

Native forest regeneration and vegetation dynamics in non-native *Pinus patula* tree plantations in Madagascar



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ABSTRACT

Today, exotic invasive alien species are considered to be one of the greatest threats to biodiversity. However, not all exotic species cause negative consequences in the ecosystems in which they settle. In some cases, artificial plantations of exotic species can act as a catalyst for the regeneration of native species. In southern central Madagascar, which has been affected by diverse disturbances (cyclones, logging, cultivation), *Pinus patula* plantations have become environments conducive to the regeneration of native species. This study aims to assess the level of understory plant diversity in these artificial plantations, describe the vegetation dynamics, and examine the effects of agricultural practices and logging on vegetation diversity and structure. Floristic inventories and biomass measurements were made on three types of vegetation that have resulted from previous human-induced disturbance: (i) cassava crops established after pine logging; (ii) fallows corresponding to cassava crops left fallow for 1–2 years; and (iii) post-logging regrowth after pine logging 3–10 years previously. Botanical surveys were conducted on 205 10 × 10 m² quadrats placed along 40 transects. A total of 125 species, 34 of which endemic, from 46 families were inventoried. The Shannon Weaver index H' values were significantly different between post-logging regrowth ($H' = 4.01 \pm 0.67$), and cultivated fields ($H' = 1.46 \pm 0.23$) and fallows ($H' = 3.31 \pm 0.78$) ($p < 0.001$). Agricultural practices, such as tillage regime, number of crop-fallow cycles (> 2 cycles) and number of fire occurrences (> 4 fires) had a greater impact on the reconstitution of vegetation than environmental parameters such as slope and topographic position. The Shannon-Weaver diversity index (H') and vegetation structure parameters (tree density, biomass) were inversely correlated with the intensity of disturbance linked to these agricultural practices. These results suggest that a low level of disturbance, such as that resulting from *Pinus* tree logging, can act as a catalyst for the establishment of native woodlands. Excessive disturbance from silvicultural and agricultural practices, such as frequent burning, heavy tillage and high number of crop/fallow cycles, may hinder, but does not block, the establishment of native woodlands.

1. Introduction

The early 1990s were marked by the emergence of new practices and research into the role of forest plantations as areas that could potentially act as catalysts for the regeneration of native species (Parrotta, 1992; Lugo, 1992; Parrotta, 1995; Telila et al., 2015). These studies show that under certain conditions, it is possible to restore both animal and plant biodiversity in degraded landscapes thanks to regeneration processes of native forest species that occur after the reforestation species, most often introduced, are logged (Parrotta et al., 1997; Lamb et al., 2005). The results of these studies, conducted in Puerto Rico,

China, Uganda, and elsewhere, provide strong evidence of the positive role of these plantations in the regeneration and implantation of native species, but they emphasize the importance of taking local specificities into account at both the ecological (landscape) and socioeconomic (land management) levels when considering how to apply the lessons learned from these researches (Lugo, 1992; Parrotta et al., 1997; Piironen et al., 2015). In Madagascar, numerous plantations of *Pinus*, *Eucalyptus*, and *Acacia* were established in the 1930s across the Central Highlands in degraded forest areas, on the edges of existing forests, and on grasslands at times far from forests and without an established forest history (Parrot, 1925; Carrière and Randriambanona, 2007;

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Randriambanona, 2010; Martin et al., 2012). While exotic species introduced with a forest plantation can disturb ecosystems and ecological habitats by modifying their structure and composition (Thébaud and Simberloff, 2001; Callaway and Ridenour, 2004), the areas planted are of undeniable interest for understanding the role of such plantations in the regeneration of native forest species in degraded areas near natural forests. These reforested areas in effect attract fruit-eating forest animals such as birds and lemurs (Martin et al., 2009, 2012; Gérard et al., 2015) that can contribute to locally increasing the dispersion of forest species seeds on these plantations, and therefore to the regeneration of these areas lying outside the forests due to nucleation (Carrière et al., 2002; Schlawin and Zahawi, 2008). The conditions of this regeneration of native or even endemic species depend as much on the structure and composition of the plantations (Sansevero et al., 2011), which affect animal movements, as the distance to the source of seeds (Jesus et al., 2012) and the effect of disturbances (agricultural and logging practices) conditioning the regeneration of pioneer species. Numerous authors deplore forest managers' preference for fast growing introduced species, but they also point to a lack of knowledge about the ecology of these plantations and the silvicultural practices associated with native and introduced species to facilitate regeneration (Lugo, 1997; Lamb et al., 2005; Pareliussen et al., 2005).

Madagascar is no exception. Indeed, in this biodiversity “hotspot” (Myers, 1988), little consideration has been given to the role of introduced forest species other than as a threat to native biodiversity through their potentially invasive character (Binggeli, 2003; Kull et al., 2007; Carrière et al., 2008). Nonetheless, these vigorous species (Perrier de la Bathie, 1931) could play a role in restoring Malagasy ecosystems (Gérard et al., 2015).

In the southern central part of the island, Ranomafana National Park and the landscapes around the commune of Androy present special features for the study of ecological restoration possibilities. The particular feature of the pine plantations (*Pinus patula* Schltdl. & Cham.) in this area (near the forest corridor linking Ranomafana and Andringitra National Parks) lies in their placement on grassy areas abandoned by agriculture rather than on lost or degraded forests (Randriambanona, 2010). The proximity of natural and artificial plant formations and the heterogeneous landscape where fluxes of birds contribute to seed dispersal (Martin et al., 2009, 2012) create an excellent site in which to understand the effect of these trees and their use (crops, logging, vegetation burning) on natural regeneration. A better understanding of the forest regeneration processes on these plantations is an important step for setting up forest restoration measures in Madagascar. It would enable the valorisation of areas with few species, such as grasslands, while also enabling the use or production of resources required for human survival (Brunet et al., 2011; Gérard et al., 2015).

