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Regeneration capacities of woody species biodiversity and soil properties in Miombo woodland after slash-and-burn agriculture in Mozambique

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ABSTRACT

Miombo woodland is the dominant tropical dry forest formation in Africa. Its importance for local populations' livelihoods and increased pressure has turned the spotlight on this ecosystem, now considered one of the five global wilderness areas prioritized for conservation and restoration. Forest regeneration is a key to restoring ecosystem services, but the characteristics, conditions and dynamics of this specific biome remain largely understudied. The aim of this study was to analyze the current status and evolution of woody species biodiversity, stand structure and soil properties of regrowth plots after slash-and-burn farming in Mozambique. Our survey focused on the area surrounding Gilé National Park in Mozambique, which is dominated by a mosaic of vegetation including mature Miombo woodland, grassland, cropland, and land abandoned after slash-and-burn cycles. We sampled 20 plots in mature woodland and 36 plots in a chronosequence of Miombo regrowth from 1 to 35 years old, grouped in four age classes: 4–6, 8–12; 20–25 and 30–35 years. We observed that woody species richness and diversity increased with time after abandonment until similar values to those in mature woodlands were reached between 20 and 25 years later. Despite the presence of the dominant Miombo tree species belonging to the genera *Julbernardia* and *Brachystegia*, after 20–35 years of regeneration species composition remained different from that of mature woodlands. Mean DBH, tree height, and carbon stock increased while tree density decreased along the chronosequence. Tree density and tree carbon stocks in 30–35-year-old Miombo regrowth exceeded those of mature woodland. Soil C stock increased during vegetation regeneration after abandonment. Results suggest that two or three decades are necessary to reach values similar to those of mature woodland. Overall, these findings show that the region has a high regeneration capacity in terms of woody species diversity and soil properties but that disturbances have a long term effect on species composition and stand structure, underlining the importance of integrated landscape management to enhance the provision of ecosystem goods and services.

1. Introduction

Miombo woodland is the most extensive tropical dry forest formation in southern Africa (Frost, 1996). The biome covers about 2.7 million km^2 (about 10% of the African continent) and seven countries from Angola in the west to Tanzania in the east, and from southern Democratic Republic of the Congo down to the northern edge of South Africa (White, 1986; Campbell, 1996; Malaisse, 1997; Pienaar et al., 2015). The floristic species richness of Miombo woodland is estimated at 8,500 species, of which 54% are endemic (Campbell, 1996; Assédé et al., 2020). These biodiversity hot spots have been identified as one of the five global wilderness areas for prioritizing conservation (Mittermeier et al., 2003). But, despite their importance for biodiversity and for the livelihoods of millions of inhabitants, Miombo woodland has received little attention from the scientific community (Gumbo et al., 2018; Siyum, 2020).

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Miombo woodland is threatened by direct and indirect human activities including conversion into agricultural land, charcoal production, overgrazing and fire (Luoga et al., 2005; Chidumayo and Gumbo, 2010; Assédé et al., 2020). In the Miombo woodland regions, slash-and-burn agriculture is the most frequent farming system and the main cause of forest loss (Malambo and Syampungani, 2008; Kalaba et al., 2013). Slash-and-burn agriculture traditionally follows a crop-fallow rotation that shapes the landscape in a complex land cover mosaic (Frost, 1996). These practices also impact the stand structure and composition of woody species regrowth and soil nutrient cycling and reduce the soil carbon stock (Walker and Desanker, 2004; Ribeiro et al., 2020). However, the resilience of Miombo woodland after slash-and-burn remains poorly studied, and only a few studies have concerned both woody species biodiversity and soil properties (Ribeiro et al., 2015).

Previous studies in Mozambique, Tanzania and Zambia reported that woody species diversity and structure (aboveground biomass and basal area) can reach values similar to mature woodland 20–30 years after abandonment (Williams et al., 2008; Kalaba et al., 2013; McNicol et al., 2015). The high regeneration capacity of Miombo woodlands is mainly due to fire resistance and vegetative reproduction from roots, and coppicing from cut stumps (Luoga et al., 2004; Shirima et al., 2015). Changes in floristic composition and the presence or absence of the dominant Miombo tree species (genera *Brachystegia* and *Julbernardia)* in early Miombo regrowth after slash-and-burn remain unclear (Strømgaard, 1986; Williams et al., 2008; Kalaba et al., 2013). Walker and Desanker (2004) in Malawi and William et al. (2008), in Mozambique, found that soil carbon stocks did not increase after the abandonment of agriculture, suggesting slow organic matter accumulation rate in these soils. To our knowledge, other changes in soil properties after abandonment have not yet been studied in Miombo woodlands.

Miombo woodland regions are characterized by significant climatic and environmental gradients, ranging from dry to wet Miombo. Consequently diversity and tree species composition recovery may vary considerably across the region and cannot be generalized (Gumbo et al., 2018; Ribeiro et al., 2020). Moreover, Miombo woodland resilience to slash-and-burn agriculture has not been studied in some countries. To our knowledge, the only study of carbon and biodiversity dynamics after slash-and-burn agriculture was by William et al. (2008) in the Sofala of Mozambique. The impacts of slash-and-burn agriculture on both floristic and soil properties (other than soil carbon stocks) have not been studied in Mozambique so far.

In this study, we analyzed Miombo woodland regeneration capacity in a new study area in Mozambique, Zambezia province, based on a long regrowth chronosequence (1–35 years). Zambezia province has the second highest rural population density and deforestation rates in the country (GoM, 2018; Montfort et al., 2020a). We used an integrated soil and floristic approach, because soil characteristics (moisture, nutrients, depth) and their dynamics are important factors influencing floristic properties whereas soil properties are influenced by forest regrowth (Campbell, 1996; Chidumayo and Gumbo, 2010).

The specific aim of this study was to assess the temporal dynamics of woody species biodiversity, stand structure and the recovery of soil properties after slash-and-burn agriculture in and around Gilé National Park, one of the largest intact area of Miombo woodland in Mozambique. We wanted to answer the two following questions: (i) how long does it takes for Miombo woodland to recover woody species biodiversity and stand structure after slash-and-burn agriculture? (ii) do soil properties return to their original level after abandonment of agriculture? Understanding the resilience of Miombo woodland and providing new information on their regeneration capacity is urgently required to predict its capacity to recover and provide goods and services, and to design sustainable land management strategies.

2. Material and methods

2.1. Study area

The study was conducted in Gilé National Park (GNAP) and vicinity located in the northeastern part of Zambezia province in Mozambique (Fig. 1). Created in 1932, originally as a game reserve for hunting, the GNAP was proclaimed a conservation area in 1999, first as a National Reserve and very recently (May 2020) as a National Park. The GNAP is divided between a fully protected core area (2,861 km^2) and a buffer zone (1,671 km^2). It is the only protected area in Mozambique with no permanent settlements in its core area and represents one of the largest areas of uninterrupted Miombo woodland in the northern part of the country (Mercier et al., 2016). About 12,500 inhabitants live in the GNAP buffer zone and 22,000 inhabitants in the main town (Gilé) located near the GNAP (Etc Terra, 2017).

