deng, S.P., Tabatabai, M.A., 1997. Effect of tillage and residue management on enzyme activities in soils: III. Phosphatases and arylsulfatase. Biol. Fertil. Soils 24, 141–146. https://doi.org/10.1007/s003740050222.

Dias-Filho, M.B., 1998. Alguns aspectos da ecologia de sementes de duas espécies de plantas invasoras da Amazônia Brasileira: implicações para o recrutamento de plântulas em áreas manejadas. In: Gascon, C., Moutinho, P. (Eds.), Floresta amazônica: dinâmica, regeneração e manejo. INPA, Manaus, pp. 233–248.

Eivazi, F., Tabatabai, M.A., 1988. Glucosidases and galactosidases in soils. Soil Biol. Biochem. 20, 601–606. https://doi.org/10.1016/0038-0717(88)90141-1.

EMBRAPA, 2017. Manual de métodos de análise de solo, 3rd ed. Embrapa, Brasília.

EMBRAPA, 2009. Manual de análises químicas de solos, plantas e fertilizantes, 2nd ed. Embrapa Informação Tecnológica, Brasília.

Faria, D., Laps, R.R., Baumgarten, J., Cetra, M., 2006. Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil. Biodivers. Conserv. 15, 587–612. https://doi.org/10.1007/s10531-005-2089-1.

Ferreira, E.B., Cavalcanti P P, Nogueira, D.A., 2013. ExpDes: Experimental Designs package.

Froufe, L.C.M., Rachwal, M.F.G., Seoane, C.E.S., 2011. Carbon sink potential of multistrata agroforestry systems at Atlantic Rain Forest. Brazilian J. For. Res. 31, 143–154. https://doi.org/10.4336/2011.pfb.31.66.143.

Hättenschwiler, S., Jørgensen, H.B., 2010. Carbon quality rather than stoichiometry controls litter decomposition in a tropical rain forest. J. Ecol. 98, 754–763. https://doi.org/10.1111/j.1365-2745.2010.01671.x.

Hättenschwiler, S., Tiunov, A.V., Scheu, S., 2005. Biodiversity and litter decomposition in terrestrial ecosystems. Annu. Rev. Ecol. Evol. Syst. 36, 191–218. https://doi.org/10.1146/annurev.ecolsys.36.112904.151932.

Hempson, G.P., Archibald, S., Bond, W.J., Ellis, R.P., Grant, C.C., Kruger, F.J., Kruger, L. M., Moxley, C., Owen-Smith, N., Peel, M.J.S., Smit, I.P.J., Vickers, K.J., 2015. Ecology of grazing lawns in Africa. Biol. Rev. 90, 979–994. https://doi.org/10.1111/brv.12145.

Holl, K., 2007. Oldfield vegetation succession in the neotropics grassland re-survey view project Islas project view project. In: Cramer, V.A., Hobbs, R.J. (Eds.), Old Fields: Dynamics and Restoration of Abandoned Farmland. Island Press, Washington, pp. 93–118.

Hooper, E., Condit, R., Legendre, P., 2002. Responses of 20 native tree species to reforestation strategies for abandoned farmland in Panama. Ecol. Appl. 12, 1626–1641. https://doi.org/10.1890/1051-0761(2002)012[1626:RONTST]2.0.CO;2.

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

Jiménez-Valverde, A, Hortal, J, 2003. Las curvas de acumulación de especies y la necesidad de evaluar la calidad de los inventarios biológicos. Revista Ibérica de Aracnología 8, 151–161.

Jose, S., 2009. Agroforestry for ecosystem services and environmental benefits: an overview. Agrofor. Syst. 76, 1–10. https://doi.org/10.1007/s10457-009-9229-7.

Leles, P.S. dos S., Resende, A.S., 2017. Controle de plantas daninhas em restauração florestal. Embrapa, Brasília.

Linder, H.P., Lehmann, C.E.R., Archibald, S., Osborne, C.P., Richardson, D.M., 2018. Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. Biol. Rev. 93, 1125–1144. https://doi.org/10.1111/brv.12388.

Lorenzi, H., Souza, H.M., Medeiros-Costa, J.T., Cerqueira, L.S.C., Ferreira, E., 2004. Palmeiras brasileiras e exóticas cultivadas. Instituto Plantarum, Nova Odessa.

Marcondes-Machado, L.O., Oliveira, M.M.A., 1987. Comportamento alimentar de aves em Cecropia (Moraceae), em mata atlântica, no Estado de São Paulo. Rev Bras Zool 4, 331–339. https://doi.org/10.1590/s0101-81751987000400005.