The objective of the present study is to describe and analyse the structure and diversity of the plant formations which have regenerated in disturbed *Pinus patula* plantations that were initially established on grasslands. By comparing different stages of regeneration before, during and after agricultural use, the study also aims to identify the key ecological factors behind the plant succession dynamics. In the present study, we set out to test the hypothesis that (i) gaps created in pine plantations due to numerous disturbances (logging, cultivation, fires) allow native species to regenerate and (ii) cultivation practices have a greater influence on the floristic diversity, structure and dynamics of the vegetation than other environmental factors.

2. Materials and methods

2.1. Study site

The study was conducted close to the forest corridor linking Ranomafana and Andringitra National Parks in the commune of Androy (21°22'S, 47°18'E; elevation 1100–1200 m), 300 km south of Antananarivo. Average annual rainfall is 1296 mm and the average

temperature is 19 °C. The soils are ferralsols according to the FAO classification, characterised by a lack of available phosphorus and exchangeable cations (Randriamalala et al., 2007). The landscape on the forest edges is heterogeneous (Martin et al., 2009, 2012) and composed of highly diverse ecological habitats: (1) dense medium-altitude rainforests dominated by *Tambourissa* and *Weinmannia* (Koechlin et al., 1974), more or less disturbed and secondary depending on the distance to villages and the presence of formerly cultivated site, (2) post-cultivation regrowth of varying ages and composition known locally as *kapoka* and *kilanjy*, (3) plantations of *Pinus* spp., *Acacia dealbata* Link and *Eucalyptus* spp., and (4) *Aristida similis* Steud. grasslands (Carrière and Randriambanona, 2007; Randriamalala et al., 2007).

2.2. The *Pinus* plantation studied

This government-owned industrial pine plantation (2300 ha) was set up between 1969 and 1972 to supply a wood pulp factory that ultimately was never constructed (Randriambanona, 2010). No fertilizer was used when the trees were planted in holes (50 × 50 × 50 cm cubic holes dug with spades) on *A. similis* grasslands (CTFT, 1967). The distance between the tropical forest of the Ranomafana-Andringitra corridor and the *Pinus* plantations varied between 200 and 600 m. The main tree species used for these plantations were *Pinus patula*. Following the selective logging of pines over the entire plantation, post-logging regrowth began to appear starting from 1994 in different gaps, and then gradually elsewhere on the entire plantation (Randriambanona, 2010). Cyclone Honorine in 1986 and Géralda in 1994 caused additional disruption (windfall), before and after the felling of trees, which cannot be quantified (personal observations). Like the logging, this led to intermittent forest regeneration phases within the plantations. These phenomena transformed the reforestation areas into forest or pre-forest regrowth plots dotted with some scattered pine trees. Beginning in 2001, the local population started to farm these post-logged regrowth areas by felling, clearing, drying and burning the vegetation (*Pinus patula*, *Vernonia garnieriana* Klatt., *Macaranga alnifolia* Baker, *Anthocleista madagascariensis* Baker) and then planting cassava. The plots were then tilled using an *angady*, a traditional spade, using two methods: (i) partial tillage immediately around the planting hole, called *kobokaka* (light tillage; < 10 cm depth, about 1 m radius around cassava cutting, which is the only crop planted with *kobokaka*) and (ii) ploughing (heavy tillage, 10–20 cm depth) (Randriamalala et al., 2012). After a two-year cassava crop cycle, the plots were left to lie fallow 3–4 years (Randriambanona, 2010). It is only after the crop cycle and during the fallow phase that post-farming natural regrowth developed, taking the form of low grasslands at the time of the study. Understory vegetation in the *Pinus* plantation site can be grouped into three vegetation types resulting from silvicultural and agricultural practices which correspond to decreasing levels of disturbance: (i) cassava plots (*Pinus* logging + cassava cultivation; Log + C), (ii) fallow, agricultural regrowth (*Pinus* logging + plot cultivation + plot abandonment; Log + C + Ab) and (iii) post-logging regrowth (*Pinus* logging + plot abandonment; Log + Ab).

2.3. Vegetation study

The vegetation inventories were made on 205 (10 m × 10 m) plots spaced 50 m apart along 40 transects spaced 100–150 m apart and of varying lengths depending on the width of the study area (Fig. 1).

This approach made it possible to take transects within the three main vegetation types present: cassava crops (Log + C), fallows (Log + C + Ab), and post-logging regrowth (Log + Ab) that had not yet been cultivated. For each plot, the following site variables were recorded: slope (in degrees), exposition, altitude and topographical position (Top, valley bottom, mid-slope, high slope, crest). For each woody individual with a diameter > 5 cm, the following parameters were recorded: species, height (h), diameter at a height of 1.30 m

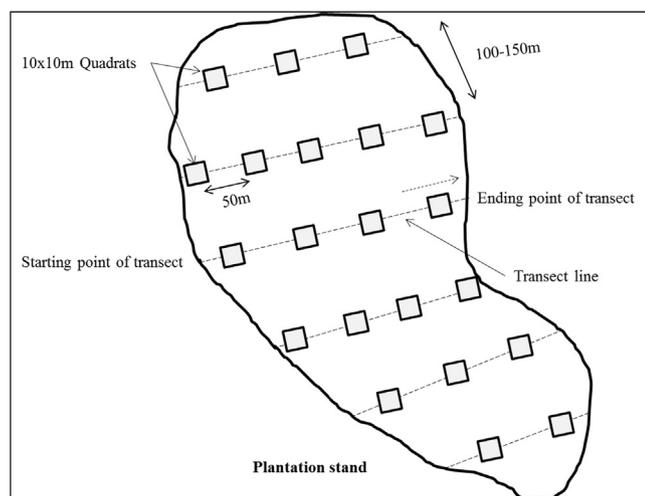


Fig. 1. Vegetation sampling.