The GNAP lies between 30 and 200 m above sea level with two distinct seasons: a wet season between November and April, and dry season between May and October (Fusari and Carpaneto, 2006). Average annual rainfall ranges from 800 to 1,000 mm and average annual temperatures range from 21 °C in the dry season to 28 °C in the rainy season (Fusari and Carpaneto, 2006). The vegetation in the core area is a semi-deciduous dry Miombo woodland (93% of the total surface area) with patches of shallow wetlands, called *dambo* (5% of the total surface area). Burned land in the core area represents an average of 18.5% of the total surface area each year (Pungulanhe, 2020). Wildfires in the core area are caused by the spread of uncontrolled fires from the opening of new agricultural fields with slash and burn technique outside the park or for hunting purposes outside and inside the park.

In the vicinity of the GNAP, the vegetation is a complex mosaic of post-cultivation Miombo regrowth of different ages, cropland (maize, cassava, beans and peanuts), mature Miombo woodland (areas that have not been cultivated in living memory, hereafter referred to as mature woodland) and wooded savannas. This landscape mosaic is driven by slash-and-burn agriculture, the main activity for 89% of the population (Mercier et al., 2016), but the landscape was also shaped by human migration during the civil war (1977–1992). Indeed, some areas represent long term forest regrowth due to the abandonment of settlement areas within the Reserve at that time. After the war, people returned to villages but only to those located close to the roads and/or remained in the main centers. Miombo woodland is key to the livelihoods of the local population as a source of energy (firewood, charcoal), construction material and non-timber forest products (mushrooms, fruits, caterpillars) (Luoga et al., 2000; Mercier et al., 2016).

2.2. Plot selection

Croplands, Miombo regrowth after slash-and-burn, and mature woodlands were sampled to represent a long chronosequence of forest regeneration (Table 1). We used three sources of information to select suitable areas: analysis of a map of changes in land use and land cover (1990–2016), field observations, and interviews with owners. All Miombo regrowth and cropland plots surveyed are located in the GNAP buffer zone and the vicinity of the GNAP (Fig. 1). All mature woodland plots are located within the core area and buffer zone of the GNAP. Floristic and stand structure and soil inventories were conducted in the dry seasons in 2015, 2016 and 2019.

2.3. Data collection

2.3.1. Floristic and stand structure sampling

Data were collected in 36 plots in four different age classes: 4–6, 8–12, 20–25 and 30–35 years (9 plots per class) containing Miombo regrowth, plus in 20 mature woodland plots.

We used circular plots, randomly positioned within the selected areas. The size of the plots varied depending on the regrowth category

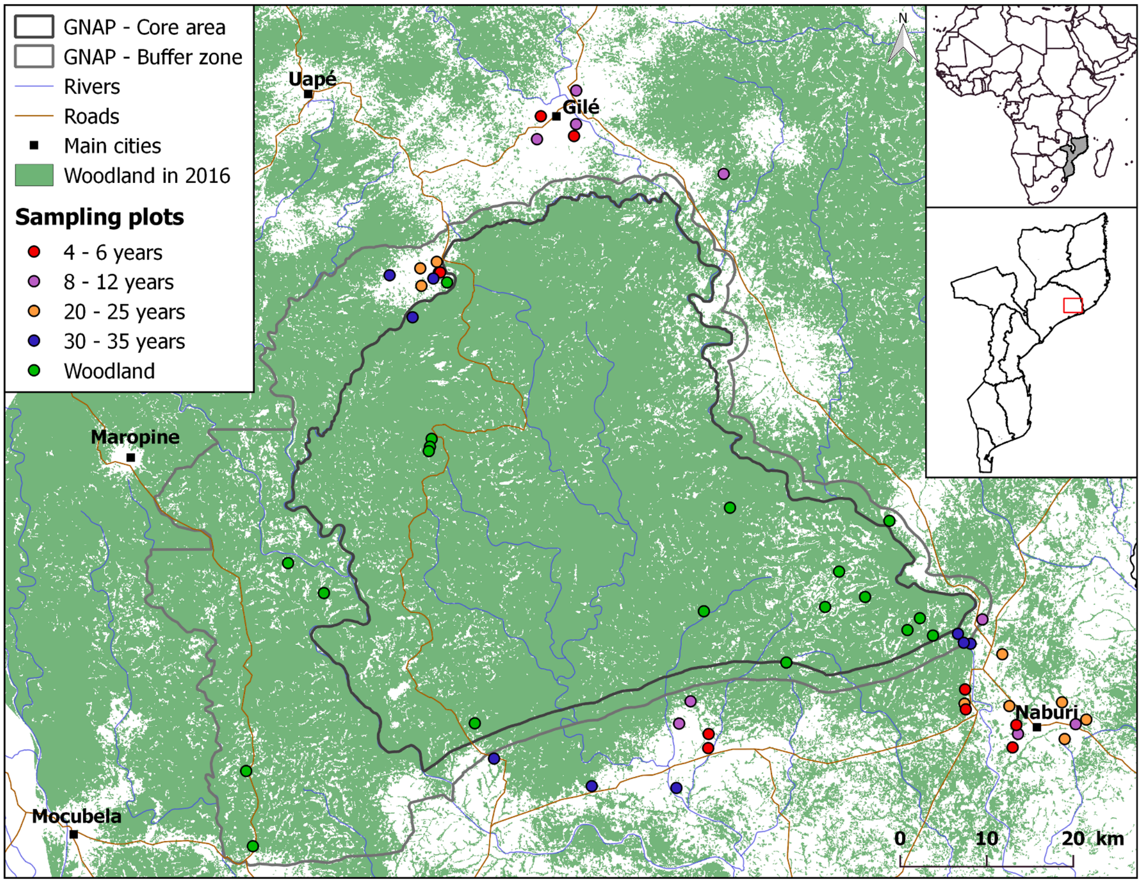

Fig. 1. Location of Gilé National Park and sampling plots.

Table 1
Description of categories.

Categories	Description
Cropland	Fields resulting from slash-and-burn agriculture for mainly maize, cassava, beans and peanuts production.
Miombo regrowth	Areas abandoned after slash-and-burn agriculture with tree regeneration and without evidence of removal of some trees after abandonment. Time since abandonment is known.
Mature woodland	Miombo forest areas that have not been cleared or cultivated in living memory.

and was identified using the species-area curve method which prevents under or over sampling of individual trees. Indeed, as the regeneration stages of Miombo are characterized by a decreasing number of species and individuals during forest succession, the use of the same fixed plot size for different stages would have led to under-representation of the composition of vegetation at mature stages or to over sampling of young regeneration stages (Syampungani et al., 2010). We used plots with a radius of 10 m for young Miombo regrowth (4–6 and 8–12 years) and plots with a radius of 16 m for older Miombo regrowth (20–25 and 30–35 years) and mature woodlands.