Markewitz, D., Davidson, E., Moutinho, P., Nepstad, D., 2004. Nutrient loss and redistribution after forest clearing on a highly weathered soil in Amazonia. Ecol. Appl. 14, 177–199. https://doi.org/10.1890/01-6016.

Martínez-Ramos, M., García-Orth, X., 2007. Sucesión ecológica y restauración de las selvas húmedas. Boletín la Soc. Botánica México Sup 69–84.

Medeiros-Costa, J., 2002. As espécies de palmeiras (Arecaceae) do Estado de Pernambuco, Brasil. In: Tabarelli, M., Silva, J.M.C. (Eds.), Diagnóstico da Biodiversidade de Pernambuco. SECTMA & Massangana, Recife, pp. 229–236.

Menz, M.H.M., Phillips, R.D., Winfree, R., Kremen, C., Aizen, M.A., Johnson, S.D., Dixon, K.W., 2011. Reconnecting plants and pollinators: challenges in the restoration of pollination mutualisms. Trends Plant Sci. 16, 4–12. https://doi.org/10.1016/j.tplants.2010.09.006.

Mesquita, R.C.G., Ickes, K., Ganade, G., Bruce Williamson, G., 2001. Alternative successional pathways in the Amazon Basin. J. Ecol. 89, 528–537. https://doi.org/10.1046/j.1365-2745.2001.00583.x.

Miccolis, A., Peneireiro, F.M., Marques, H.R., Vieira, D.L.M., Arco-Verde, M.F., Hoffmann, M.R., Rehder, T., Pereira, A.V.B., 2016. Restauração ecológica com sistemas agroflorestais: como conciliar conservação com produção: opções para Cerrado e Caatinga. Centro Internacional de Pesquisa Agroflorestal, Brasília.

Mouga, D., Krug, C., 2010. Comunidade de abelhas nativas (Apidae) em Floresta Ombrófila Densa Montana em Santa Catarina. Zoologia 27, 70–80. https://doi.org/10.1590/S1984-46702010000100011.

Mueller-Dombois, D., Ellenberg, H., 1974. Aims and Methods of Vegetation Ecology. John Wiley & Sons, New York.

Nepstad, D.C., Uhl, C., Serrao, E.A.S., 1991. Recuperation of a degraded Amazonian landscape: forest recovery and agricultural restoration. Ambio 20, 248–255.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2017. vegan: Community Ecology Package.

Opuni-Frimpong, E., Nyarko-Duah, N.Y., Belford, E.J.D., Storer, A.J., 2014. Silvicultural systems for restoration of mahogany in degraded landscapes in Africa: influence of mixed rainforest plantation on growth and pest damage. Open J. For. 04, 414–425. https://doi.org/10.4236/ojf.2014.44046.

Peneireiro, F.M., 1999. Sistemas agroflorestais dirigidos pela sucessão natural: um estudo de caso. ESALQ/USP, Piracicaba.

Piotto, D., Montagnini, F., Thomas, W., Ashton, M., Oliver, C., 2009. Forest recovery after swidden cultivation across a 40-year chronosequence in the Atlantic forest of southern Bahia, Brazil. Plant Ecol. 205, 261–272. https://doi.org/10.1007/s11258-009-9615-2.

Poorter, L., Bongers, F., Aide, T.M., Almeyda Zambrano, A.M., Balvanera, P., Becknell, J.M., Boukili, V., Brancalion, P.H.S., Broadbent, E.N., Chazdon, R.L., Craven, D., De Almeida-Cortez, J.S., Cabral, G.A.L., De Jong, B.H.J., Denslow, J.S., Dent, D.H., DeWalt, S.J., Dupuy, J.M., Durán, S.M., Espírito-Santo, M.M., Fandino, M.C., César, R.G., Hall, J.S., Hernandez-Stefanoni, J.L., Jakovac, C.C., Junqueira, A.B., Kennard, D., Letcher, S.G., Licona, J.C., Lohbeck, M., Marín-Spiotta, E., Martínez-Ramos, M., Massoca, P., Meave, J.A., Mesquita, R., Mora, F., Munõz, R., Muscarella, R., Nunes, Y.R.F., Ochoa-Gaona, S., De Oliveira, A.A., Orihuela-Belmonte, E., Penã-Claros, M., Pérez-Garciá, E.A., Piotto, D., Powers, J.S., Rodríguez-Velázquez, J., Romero-Pérez, I.E., Ruíz, J., Saldarriaga, J.G., Sanchez-Azofeifa, A., Schwartz, N.B., Steininger, M.K., Swenson, N.G., Toledo, M., Uriarte, M., Van Breugel, M., Van Der Wal, H., Veloso, M.D.M., Vester, H.F.M., Vicentini, A., Vieira, I.C.G., Bentos, T.V., Williamson, G.B., Rozendaal, D.M.A., 2016. Biomass resilience of Neotropical secondary forests. Nature 530, 211–214. https://doi.org/10.1038/nature16512.