(DBH), life form (tree, shrub, grass, lianas) and main mode of seed dispersal (anemochory, zoochory, barochory). The following parameters were calculated for each plot:

- species richness (S), defined as the total number of species found per plot;
- Shannon-Weaver diversity index (Shannon and Weaver, 1949);
- evenness index, $R = H/H_{max}$, where H is the Shannon-Weaver index and H_{max} is the maximum value of H in the community, if all of the plant species are equally frequent (Pielou, 1966);
- tree density ($N \text{ ha}^{-1}$);
- total biomass (TB) composed by above-ground biomass (AGB) and below-ground biomass (BGB). The AGB (Mg ha^{-1}) was assessed using the full harvest method in 15 randomly chosen plots in each vegetation type. This method consisted of cutting close to the ground all standing plant material in a $2 \text{ m} \times 2 \text{ m}$ square (Pfund et al., 1997); four squares per plot were measured. The weight of the fresh material was recorded in the field and the dry matter content was determined after drying in an oven (85°C for 24 h). BGB was measured by assessing fine root biomass (diameter $< 2 \text{ mm}$) with the coring method (Böhm, 1979) in the same squares as the AGB using a sensor (XOK-37000, Lindquist International) with an 80 mm inner diameter, with 9 samples taken on the 0–10, 10–20, 20–30, 30–40, 40–50, 50–75, 75–100, 100–125, 125–150 cm horizons. The roots were cleaned of dirt using a double screen under a spray of water, then rinsed, manually sorted and dried in an oven (85°C for 24 h), and weighed.

2.4. Agro-ecological variables

To retrace the silvicultural and agricultural history of studied plots, questionnaires were used among the populations and, for the cultivated plots, the farmers. The information collected concerned the following silvicultural and agricultural variables: (i) number of successive fires since first clearing (FN-1: 1 fire, FN-2: 2 fires, FN-3: 3 fires, FN-4: 4 fires); (ii) crop-fallow cycle number (CC-0: uncultivated, CC-1: one cycle, CC-2: two cycles); (iii) duration since the first pine logging (DEF-3: 3 years, DEF-4: 4 years; DEF-5: 5 years); (iv) fallow ages (FA-0: uncultivated and/or under cultivation, FA-1: fallow 1 year-old, FA-2: fallow 2 year-old), and (v) tillage regime (T-0: no-tillage, T-1: light tillage, *kobokaka*, T-2: heavy tillage, soil ploughing). Environmental parameters such as (vi) slope values (low $< 10^\circ$, middle, between 10 and 20° and high $> 20^\circ$) and (vi) topographic positions (Top-1: valley bottom, Top-2: middle slope, Top-3: upper slope and Top-4: crest).

2.5. Data analysis

A co-inertia analysis was conducted to determine the factors determining the distribution of plant species in the vegetation types (Dray et al., 2003). This method aims to describe the common structure of two tables: the first is represented by 125 species \times 205 plots table (presence/absence of species criteria) and the second by agro-ecological variables (number of successive fires, crop-fallow cycle number, duration since the first pine logging, fallow ages, tillage regime, slope values and topographic position). Another co-inertia analysis linking vegetation diversity and structure (biomass, tree density) and agro-ecological variables was also performed. An analysis of variance (ANOVA) was preceded by a test of homoscedasticity that was used to test variations of structure and diversity variables (species richness, Shannon and Evenness index, seed dispersal mode and life forms) by (i) agro-ecological variables affecting them the most according to co-inertia analysis and by (ii) vegetation types. The analyses were made using ADE-4 statistical software (Thioulouse et al., 1999).

3. Results

3.1. Floristic composition

One hundred and twenty-five species belonging to 91 genera and 46 families were identified in the whole plots. The most represented families are the Asteraceae (19 species), followed by the Poaceae and the Rubiaceae with 14 species each. Thirty-four species are endemic. In total, 30 tree species, 32 shrub species, 51 herbaceous species and 12 liana species were counted. The majority of woody species (trees and shrubs) were native or endemic. The species associated with cassava crops (Log + C) are *Manihot* sp. (Euphorbiaceae) and annual herbaceous belonging to the Asteraceae family, such as *Bidens pilosa*, *Erigeron naudinii* (Bonnet) Humbert, those associated with fallows (Log + C + Ab) are essentially *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae), *Rhynchelytrum repens* (Willd.) C.E. Hubb. (Poaceae), and *Imperata cylindrica* (L.) Rausch (Poaceae). Post-logging regrowth (Log + Ab) are essentially characterized by woody species such as *V. garnieriana*, *Syzygium emirnense* (Baker) Labat and G.E. Schatz (Myrtaceae), *Weinmannia rutenbergii*, *Tambourissa purpurea* (Drake) (Monimiaceae), *Polycias ornifolia* Baker Harms (Araliaceae).

The dependence between the species and the variables considered is significant ($p < 0.001$, RV coefficient = 0.447). The first co-inertia axis (68% of the total co-inertia) opposes: (i) plots that are characterized by a low frequency of fires (FN-2), with soil never tilled (T-0), not cultivated (CC-0), and located at the crest of hills (Top-4), to (ii) plots that underwent one (CC-1) or two crop cycles (CC-2); were lightly tilled (*kobokaka*; T-1) or ploughed (T-2), frequently burned (FN-3 and FN-4) and located at the valley bottom (Top-1) (Fig. 2).