We measured the diameter at breast height (DBH 1.3 m above the ground, in centimeters) and height (in meters) of all living woody species with a diameter > 5 cm. Species names were recorded from local field guides in Lomwe language. The scientific names were then identified using a document produced by the field team (Montfort et al., 2020b) and the checklist of the vernacular names of vascular plants in Mozambique (de Koning, 1993). Field identification books were used to confirm identification and to identify species local field guide was unable to identify (Smith and Allen, 2004; Wyk and Wyk, 2013).

2.3.2. Soil sampling and laboratory analysis

Soil samples were collected in the same plots as the plots used for floristic and woody structure. We selected six out of the nine plots in the age classes 4–6, 8–12, 20–25 and mature woodlands, and four plots in cropland areas.

Within each plot, four soil samples were collected in three different soil layers: 0–10 cm, 10–20 cm, 20–30 cm, using auger holes and all samples were pooled to form a composite sample per plot for laboratory analysis. The following physical and chemical properties were measured in a soil laboratory: pH, soil texture (sand, silt, clay), soil organic carbon (SOC), using the Walkley-Black method, soil nutrients (available phosphorus, potassium, calcium, magnesium, sodium) and micronutrients (iron, zinc, manganese, copper). Bulk density was also measured in each plot using the cylinder method (soil samples sieved to 2 mm). Soil analyses were performed in two laboratories (Labserve Nelspruit and Omnia in Bryanston, South Africa). Details of the methods used in the laboratory for each soil property are listed in Appendix A. For available phosphorus a correction factor of 0.83 was applied for conversion between values obtained using Bray I and Ambic I extraction methods (White et al., 2020). Soil organic carbon stocks were calculated using the equation:

$$SOC = CxBDxSD \quad (1)$$

where C is the concentration of soil organic carbon (%), BD bulk density (g/cm-3) and SD soil sampling depth (30 cm).

2.4. Data analysis

We used the Chao 1 estimator (abundance-based estimator) for species richness and the Shannon-Wiener species diversity index (Chao, 1987; Scherer and Pallmann, 2017). Tree density (number of trees per hectare) and tree mean height and DBH were calculated for each plot to assess the stand structure.

Tree carbon stock was calculated as the sum of aboveground (AGB) and belowground biomass (BGB). AGB was calculated using the Chave et al. (2014) allometric equation for mixed species and dry forests based on a total of 1,891 harvested trees, including 321 harvested trees in dry Miombo woodland:

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

where ρ is wood density, DBH is the diameter at breast height (1.3 m above the ground) and H is tree height.

Wood density for each species was obtained from the global wood density database (Chave et al., 2009; Zanne et al., 2009). BGB was calculated by multiplying the aboveground biomass AGB by the default value of root-to-shoot ratio provided by IPCC for dry tropical forests, i.e. 0.56 if the aboveground biomass is <20 tdm/ha and 0.28 if the aboveground biomass is >20 tdm/ha (IPCC, 2019).

All floristic and soil indicators for different classes were compared using a one-way or single factor analysis of variance (ANOVA), followed by a pairwise Tukey's HSD test. Results of the statistical analyses were considered significant if the p-value < 0.05. These analyses were carried out after checking the normality and homoscedasticity of the data, in the case of non-compliance with these conditions a non-parametric Kruskal-Wallis test was performed (noted KW).

A principal coordinates analysis (PCoA) based on square-root-transformed species abundance data was used to obtain a graphical representation of similar species composition among plots (Legendre and Legendre, 2012). In the PCoA, the Chao-Jaccard index was used as distance index to assess species composition similarity (beta diversity) between categories because it reduces undersampling bias by accounting for unseen shared species and can be used to compare plots of different sizes (Chao et al., 2005). Differences among categories were statistically tested using permutational multivariate analysis of variance (PERMANOVA) on coordinates along the two axes of the PCoA (Anderson, 2001).

The importance value index (IVI) based on the relative frequency, density and dominance of each species was used to characterize the floristic structure and composition of the plots (Curtis and McIntosh, 1951):

$$IVI = (\text{relative frequency} + \text{relative basal area} + \text{relative density})/3 \quad (3)$$

$$\text{Relative frequency} = \frac{\text{Frequency of respective woody species}}{\text{Total frequency of all woody species}} x100 \quad (4)$$

$$\text{Relative basal area} = \frac{\text{Basal area of respective woody species}}{\text{Total basal area of all woody species}} x100 \quad (5)$$

$$\text{Relative density} = \frac{\text{Abundance of respective woody species}}{\text{Total abundance of all woody species}} x100 \quad (6)$$

Differences in soil properties between categories were tested using a PERMANOVA based on the Euclidean distance matrix calculated on log transformed soil data (Organic carbon %, Zn, Mn, Fe, Cu, pH, P, K, Ca, Mg, Na, Bulk density).

All statistical tests were performed in R software using the "vegan" and "simboot" packages (Oksanen, 2015; Scherer and Pallmann, 2017; R Core Team, 2020).

3. Results

3.1. Changes in woody species richness and diversity

Woody species richness (Chao 1 estimator) increased with time after abandonment from 9.0 ± 4.0 species (at 4–6 years old) to 26.4 ± 11.8 species (at 30–35 years old) and decreased for mature woodland (18.9 ± 7.9 species) (Fig. 2). The same pattern was observed with the Shannon-Wiener index. With both estimators, the difference between young Miombo regrowth and mature woodland was significant (p-value < 0.05 – Fig. 2) but no significant differences were found between mature woodland and the 20–25 or 30–35-year-old Miombo regrowth (Fig. 2). Although not significant (p-value < 0.05), the species diversity and the species richness of the 30–35-year-old Miombo regrowth exceeded that of mature woodland (Fig. 2).

The highest number of species was found in the 20–25 and 30–35-year-old Miombo regrowth classes, 74 species belonging to 29 families. The young Miombo regrowth (4–6 and 8–12 years) was composed of 55 species belonging to 19 families, and mature woodland of 54 species belonging to 20 families. In all categories, the most diverse families were Fabaceae (25 species), Euphorbiaceae (9 species) and Rubiaceae (8 species).

3.2. Species composition recovery

Ranked by their IVI (Table 2), the dominant species in mature woodland were *Brachystegia boehmii, Brachystegia spiciformis* and *Julbernardia globiflora,* which are typical of dry Miombo vegetation (Timberlake and Chidumayo, 2011). Young Miombo regrowth (4–6 and 8–12 years) was dominated by fire tolerant species such as *Erythrophleum africanum* and *Annona senegalensis,* or cultivated species such as *Anacardium occidentalis* (Carrière, 1994; Smith and Allen, 2004). Twenty years after abandonment, a large number of dominant species were the same as those found in mature woodland.