R Development Core Team, 2018. R: a language and environment for statistical computing.

Reflora, 2019. Reflora – Virtual Herbarium [WWW Document]. URL http://reflora.jbrj.gov.br/reflora/herbarioVirtual/.

Ribeiro, R.S., Bento, M.A., Neves, T.G., Agostini, K., 2010. Visitantes florais de *Lantana camara* (Verbenaceae) no campus Taquaral da Universidade Metodista de Piracicaba. In: 8ª Mostra Acadêmica/18°Congresso de Iniciação Científica. UNIMEP, Piracicaba, pp. 1–3.

Rauh, L.K., 2008. Avaliação da atividade antiinflamatória tópica da *Vernonia scorpioides* (Lam) Persons em modelos de inflamação cutânea em camundongos. UFPR.

Ruas, R.A.A., Lima, J.C.L., Appelt, M.F., Dezordi, L.R., 2012. Controle de Brachiaria decumbens Stapf com adição de ureia à calda do glifosato. Pesqui. Agropecu. Trop. 42, 455–461. https://doi.org/10.1590/S1983-40632012000400013.

Salomão, R.P., Vieira, I.C.G., Brienza Junior, S., Amaral, D.D., Santana, A.C., 2012. Sistema capoeira classe: uma proposta de sistema de classificação de estágios sucessionais de florestas secundárias para o estado do. Pará. Bol. do Mus. Para. Emílio Goeldi. Ciências Nat. 7, 297–317.

Sang, P.M., Lamb, D., Bonner, M., Schmidt, S., 2013. Carbon sequestration and soil fertility of tropical tree plantations and secondary forest established on degraded land. Plant Soil 362, 187–200. https://doi.org/10.1007/s11104-012-1281-9.

Santos, F.M., Balieiro, F.D.C., Fontes, M.A., Chaer, G.M., 2017. Understanding the enhanced litter decomposition of mixed-species plantations of Eucalyptus and Acacia mangium. Plant Soil 1–15. https://doi.org/10.1007/s11104-017-3491-7.

Santos, D.A., Fuku, i, M.J., Dhammika, N.P.N, et al., 2010. Anti-inflammatory and antinociceptive effects of *Baccharis dracunculifolia* DC (Asteraceae) in different experimental models. J Ethnopharmacol 127, 543–550. https://doi.org/10.1016/j.jep.2009.09.061.

Santos, M.J.L., Machado, I.C., 1998. Biologia floral e heterostilia em Vismia Guianensis (Aubl.) choisy (clusiaceae). Acta Bot Brasilica 12, 451–464. https://doi.org/10.1590/S0102-33061998000400014.

Santos, F.M., Terra, G., Chaer, G.M., Monte, M.A., 2018. Modeling the height–diameter relationship and volume of young African mahoganies established in successional agroforestry systems in northeastern Brazil. New For. https://doi.org/10.1007/s11056-018-9665-1.

Santos, P.Z.F., Crouzeilles, R., Sansevero, J.B.B., 2019. Can agroforestry systems enhance biodiversity and ecosystem service provision in agricultural landscapes? A meta-analysis for the Brazilian Atlantic Forest. For. Ecol. Manage. 433, 140–145. https://doi.org/10.1016/j.foreco.2018.10.064.

Santos, F.M., Terra, G., Monte, M.A., Chaer, G.M., 2020. Growth, yield and stem form of young African mahoganies (*Khaya* spp.) in mixed-species plantations and successional agroforestry systems. New Forests. Submitted for publication.

Sato, T.M., Passos, F.D.C., Nogueira, A.C., 2008. Frugivoria de morcegos (Mammalia, Chiroptera) em *Cecropia pachystachya* (Urticaceae) e seus efeitos na germinação das sementes. Pap. Avulsos Zool. 48, 19–26. https://doi.org/10.1590/S0031-10492008000300001.

Schnurer, J., Rosswall, T., 1982. Fluorescein diacetate hydrolysis as a measure of total microbial activity in soil and litter. Appl. Environ. Microbiol.