The species associated with type (i) plots are mainly trees and shrubs such as *V. garnieriana*, *Gaertnera macrostipula* Baker (Rubiaceae), *S. emirnense*, *W. bojeriana*, *Myrica phyllireaefolia* Baker (Myricaceae), *Rytiginia* sp. (Rubiaceae), *Oncostemum bojerianum* A. DC. (Myrsinaceae), *Vaccinium emirnense* (Ericaceae), *Allophylus* sp. (Sapindaceae), *T. purpurea*, *Anthocleista madagascariensis* Baker (Loganiaceae), *P. ornifolia*. Some lianas are present: *Cissus lemurica* Desc (Vitaceae), *Ligodium lanceolatum* Desv. (Schizaceae). The species associated with the second type of plots (ii) are essentially annual herbaceous species belonging to the Asteraceae family (*Ageratum conyzoides* L. and *Helichrysum attenuatum* Humb.), the Poaceae family: *Imperata cylindrica* (L.) Rausch, *R. repens* and a fern species *Pteridium aquilinum*. They are associated with a few shrub species: *Trema orientalis* L. (Ulmaceae), *Solanum auriculatum* Aiton (Solanaceae).

The second axis (16%) opposes plots that were: (iii) logged, cultivated, and then left fallow one year (FA-1) or two years (FA-2), to those (iv) under cultivation (FA-0) and recently cleared (3 years, DEF-3). The species associated with type (iii) plots are Poaceae such as *Paspalum* sp.,

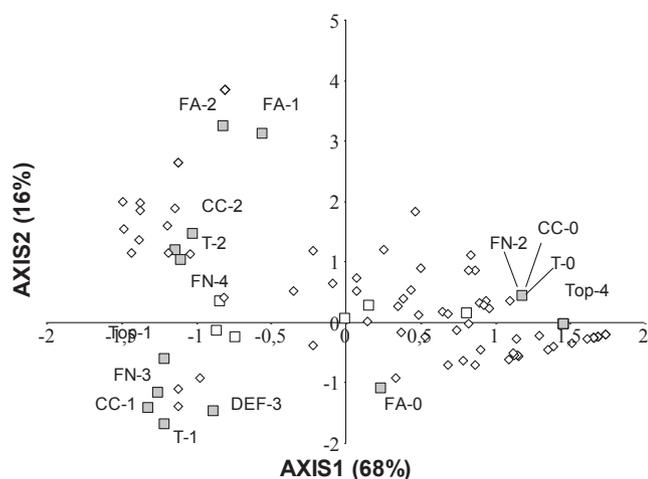


Fig. 2. Co-inertia analysis: relation between agro-ecological variables and species distribution. **CC:** crop-fallow cycle (0: No, 1: CC; 2: 2 CC); **FA:** fallow age (0 year; 1 year; 2 years); **FN:** Fire frequency since first clearing (2: ≤ 2 fires; 3: ≤ 4 fires; 4: ≥ 4 fires); **T:** tillage regime (0: no tillage; 1: light tillage; 2: heavy tillage); **Top:** plot's topographical localisation (1: bottom; 4: crest). Diamond: species; Grey squares: agro-ecological variables that affect species distribution; White squares: other agro-ecological variables.

Panicum sp., Asteraceae *Elephantopus scaber*, *Helichrysum cordifolium*, Rubiaceae *Morinda* sp., *Oldelandia herbacea* D. C., *Danais fragrans* (Comm. Ex. Lam) Pers., some Fabaceae (*Hyposestes* sp., *Crotalaria uncinella* Lamk) and Rosaceae (*Rubus rosaeifolius* J. E. Smith), as well as some shrubs such as *Dodonaea viscosa* Jacquin (Sapindaceae), *Halleria ligustrifolia* Bak. (Scrophulariaceae) and *Morinda* sp. (Rubiaceae). The species associated with type (iv) plots are cassava *Manihot* sp. (Euphorbiaceae) and *B. pilosa* (Asteraceae). In the end, the co-inertia analysis linking species and agro-ecological variables made it possible to distinguish three vegetation types: (i) plots less disturbed since the pinus trees were planted, (ii) plots abandoned 1 or 2 years previously after having been cultivated and subjected to intense tillage and fires, located on the lower slopes, and (iii) plots under cultivation that were cleared some time ago (5 years). The effect of slope was not significant. Human practices represented by the number of crop-fallow cycles, the number of successive fires, and the tillage regime had the greatest impact on the distribution of species in the study site.

3.2. Effects of silvicultural and agricultural practices and other ecological variables on vegetation diversity and structure

The dependence between vegetation diversity and structure and considered agro-ecological variables is significant ($p < 0.001$, RV coefficient = 0.516). The first co-inertia axis (97% of the total co-inertia) is characterized by Below-Ground Biomass (BGB), Total Biomass (TB), Above-Ground Biomass (AGB), Tree Density (D), and Shannon Index (H') (Fig. 3).

The same first co-inertia axis showed that frequent fires, crop-fallow cycles and soil ploughing reduce biomass values and, to a lesser extent, the Shannon-Weaver index values (H'), tree density (D) and total biomass (TB) (Fig. 3). In fact, there is a global and negative dependency between (i) these structure and diversity parameters (H' , BGB, AGB, TB and D) and agricultural and silvicultural variables (fire number, tillage regime, crop-fallow number) (Figs. 4–6).

Diversity index, densities and biomass of the main vegetation groups are summarized in Table 1. Cassava crops plots have the lowest species richness ($S = 6$), only a few weeds grow there (e.g., *B. pilosa*, *A. conyzoides*); Post-logging regrowth have the highest species richness ($S = 33$).