The Venn diagram shows that mature woodland and 4–12-year-old Miombo regrowth had few unique species (4 and 5, respectively) whereas 20–35-year-old Miombo regrowth had a large number (26 species) (Fig. 3). In each category, between 38 and 70% of the species were found in all categories.

The PERMANOVA showed no significant difference in species composition among Miombo regrowth categories whereas the differences in species composition between mature woodlands and young Miombo regrowth (4–12 years) or 20–35-year-old Miombo regrowth were significant (pairwise PERMANOVA: F-Model = 3.434, p-value = 0.001 and F-Model = 3.188, p-value = 0.001 respectively). The 20–35-year-old Miombo regrowth had intermediate species composition (Appendix B).

3.3. Changes in vegetation structure

The mean DBH and height, and the tree carbon stock increased along the chronosequence whereas tree density decreased (Fig. 4). Wood density remained stable. There was no significant difference in mean DBH and height between mature woodland (DBH: 15.4 ± 4.9 cm; H: 10.7 ± 2.2 m) and 30–35-year-old Miombo regrowth (DBH: 16.4 ± 2.6 cm; H: 9.1 ± 1.4 m) (ANOVA, p-value > 0.05) (Fig. 4). Tree carbon stocks in mature woodland differed significantly from tree carbon stocks in young Miombo regrowth (4–6 years) but not in the 8–12 and 20–25-year-old Miombo regrowth (Fig. 4). Tree carbon stocks were significantly higher in the 30–35-year-old Miombo regrowth (56.7 ± 18.8 MgC/ha) than in mature woodland (36.0 ± 22.6 MgC/ha) (ANOVA: df = 4, F = 12.54, p-value = 3.55–07, Tukey's HSD: p-value = 0.032) because the 30–35-year-old Miombo regrowth had on average larger diameters and significantly more individuals than mature woodlands (Fig. 4).

3.4. Changes in soil properties

Soil organic carbon (SOC) stocks in the top 30-cm soil layer were 16.9 MgC/ha (±3.5 MgC/ha) in mature woodland and 9.6 MgC/ha (±3.2 MgC/ha) in cropland (Fig. 5). This corresponds to a difference of 7.3 MgC/ha, or a 43% reduction in soil carbon stocks in cropland compared to mature woodland. SOC stocks in mature woodland soil

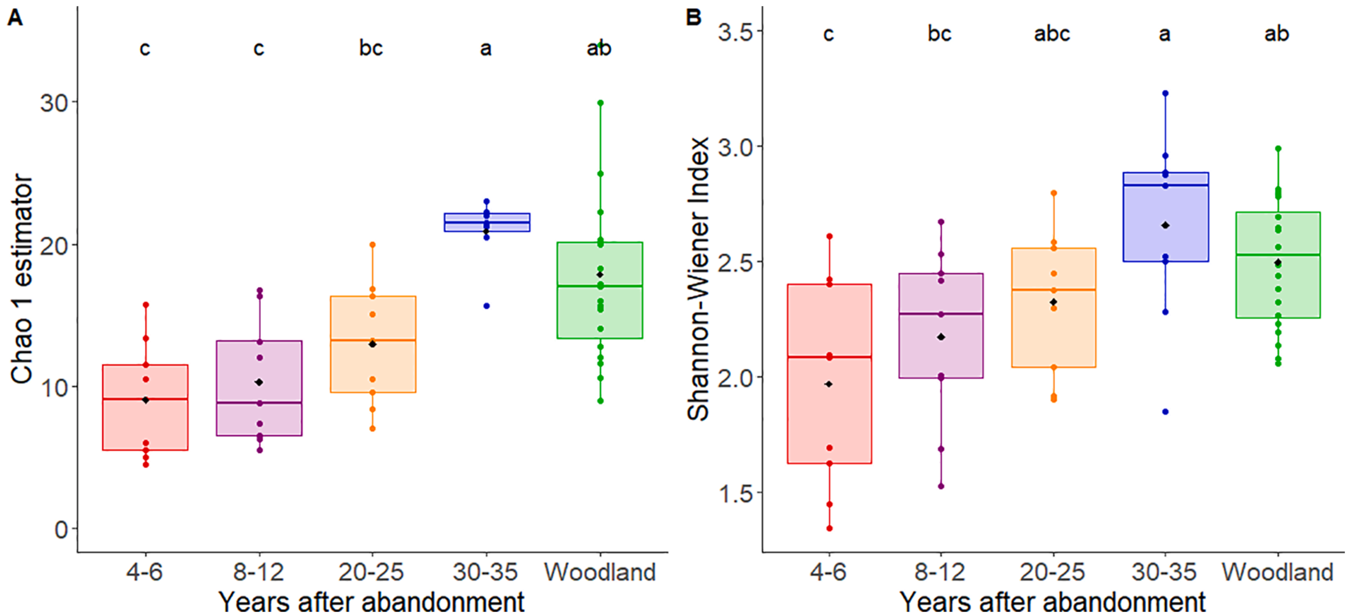

Fig. 2. (A) Woody species richness (Chao 1 estimator) and (B) diversity (Shannon-Wiener index) for Miombo regrowth and mature woodland. Letters ([a], [b], [c]) indicate statistically significant differences (ANOVA, pairwise Tukey's HSD test, $p < 0.05$). The bounding box of each variable in the boxplot represents quartile values, the straight line represents the mean value.

Table 2
The ten most dominant species in Miombo regrowth and mature woodland ranked with the importance value index (IVI).

Rank	4–6 years	8–12 years	20–25 years	30–35 years	Woodland
1	Diplorhynchus condylocarpon	Millettia stuhlmannii	Julbernardia globiflora	Brachystegia spiciformis	Brachystegia spiciformis
2	Pteleopsis myrtifolia	Strychnos madagascariensis	Pterocarpus angolensis	Annona senegalensis	Brachystegia boehmii
3	Millettia stuhlmannii	Brachystegia spiciformis	Millettia stuhlmannii	Pterocarpus angolensis	Diplorhynchus condylocarpon
4	Erythrophleum africanum	Xylopia aethiopica	Strychnos madagascariensis	Julbernardia globiflora	Julbernardia globiflora
5	Anacardium occidentale	Anacardium occidentale	Erythrophleum africanum	Strychnos madagascariensis	Dalbergia nitudila
6	Albizia versicolor	Combretum zeyheri	Diplorhynchus condylocarpon	Brachystegia boehmii	Pseudolachnostylis maprouneifolia
7	Xylopia aethiopica	Julbernardia globiflora	Brachystegia boehmii	Albizia versicolor	Millettia stuhlmannii
8	Annona senegalensis	Terminalia sericea	Dalbergia nitudila	Pteleopsis myrtifolia	Phyllocosmus lemaireanus
9	Bauhinia petersiana	Albizia adianthifolia	Byrsocarpus orientalis	Strychnos spinosa	Pterocarpus angolensis
10	Julbernardia globiflora	Annona senegalensis	Combretum zeyheri	Millettia stuhlmannii	Combretum zeyheri

were significantly higher than SOC stocks in young Miombo regrowth (4–6 years and 8–12 years) (KW, p-value < 0.05). There was no significant difference between 20 and 25-year-old Miombo regrowth and mature woodland (KW: chi2 = 8.53, df = 4, p-value 0.07, Tukey's HSD p-value > 0.05).