Sforcin, J.M., Sousa, J.P.B., Silva-Filho, A.A., et al., 2012. *Baccharis dracunculifolia*: uma das principais fontes vegetais da própolis brasileira. Editora Unesp, São Paulo.

Silva, D.K.A., Oliveira Freitas, N., Souza, R.G., Silva, F.S.B., Araujo, A.S.F., Maia, L.C., 2012. Soil microbial biomass and activity under natural and regenerated forests and conventional sugarcane plantations in Brazil. Geoderma 189–190, 257–261. https://doi.org/10.1016/j.geoderma.2012.06.014.

Silva, E.E., Azevedo, P.H.S., De-Polli, H., 2007. Determinação da respiração basal (RBS) e quociente metabólico do solo (qCO2). Seropédica.

Siminski, A., Fantini, A.C., Guries, R.P., Ruschel, A.R., Sedrez, M., Reis, D., Loustau, D., Steinman, A.D., 2011. Secondary forest succession in the Mata Atlantica, Brazil: floristic and phytosociological trends. Int. Sch. Res. Netw. ISRN Ecol. 2011, 1–19. https://doi.org/10.5402/2011/759893.

Santos, L.M., 2018. Guia de plantas: flores no campo rupestre. CVRD, Nova Lima.

Szott, L.T., Palm, C.A., Buresh, R.J., 1999. Ecosystem fertility and fallow function in the humid and subhumid tropics. Agrofor. Syst. 47, 163–196. https://doi.org/10.1023/A:1006215430432.

Tabatabai, M.A., 1994. Soil Enzymes. In: Weaver, R.W., Angle, S., Bottomley, P., Bezdicek, D., Smith, S., Tabatabai, A., Wollum, A. (Eds.), Methods Soil Anal. SSSA Book Series, Madison, pp. 775–833. https://doi.org/10.2136/sssabookser5.2.c37.

Toledo, R.E.B., Filho, R.V., Alves, P.L.C.A., Pitelli, R.A., Lopes, M.A.F., 2003. Weed control strip on Eucalyptus plants growth. Sci. For. 64, 78–92.

Turner, B.L., Hopkins, D.W., Haygarth, P.M., Ostle, N., 2002. β-glucosidase activity in pasture soils. Appl. Soil Ecol. 20, 157–162. https://doi.org/10.1016/S0929-1393(02)00020-3.

Uhl, C., Buschbacher, R., Serrao, E.A.S., 1988. Abandoned pastures in Eastern Amazonia. I. Patterns of plant succession. J. Ecol. 76, 663. https://doi.org/10.2307/2260566.

Vance, E.D., Brookes, P.C., Jenkinson, D.S., 1987. An extraction method for measuring soil microbial biomass C. Soil Biol. Biochem. 19, 703–707. https://doi.org/10.1016/0038-0717(87)90052-6.

Vieira, D.L.M., Holl, K.D., Peneireiro, F.M., 2009. Agro-successional restoration as a strategy to facilitate tropical forest recovery. Restor. Ecol. 17, 451–459. https://doi.org/10.1111/j.1526-100X.2009.00570.x.

Vilela, F. de S., Flesher, K.M., Mauro, Ramalho, 2012. Dispersal and predation of Eschweilera ovata seeds in the Atlantic Forest of Southern Bahia. Brazil. J. Trop. Ecol. 28, 223–226. https://doi.org/10.1017/S0266467411000514.

Wieland, L.M., Mesquita, R.C.G., Bobrowiec, P.E.D., Bentos, T.V., Williamson, G.B., 2011. Seed rain and advance regeneration in secondary succession in the Brazilian Amazon. Trop. Conserv. Sci. 4, 300–316. https://doi.org/10.1177/194008291100400308.

Williamson, G.B., Bentos, T.V., Longworth, J.B., Mesquita, R.C.G., 2014. Convergence and divergence in alternative successional pathways in Central Amazonia. Plant Ecol. Divers. 7, 341–348. https://doi.org/10.1080/17550874.2012.735714.

Yeomans, J.C., Bremner, J.M., 1988. A rapid and precise method for routine determination of organic carbon in soil. Commun. Soil Sci. Plant Anal. 19, 1467–1476. https://doi.org/10.1080/00103628809368027.

Young, K., 2017. Mimicking nature: a review of sucessional agroforestry systems as an analogue to natural regeneration of secondary forest stands. In: Montagnini, F. (Ed.), Integrating Landscapes Agroforestry for Biodiversity Conservation and Food Sovereignty. Springer International Publishing, pp. 179–209.