The species richness of cassava crops is thus significantly lower than

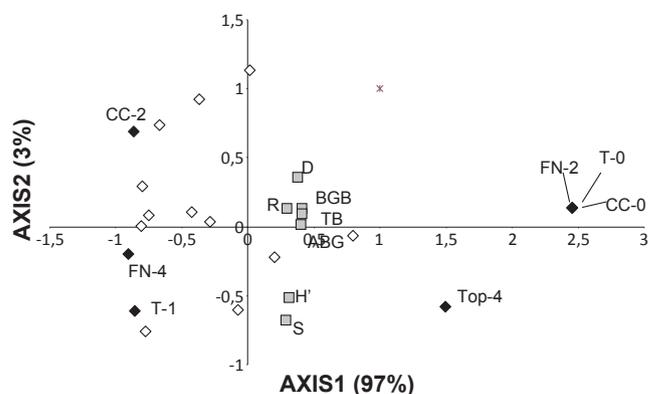


Fig. 3. Co-inertia analysis: relation between agro-ecological variables and vegetation diversity and structure. **CC:** crop-fallow cycle (0: No CC; 2: 2 CC); **FN:** Fire frequency since first clearing (2: ≤ 2 fires; 3: ≤ 4 fires; 4: ≥ 4 fires); **T:** tillage regime (0: No tillage; 1: light tillage; 2: heavy tillage); **Top:** plot's topographical localisation (1: Valley bottom; 4: crest). Black diamonds: agro-ecological variables that affect vegetation diversity and structure; White diamonds: agro-ecological variables; Grey squares: vegetation diversity and structure variables: **S:** species richness, **H'**: Shannon-Weaver index, **R:** Evenness index, **D:** Tree density, **BGB** Below-Ground Biomass, **AGB** Above-Ground Biomass; **TB:** Total Biomass.

that of the fallows and post-logging regrowth groups ($p < 0.001$). Between the latter two groups, the difference of mean species richness is not significant ($p > 0.05$). The highest tree density (6843 N ha^{-1}) was recorded in post-logging regrowth and the lowest value (297 N ha^{-1}) in cassava crops. A significant difference was observed between the total biomass values of post-logging regrowth ($28.6 \pm 5.67 \text{ Mg ha}^{-1}$) and fallows ($5.83 \pm 1.5 \text{ Mg ha}^{-1}$) ($p < 0.001$).

3.3. Life forms and dispersal mode of vegetation types

A significant difference was observed between the vegetation types in terms of biological forms (Table 2).

While post-logging regrowth is composed of trees ($35.0\% \pm 12.2$), in fallows, trees represent only $15.6\% \pm 6.5$ of the species. In cassava plot and post-logging regrowth, the trees are mainly pines that were not felled during logging or which were spared by the farmer when crop farming. A significant difference for shrubs was observed between the three main vegetation types ($F = 55.042$; $p < 0.001$). Lianas are significantly more abundant in post-logging regrowth compared to fallows and cassava crops ($F = 3.028$; $p < 0.01$). With regard to seed dispersal, anemochorous species represented 42% of all species, zoochorous 40%, and barochorous 18%. Anemochorous species are more abundant in cassava crops compared to fallows and post-logging regrowth ($F = 24.642$; $p < 0.001$). In contrast, zoochorous species are more abundant in post-logging regrowth than in fallows and cassava crops ($F = 46.710$; $p < 0.001$). Barochorous species represent a very low percentage in the cassava crop ($1.7\% \pm 5.3$) and reach $14.0\% \pm 9.7$ in post-logging regrowth ($F = 4.840$; $p < 0.05$).

4. Discussion

4.1. Disturbed *Pinus* plantations as forest regeneration foci

The results of this study confirm for the first time in Madagascar that logged forest plantations operate as regeneration foci (Parrotta et al., 1997; Holl et al., 2011; Zahawi et al., 2013) as defined by nucleation theory (Corbin and Holl, 2012; Piironen et al., 2015), which enable an afforestation process to begin. The species-poor *Pinus* plantations disturbed by logging have enabled the dispersion, natural regrowth, and establishment of native and even endemic forest species

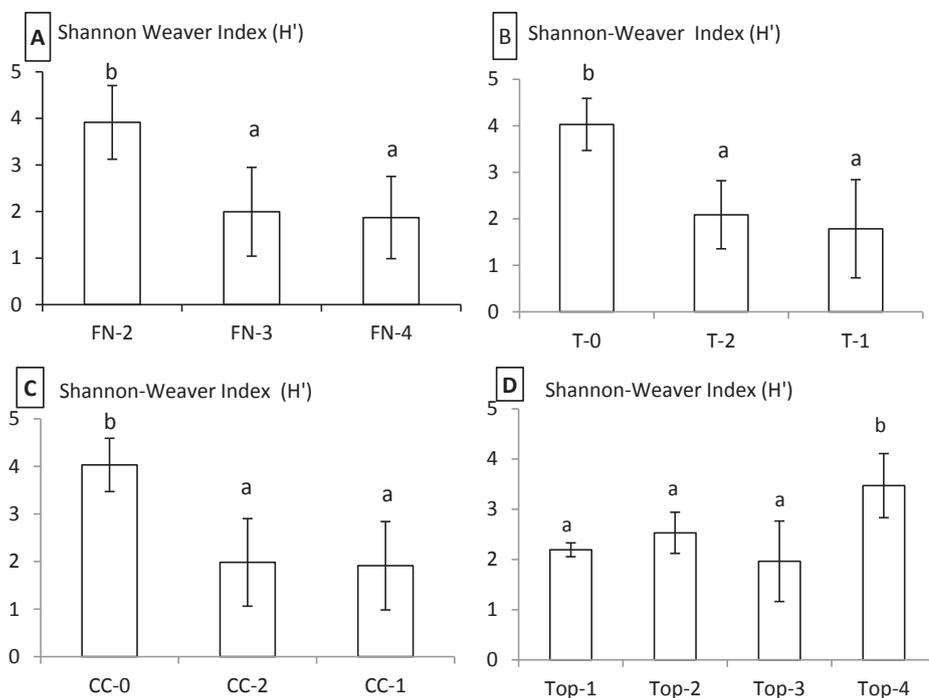


Fig. 4. Effect of cropping history and environmental variables on Shannon-Weaver index. FN: Fire frequency since first clearing (2: ≤ 2 fires; 3: ≤ 4 fires; 4: ≥ 4 fires); CC: crop-fallow cycle (0: No; 1: 1 CC; 2: 2 CC); T: tillage regime (0: no tillage; 1: light tillage; 2: heavy tillage); Top: plot's topographical localisation (1: valley bottom; 4: crest). Vertical bars stand for S.E.

such as *T. purpurea*, *Evodia madagascariensis* Baker, *V. garnieriana*, *Nuxia capitata*, *N. sphaerocephala* and *Aphloia theiformis* (MBG, Tropicos Data Base) in areas that previously had been grasslands.