Mature woodland soils had significantly higher concentrations of available phosphorus and lower concentrations of calcium and copper than those of cropland (KW, p-value < 0.05) (Appendix C). The concentration of available phosphorus increased along the forest regeneration chronosequence of while that of calcium decreased. Magnesium, potassium, sodium and zinc concentrations were higher in young Miombo regrowth (4–6 years and 8–12 years) than in cropland and mature woodland.

The PERMANOVA revealed a significant difference in soil properties (organic carbon %, Zn, Mn, Fe, Cu, pH, P, K, Ca, Mg, Na, Bulk density) between mature woodland, young Miombo regrowth and, cropland (Pairwise PERMANOVA, p-value < 0.05) but no significant difference in soil properties between mature woodland and 20–25-year-old Miombo regrowth (Pairwise PERMANOVA: F-Model = 1.03; p-value = 0.418).

On average, plots were characterized by low nutrient and micronutrient concentrations and acidic soil conditions (mean pH 5.1) (Appendix C). Bulk density and soil texture did not significantly differ among the plots (Appendix C). All the plots were characterized by a bulk density of between 1.31 and 1.56 g/cm^3 and were dominated by sand, loamy sand and sandy loam soils (Range: Sand = 75–94%; Silt = 1–13%, Clay = 2–13%).

4. Discussion

This study provides information on Miombo woodland biodiversity, woody structure, and soil properties, previously undocumented in central Mozambique. Our results show that floristic, stand structure and soil properties gradually approach those of mature woodland over time and the time needed to recover the characteristics of mature woodland for each property in the study area.

4.1. How long does it takes for Miombo woodland to recover woody species biodiversity and woody structure after slash-and-burn agriculture?

Our results showed that the floristic characteristics (woody species richness and diversity, stand structure and biomass) of mature woodland in the vicinity of the GNAP can recover in two to four decades after slash-and-burn is abandoned, showing that Miombo woodland in the study area has a high regeneration capacity after disturbances caused by slash-and-burn agriculture. In comparison, in 56 sites comprising dry, moist, and wet forest in the Neotropics, Rozendaal et al. (2019) showed that the median time span to return to old forest values was 54 years for species richness. The observed capacity of resilience of these forests is consistent with studies in other Miombo regions (Williams et al., 2008; Chinuwo et al., 2010; Kalaba et al., 2013; McNicol et al., 2015). Indeed, other

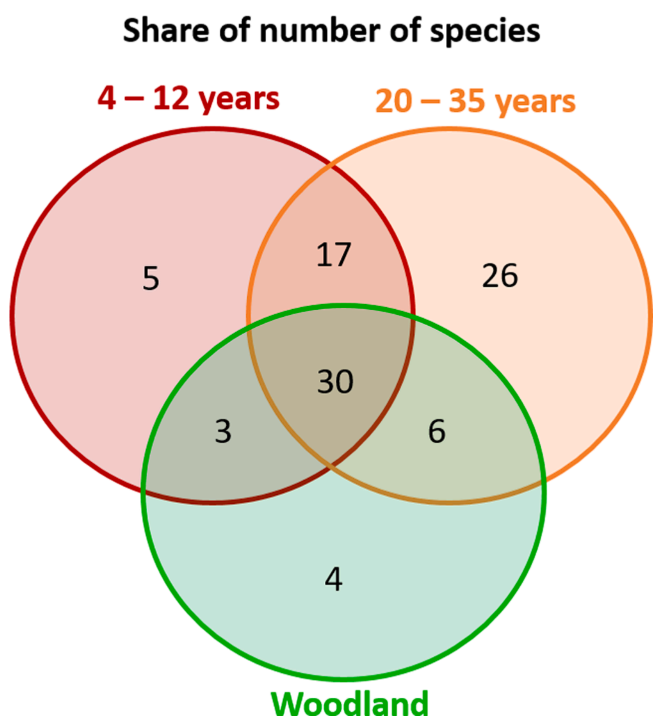

Fig. 3. Venn diagram showing the number of species common to Miombo regrowth and mature woodland.

authors showed that after cultivation has been stopped, vegetation can grow from the soil seed bank, existing vegetative material (stem, stump, sucker, root) that was only slightly affected by fire, or seeds originating from nearby or remnant trees (Floret and Pontanier, 2001; Timberlake and Chidumayo, 2011). The ability of species to regrow vegetatively depends on a number of factors including forest type, the age and size of the tree, rainfall and fire (Faye et al., 2002; Luoga et al., 2004). Several studies have shown that Miombo formations regenerate mainly through regrowth of coppice and root suckers rather than seeds, which may explain the rapid regrowth reported (Luoga et al., 2004; Backéus et al., 2006; Chidumayo, 2013; Chirwa et al., 2014).

In our study, species richness, species diversity and biomass were higher in old Miombo regrowth than in mature woodland. Higher species richness and diversity in secondary vegetation areas has been reported in other studies (e.g. Williams et al., 2008; McNicol et al., 2015) and can be explained by the intermediate disturbance theory which postulates that, at an intermediate level of disturbance, the environment will allow the co-existence of both early and late-succession species as a result of the creation of a greater variety of ecological niches (Connell and Slatyer, 1977). The higher biomass can be explained by the larger number of individuals and larger diameters due to regrowth of new shoots from well-established stumps and roots that were not affected by fire or clearing (Luoga et al., 2004; Syampungani et al., 2015).

Tree species diversity in mature woodland, obtained with the Shannon-Weiner index estimator (H'), was 2.5, indicating moderate diversity of Miombo woodland according to Barbour et al. (1998). Our results are thus situated between those obtained by Williams et al. (2008) (H': 1.9) in a dry Miombo zone (average rainfall of 680 mm/year) in Sofala province, Mozambique, and Kalaba et al. (2013) (H': 2.8) in a wet Miombo zone (average rainfall 1,200 mm/year) in Zambia. The differences in species diversity and richness are mainly due to differences in anthropogenic pressure and in rainfall regimes between the study areas.