In this regrowth, mainly composed of trees, shrubs and lianas, the proportion of herbaceous species is low compared to post-crop regrowth of the same age and the absence of shrub species in cassava crops is mainly due to clearing, burning, tillage, and weeding operations before crop farming (Randriamalala et al., 2007, 2012). The regeneration and presence of tree species and shrubs in post-logging regrowth and fallows is therefore more important than in cassava plots. This also may be due to the competition imposed by herbaceous species

(heliophilous), which establish rapidly in cassava plots and can block for a time the regeneration of pioneer shrubs and tree species (more sciaphilous) (Carrière et al., 2002; Randriamalala et al., 2007, 2012). Shrub canopy closure reduced herbaceous cover and favoured the development of tree and shrub species in fallows and post-logging plots (Table 2).

The plant composition and levels of species diversity are similar to those observed in post-cultivation forest regrowth originating from slash-and-burn agriculture and the secondary forests in the study area (Goodman and Razafindratsita, 2001; Randriamalala et al., 2007, 2012; Randrianarison et al., 2015). The species diversity of this regrowth (H'

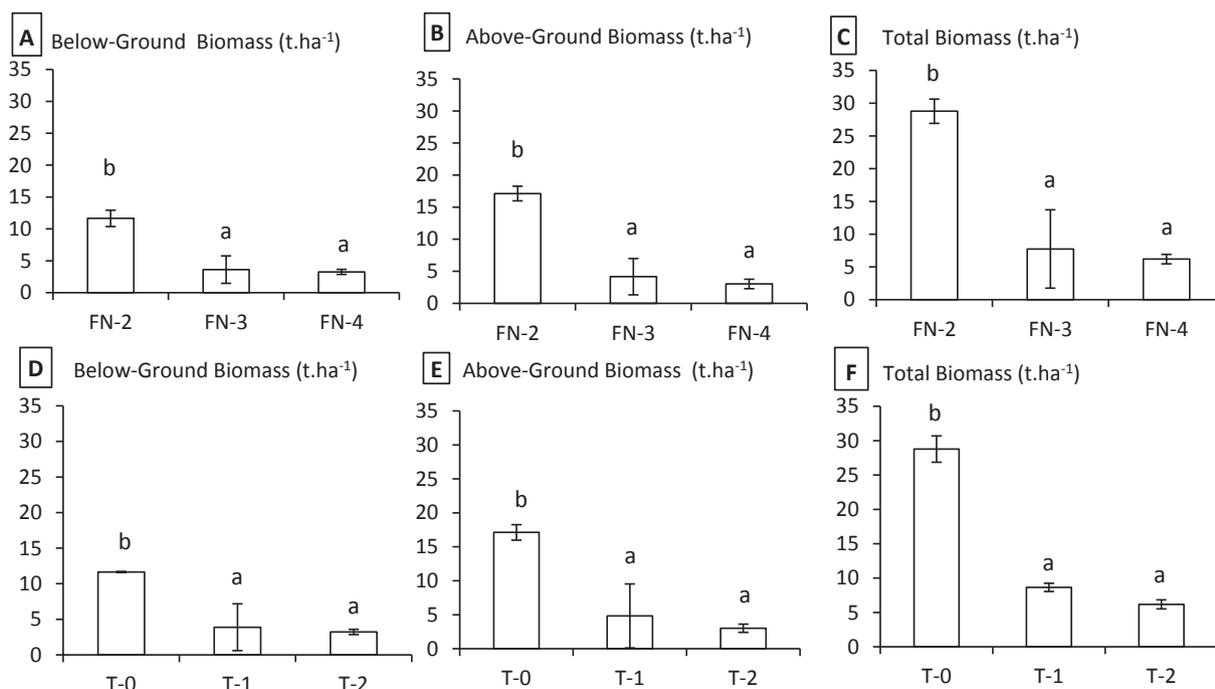


Fig. 5. Effect of cropping history and environmental variables on biomass. FN: Fire frequency since first clearing (2: ≤ 2 fires; 3: ≤ 4 fires; 4: ≥ 4 fires); T: tillage regime (0: no tillage; 1: light tillage; 2: heavy tillage). Vertical bars stand for S.E.