Species composition and species dominance changed notably with the number years after abandonment. In agreement with Kalaba et al. (2013) but in contrast to Williams et al. (2008) and Stromgaard (1986), in our study the dominant Miombo tree species (*Brachystegia spiciformis, Brachystegia boehmii, Julbernadia globiflora*) were present in all stages of regeneration. The differences between similar studies are probably due to the different land histories in the study areas concerned. Jew et al. (2016) showed that the dominant Miombo tree species are present in areas under low pressure but are replaced by other species in areas under high pressure. Disturbance in our study area is still quite low due to the proximity to the National Park and to the past population's migration away from the protected area. Yet, in the present study, despite the presence of the dominant Miombo species, after 20–35 years of regeneration, the species composition was still different from that of mature woodlands. This result is in line with the result of other studies on Miombo regeneration after slash-and-burn (Williams et al., 2008; Kalaba et al., 2013; Gonçalves et al., 2017). Kalaba et al. (2013), who studied the most extensive chronosequence known in Miombo woodland (1 to 58 years of abandonment), showed that even after six decades of set-aside, species composition did not match that of mature woodland. Analysis of the species composition recovery time would require long-term studies covering several human generations which are unlikely due to time and cost constraints. Rozendaal et al. (2019) suggest that recovery to reach the species composition of mature forest in neotropical lowland forest sites takes centuries but, in some cases, it is not known if the original composition will ever be completely recovered.

In this study, we used a synchronic approach (one sampling of different plots in a chronosequence) which is widely used to investigate forest succession after disturbance. However, this approach has some limitations due to the spatial heterogeneity of soil properties or the landscape context and the difficulty involved in obtaining the complete history of land-use practices, and of the occurrence of fire (Chazdon et al., 2007; Quesada et al., 2009). Several authors suggest that the use of permanent plots (diachronic approach) is more appropriate to study forest ecological succession (Quesada et al., 2009; Gumbo et al., 2018), as permanent plots allow continuous monitoring of the stand and consistent knowledge of regeneration dynamics can be acquired by comparing successive samples. Biases related to the use of chronosequence were limited by selecting areas where a maximum of reliable information was collected on the land use history. In addition, plots are relatively homogeneous in terms of soil properties and agricultural practices.

4.2. Do soil properties return to their original level after abandonment of agriculture?

The results of the present study showed that many soil properties reach values similar to those of mature woodland after 20 years of abandonment. After abandonment, soil C stock increased steadily during vegetation regeneration, and two or three decades were required to reach a value comparable to that in mature woodland. Our results also suggest that the soil disturbances associated with the slash-and-burn system (export of biomass, burning of crop residues, soil tillage, and high soil temperature) leads to a significant decline in soil carbon stocks. Indeed, we observed a 43% drop in carbon stocks in cropland soil compared to mature woodland. A similar pattern was observed by Walker and Desanker (2004) in Malawi (40% less carbon stocks in cropland soils than in mature woodland) and lower values were reported by Williams et al. (2008) in Mozambique (20% less carbon stocks than in mature woodland soil). In contrast, Magalhães and Mamugy (2020) found no significant impact of the conversion of mature woodland into cropland on soil organic carbon stock in Zambezia province (Mozambique). Farmers' practices, fire intensity and the stage of cultivation when sampling was performed (immediately after slash-and-burn or a few years later) may explain those differences.

Soil carbon stocks in mature woodland reported in this study were relatively low (16.9 MgC/ha ± 3.5 MgC/ha) compared with other studies in Mozambique. Ribeiro et al. (2013) found an average of 34.72 MgC/ha (±17.93 MgC/ha) of soil carbon stocks in the top 30 cm soil

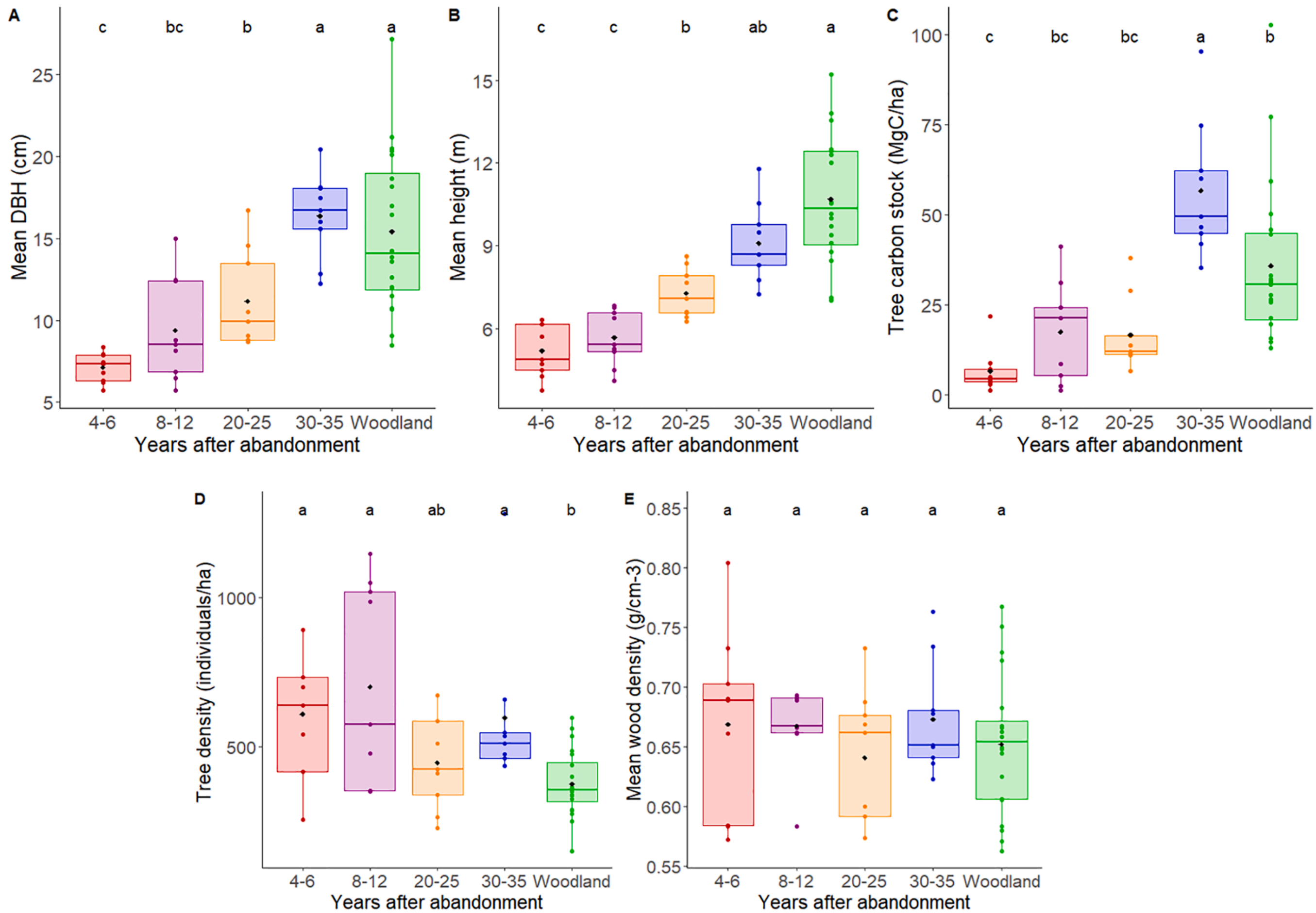

Fig. 4. Stand properties in Miombo regrowth and in mature woodland. (A) tree mean DBH, (B) mean height, (C) tree carbon stock, (D) tree density and (E) mean wood density. Letters ([a], [b], [c]) indicate statistically significant differences (ANOVA, pairwise Tukey's HSD test, $p < 0.05$). The bounding box of each variable in the boxplot represents quartile values, the straight line represents the mean value.