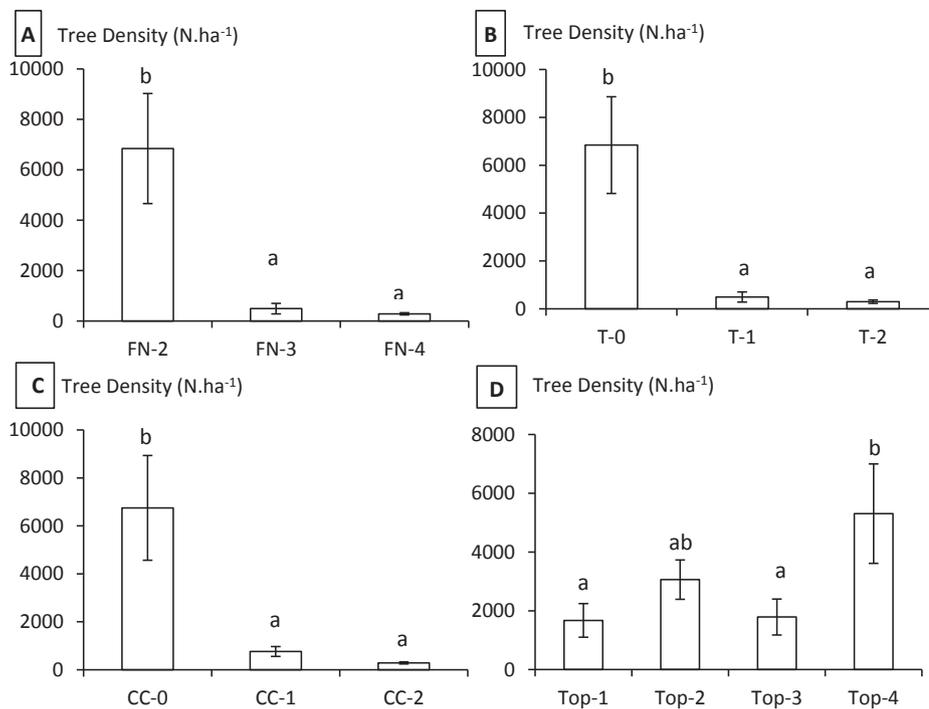


Fig. 6. Effect of cropping history and environmental variable on tree density. FN: Fire frequency since first clearing (2: ≤2 fires; 3: ≤4 fires; 4: ≥4 fires); CC: crop-fallow cycle (0: no CC; 2: 2 CC); T: tillage regime (0: no tillage; 1: light tillage; 2: heavy tillage); **Top:** plot's topographical localisation (1: valley bottom; 4: crest). Vertical bars stand for S.E.

= 3.31) is comparable to that observed ($H' = 3.54$) in the regrowth on *Pinus patula* and *Cupressus lusitanica* plantations in Colombia (Cavelier and Tobler, 1998). This value is in contrast superior to that obtained by Senbeta et al. (2002) in regrowth on a *Eucalyptus* plantation in Ethiopia. In terms of tree density, the value obtained in this study ($D = 6843 \text{ N ha}^{-1}$) is higher than that obtained by Senbeta et al. (2002) and Yirdaw (2001) in the same type of plantation in Ethiopia ($D = 2325\text{--}4495 \text{ N ha}^{-1}$) (Table 3). The age of these plantations may be the reason for this difference, with the plantations in Ethiopia being younger (less than 30 years). Moreover, the *Pinus* plantations in the study area were never maintained (weeding and cleaning), allowing woody species to develop and multiply rapidly. The tree density obtained ($D = 6843 \text{ N ha}^{-1}$) is in the same range as that obtained by Lee et al. (2005) in Hong Kong ($9031 < D < 10,000$). However, it is less than that recorded on the *Acacia* plantations ($7273 < D < 11,169$) established in the 1920s in the same study area (Randriambanona, 2010). These comparisons do not enable a conclusion to be drawn regarding the factors determining the tree density values (Table 3). The total plant biomass values of this natural regrowth (28.6 Mg ha^{-1}) are similar to those of an *Acacia* plantation (70 years old) in the same study area (Randriambanona, 2010). However, they are greater than those of regrowth in four-year-old *Albizia lebeck* plantations in Puerto Rico (7.71 Mg ha^{-1}) (Parrotta, 1992).

The results of this study show: (1) the capacity of these logged *Pinus* sites composed of few species to attract both zoochorous and anemochorous plant species (Schlawin and Zahawi, 2008; Zahawi et al.,

Table 2

Life forms and species mode dispersion in percentage (means ± S.E) of each vegetation type. The means identified with the same letter are the lines representing statistically homogeneous groups at a 5% probability level according to the Newman-Keuls test. Log: Pine Logging; C: Cultivation, Ab: Abandonment.

Life forms Dispersal mode	Cassava crops (Log + C)	Fallows (Log + C + Ab)	Post-logging regrowth (Log + Ab)	<i>P</i> -value
Trees	00.0 ± 0.0a	15.6 ± 6.5a	35.0 ± 12.2b	< 0.0001
Shubs	00.0 ± 0.0a	27.3 ± 8.1b	23.7 ± 9.9b	< 0.0001
Grass	97.5 ± 7.9c	52.1 ± 11.8b	28.6 ± 19.6a	< 0.0001
Lianas	2.5 ± 1.9a	5.0 ± 4.1a	12.7 ± 7.7b	< 0.0051
Anemochorous	79.3 ± 6.8c	60.9 ± 12.7b	35.7 ± 11.9a	< 0.0001
Zoochorous	19.0 ± 5.2a	34.0 ± 10.5b	50.3 ± 9.1c	< 0.0001
Barochorous	1.7 ± 5.3a	5.1 ± 5.3a	14.0 ± 9.7b	< 0.002

2013; Traverset et al., 2014), (2) Malagasy forest plant species can spread outside forests, and this despite a limited community of seed dispersing animals (Goodman and Ganzhorn, 1997), and (3) the capacity of these forest species to grow in more or less unfavourable conditions to start a diversified forest succession dynamic. In effect, Parrat (1966) noted the negative features of the physical and chemical characteristics of the soil (shallow soil with pseudo-concretions, deficient in phosphorous and exchangeable bases) of the Androy *Pinus* plantation schemes studied here. The diversity of forest species observed in this regrowth is partially related to their proximity to seed sources such as

Table 1

Diversity index, densities and biomass of vegetation groups (means ± S.E). The means identified with the same letter are the lines representing statistically homogeneous groups at a 5% probability level according to the Newman-Keuls test. Log: Pine Logging; C: Cultivation, Ab: Abandonment.