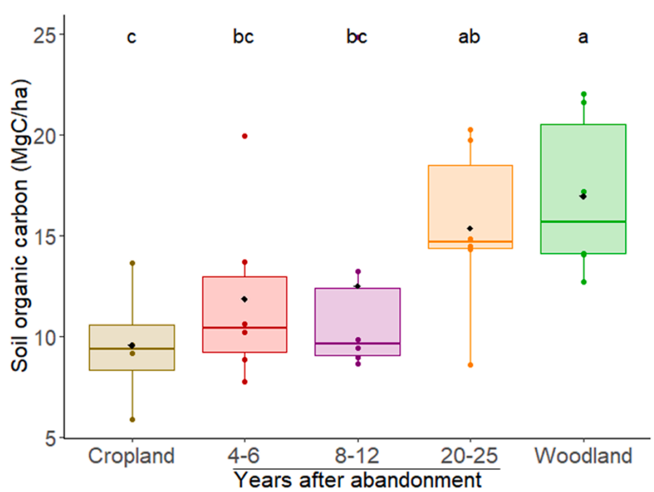

Fig. 5. Soil organic carbon in the top 30-cm soil layer for cropland, Miombo regrowth and mature woodland. Letters ([a], [b], [c]) indicate statistically significant differences (KW, pairwise Tukey's HSD test, $p < 0.05$).

layer using the same method (Walkley-Black) and, using a dry combustion method (CN analyzer), Williams et al. (2008) found that the average carbon stock in soil can exceed 100 MgC/ha. The use of the Walkley-Black method is known to underestimate soil carbon content compared to dry combustion method (Walkley, 1947), but alone, this underestimation cannot explain the differences between our results and those reported by William et al. (2008). Beyond the differences in the soil laboratory methods used, several authors have reported high variability of soil C contents related to topography, soil texture and fire frequency (Ryan et al., 2011; Woollen et al., 2012). In the present study, the low soil carbon stock can be explained by the low soil clay (2–13%) and silt (1–13%) contents, these elements being known to limit the decomposition of organic matter by soil microbial communities (Hassink, 1997; Walker and Desanker, 2004).

We also observed a regular increase in the concentration of available phosphorus during forest regeneration until, after two or three decades, it reached a value comparable to that in mature woodland. Like soil carbon stocks, this results suggest that slash-and-burn system leads to a significant decline in available phosphorus (cropland soils contained 47% less soil available phosphorus than mature woodland). Available phosphorus is currently poorly documented even though it is known to be a key limiting resource for crops and Miombo trees. Mycorrhizal associations play an important role by allowing plants to directly absorb phosphorus from organic matter (Högberg, 1982; Campbell, 1996).

Higher concentrations of exchangeable soil cations (Mg, K, and Na) were observed in Miombo regrowth than in mature woodland. These results are in agreement with those of other studies (Strømgaard, 1992; Markewitz et al., 2004). Authors suggest that this is linked to the amount of imported nutrients in the soil through litter fall or rain and dust fall in Miombo regrowth that exceeds nutrient exports into the growing vegetation and leaching (Nye and Greenland, 1960). Further studies are needed to understand nutrient cycling between vegetation and soil after slash-and-burn agriculture and during Miombo regeneration.

Soils in Miombo woodland are generally nutrient poor (Frost, 1996; Ribeiro et al., 2020), which is also the case in the Gilé area where the soils are sandy and acidic with low water and nutrient retention properties. This highlights the high adaptability of Miombo tree species to unfavorable soil conditions.

4.3. Implications for land management and restoration

The results of the present study show that Miombo has a high regeneration capacity in terms of woody species diversity, richness, carbon stocks and soil properties in low intensity and short-duration disturbance conditions. In the context of large-scale ecosystem restoration, natural regeneration is a cost-effective natural solution (Chazdon et al., 2016; Rozendaal et al., 2019) and is recognized as a climate mitigation strategy (Cook-Patton et al., 2020). Natural regeneration allows the establishment of species adapted to local conditions, species that should be more resistant than others to climatic variations and disturbances (Kalaba et al., 2013). However, our results also show that species composition does not recover rapidly after slash-and-burn (35 years were required in the present case). Different species composition in Miombo regrowth can nevertheless provide some interesting ecosystem services for local communities (e.g. provision of non-timber forest products, improved soil fertility) and for wildlife (Amaya et al., in prep). Yet, it is also important to conserve sufficient areas of intact Miombo woodland to preserve typical biodiversity of mature Miombo and seed banks as a reserve for future possible restoration projects as mature Miombo remains a key habitat and a source of natural resources.

Although regeneration capacity appears to be relatively good, the soil property dynamics and changes in species composition we observed suggest that regeneration rates and capacity may depend on the past land use (number of cycles, length of fallow), past disturbances (type, intensity) and soil properties. Knowledge is still lacking on the impact of these factors on the regeneration capacity of Miombo woodland (Ribeiro et al., 2015). The analysis of the influence of these factors and the spatial distribution of human pressure could be useful for land use planning of woodland restoration. In addition, socio-economic aspects should be taken into account in spatial planning and land tenure, agricultural and forest policy also require a full investigation to insure the success of restoration plans.

5. Conclusion

We demonstrated that the Miombo ecosystem in the Zambezia province (North of Mozambique) showed high resilience after disturbance of low intensity and short-duration. The land in this landscape dominated by smallholder farming was able to recover after 20–25 years of abandonment in terms of woody species diversity, species richness, soil properties and, after 30–35 years in terms of floristic structure (DBH and height). Even though this looks promising for land managers and environmentalists, much longer is needed for species composition to become similar to that of the original natural ecosystem.

The government of Mozambique is committed to restoring one million hectares of degraded forestland through the African Landscape Forest Restoration 100 Initiative (AFR 100). This study provides new insights into the impacts of slash-and-burn and regeneration dynamics that could help define passive or assisted forest restoration strategies that are suitable for Miombo woodland to achieve Mozambican commitments to ecosystem restoration. Further, our findings emphasizes the importance of natural mature forests for biodiversity conservation and argue for integrated landscape management of both human and natural ecosystems to enhance the provision of ecosystem goods and services (climate change mitigation, biodiversity, supporting livelihood).

CRediT authorship contribution statement

Frédérique Montfort: Conceptualization, Methodology, Investigation, Formal analysis, Writing - original draft, Writing - review & editing. **Marie Nourtier:** Conceptualization, Methodology, Writing - review & editing, Supervision. **Clovis Grinand:** Conceptualization, Methodology, Writing - review & editing. **Solène Maneau:** Investigation, Formal analysis. **Corentin Mercier:** Conceptualization, Writing - review & editing, Supervision. **Jean-Baptiste Roelens:** Investigation, Writing - review & editing. **Lilian Blanc:** Conceptualization, Writing - review & editing, Supervision.

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.

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Appendix A

Laboratory methods used to test each soil property.

Properties	Method	Unit
Bulk density	Cylindre	g/cm^3
pH	KCL	pH unit
Sand	Hydrometer	%
Silt	Hydrometer	%
Clay	Hydrometer	%
Organic Carbon	Walkley-Black	%
Calcium	NH_4OAc & Ambic I	mg/kg
Magnesium	NH_4OAc & Ambic I	mg/kg
Phosphorus	Bray I & Ambic I	mg/kg
Potassium	NH_4OAc & Ambic I	mg/kg

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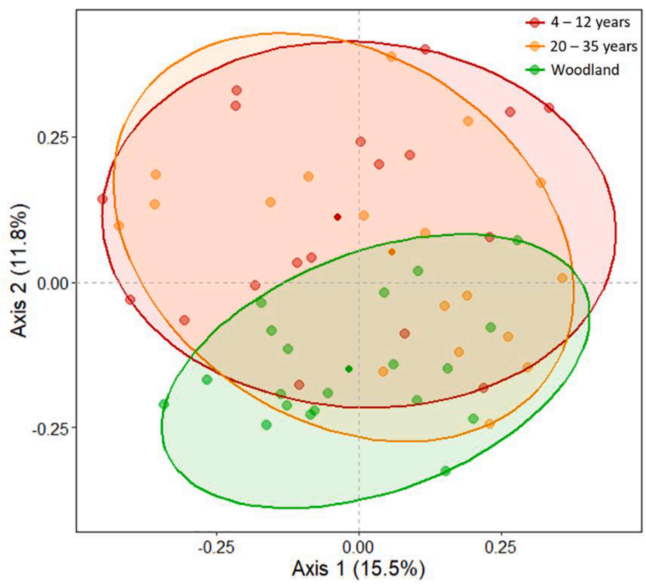
Properties	Method	Unit
Sodium	NH_4OAc & Ambic I	mg/kg
Iron	DTPA & Ambic I	mg/kg
Zinc	DTPA & Ambic I	mg/kg
Manganese	DTPA & Ambic I	mg/kg
Copper	DTPA & Ambic I	mg/kg

Appendix B

Principal coordinates analysis (PCoA) based on the Chao dissimilarity index calculated on abundance data (54 plots × 96 species). The first and second axes of the PCoA accounted for respectively, 15.5% and 11.8% of the inertia. Axis 1 was interpreted as representing site-to-site variations and does not differentiate between regeneration categories. Species composition in 4–12-year-old and 20–35-year-old regeneration categories was more heterogeneous than in mature woodlands. The second axis reveals that changes in species composition were associated with a land-use gradient with regeneration categories on the one hand and forest on the other.



Appendix C

Soil physical properties. Means with different letters ([a], [b], [c]) are statistically significant different (KW, pairwise Tukey's HSD test, $p < 0.05$).

Categories	pH	Bulk density (g/cm^3)	Sand (%)	Silt (%)	Clay (%)
Cropland	6.2 ± 0.4 [a]	1.41 ± 0.06 [a]	82.3 ± 5.7 [a]	10.8 ± 2.2 [a]	7.0 ± 5.8 [a]
4–6 years	4.6 ± 0.4[c]	1.41 ± 0.10 [a]	83.8 ± 4.4 [a]	6.8 ± 3.3 [ab]	9.3 ± 1.6 [a]
8–12 years	5.2 ± 0.3[b]	1.47 ± 0.05 [a]	84.3 ± 4.5 [a]	6.3 ± 3.6[b]	9.3 ± 1.0 [a]
20–25 years	4.7 ± 0.3[c]	1.47 ± 0.08 [a]	81.7 ± 4.2 [a]	8.3 ± 3.1 [ab]	10.0 ± 1.3 [a]
Woodland	5.2 ± 0.3[b]	1.40 ± 0.05 [a]	84.2 ± 5.6 [a]	7.0 ± 2.2 [ab]	8.8 ± 4.2 [a]

Mean soil nutrient concentrations (mg/kg) for each category. Means with different letters ([a], [b], [c]) are statistically significant different (KW, pairwise Tukey's HSD test, $p < 0.05$).

Categories	Calcium (Ca)	Magnesium (Mg)	Phosphorus (P)	Potassium (K)	Sodium (Na)
Cropland	380.91 ± 201.65 [a]	47.52 ± 22.43 [a]	1.05 ± 0.10[b]	49.44 ± 14.85 [ab]	4.52 ± 1.50[b]
4–6 years	244.67 ± 33.46 [ab]	88.33 ± 42.50 [a]	1.39 ± 0.46 [ab]	99.00 ± 46.29 [a]	9.67 ± 8.98 [ab]
8–12 years	402.50 ± 261.36 [a]	115.17 ± 105.21 [a]	1.40 ± 0.46 [ab]	162.00 ± 131.63 [a]	6.00 ± 1.79 [ab]
20–25 years	168.50 ± 69.27[c]	50.33 ± 24.82 [a]	1.68 ± 0.54 [ab]	62.67 ± 30.64 [ab]	7.00 ± 1.67 [a]
Woodland	176.00 ± 80.69 [bc]	56.90 ± 30.34 [a]	2.20 ± 1.11 [a]	43.63 ± 23.30[b]	4.61 ± 1.06[b]

Mean soil micronutrient concentrations (mg/kg) for each category. Means with different letters ([a], [b], [c]) are statistically significant different (KW, pairwise Tukey's HSD test, $p < 0.05$).

Categories	Copper (Cu)	Iron (Fe)	Manganese (Mn)	Zinc (Zn)
Cropland	0.98 ± 0.57 [a]	16.10 ± 7.65 [ab]	24.41 ± 10.94 [a]	0.19 ± 0.07[c]
4–6 years	0.42 ± 0.12[c]	17.55 ± 9.23 [ab]	17.40 ± 14.10 [ab]	0.35 ± 0.15 [a]
8–12 years	0.60 ± 0.11 [ab]	10.47 ± 1.92[b]	8.09 ± 6.74[b]	0.42 ± 0.10 [a]
20–25 years	0.42 ± 0.10[c]	12.95 ± 6.13 [ab]	22.22 ± 16.20 [a]	0.33 ± 0.05 [ab]
Woodland	0.51 ± 0.23 [bc]	17.83 ± 5.47 [a]	25.41 ± 12.11 [a]	0.25 ± 0.08 [bc]

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