Vegetation type	Cassava crops (Log + C)	Fallows (Log + C + Ab)	Post-logging regrowth (Log + Ab)	<i>p</i> -value
Species richness	6 ± 1.89a	29 ± 6.40b	33 ± 9.00b	< 0.001
Shannon index	1.46 ± 0.23a	3.31 ± 0.78b	4.01 ± 0.67b	< 0.001
Evenness index	0.59 ± 0.06a	0.66 ± 0.16a	0.80 ± 0.10b	< 0.001
Tree density (N ha ⁻¹)	297 ± 68b	492 ± 212b	6843 ± 2276.8b	< 0.001
Above-ground biomass (Mg ha ⁻¹)	2.02 ± 0.13a	2.73 ± 0.24a	17.06 ± 0.02b	< 0.001
Below-ground biomass (Mg ha ⁻¹)	0.91 ± 0.02a -	3.10 ± 0.71a	11.60 ± 1.40b	< 0.004
Total biomass (Mg ha ⁻¹)	2.93 ± 0.27a -	5.83 ± 1.5a	28.66 ± 5.67b	< 0.000

Table 3
Trees density of the native species on the different plantations studied.

Sites	Altitude, rainfall and annual temperatures	Type of plantations (age)	Tree density D (N ha ⁻¹)	Sources
Madagascar 21°23'S–47°18'E	1000–1200 m	<i>Pinus patula</i> (35)	6843	This study Randriambanona (2010)
	1370 mm 17.7 °C	<i>Acacia dealbata</i> (80)	7273–11,169	
Uganda 0°13'–0°41'N 30°19'–30°32'E	1250 m	<i>Cupressus lusitánica</i> (27)	2170	Kasenene (2007)
	1740 mm	<i>Pinus caribaea</i> (27)	2309	
	–	<i>Eucalyptus</i> sp. (27)	1513	
Ethiopia 7°13'N 38°37'E	2100–2700 m	<i>Pinus patula</i> (10)	2325	Senbeta et al. (2002)
	1250 mm	<i>Pinus patula</i> (21)	3750	
	20 °C	<i>Pinus patula</i> (28)	2525	
Ethiopia 7°6'N 38°37'E	1800–2100 m	<i>Pinus patula</i> (16)	4495	Yirdaw (2001)
	1200 mm	<i>Cupressus lusitánica</i> (14–16)	8218	
	19–25 °C	<i>Grevillea robusta</i> (14–15)	5470	
	–	<i>Juniperus procera</i> (16)	5498	
Puerto Rico 18°27'N 66°10'O	–	<i>Leucaena leucocephala</i> (4,5)	9500	Parrotta (1995)
	1600 mm	<i>Casuarina equisetifolia</i> (4,5)	7100	
	23.8–29.4 °C	<i>Eucalyptus robusta</i> (4,5)	4800	
	–	<i>Eucalyptus</i> + <i>Leucaena</i> (4,5)	6350	
	–	<i>Casuarina</i> + <i>Leucaena</i> (4,5)	8300	
Hong-Kong 22°08'N 113°49'E	–	<i>Acacia confusa</i> (15–35)	9031	Lee et al. (2005)
	2616 mm	<i>Lophostemon cofertus</i> (25–35)	9094	
	16.9–28.8 °C	<i>Melaleuca quinquenervia</i> (23–30)	10,000	
Sri-Lanka 6°21'–6°27'N 80°21'–80°38'E	210–800 m	<i>Pinus caribaea</i> (22–28)	358–2828	Shibayama et al. (2006)
	3600–6000 mm	–	–	
	25 °C	–	–	

the “mature” forest (less than one km), the existence of shred forest, the presence of extensive post-agricultural forest regrowth rich in species (Randriamalala et al., 2015), and the presence of numerous isolated trees and copses which contribute to the spatial heterogeneity of the landscape and thus promote fluxes of fruit-eating animals dispersing seeds (Fournier et al., 2001; Martin et al., 2009, 2012). These heterogeneous landscapes composed of numerous and diverse wooded areas (Martin et al., 2012) are important seed sources and are decisive in the evolution of the vegetation beyond the young stages. Indeed, the frugivorous forest species present in the landscape were found to occupy almost exclusively areas with trees because they remain highly dependent on the arboreal structures distributed in the landscape, as has been demonstrated in several studies elsewhere (De Clerck et al., 2010; Harvey et al., 2006; Söderström et al., 2003). These structures, including *Pinus* plantation regrowth, may thus also serve as stepping stones, refuges and complementary habitats for birds and other species fluxes in the agricultural mosaic (Fischer and Lindenmayer, 2002; Harvey et al., 2006; Manning et al., 2006). These fluxes are what largely determine the nucleation observed (Yarranton and Morrison, 1974).

4.2. The effect of silvicultural and agricultural practices on regrowth

The cultivation of *Pinus* regrowth after logging modifies the structure and composition through clearing, which periodically eliminates the present vegetation, possible tillage that can destroy stumps and shoots, and the repeated burning of preceding crops (Randriamalala et al., 2007, 2012). Compared to the other ecological variables (slope and topographic position), silvicultural and agricultural practices variables (number of successive fires since first clearing, crop-fallow cycle number and tillage regime) are the main drivers of this area's vegetation dynamics.

These results corroborate those obtained in the same study area by Randriamalala et al. (2012) and by Randrianarison et al. (2015) in post-farming forest regrowth that follows slash-and-burn agriculture in natural forests. Soil variables have only a slight influence on the post-crop regeneration dynamics (Randriamalala et al., 2007). Likewise, Pfund (2000) obtained the same results on the same type of tropical

rain forest in Beforona further north in Madagascar. These studies also indicated that environmental factors such as slope, altitude, exposure, and topographical position had a weak influence on regeneration dynamics.

Agricultural practices reduced species diversity (S and H'), especially for woody species (Mitja and Puig, 1991). Furthermore, the effect of fire, which can produce temperatures of up to 310 °C on the surface of the soil, also contributes to the reduced diversity and abundance of the seed bank in the soil on the cultivated plots (Uhl and Saldarriaga, 1987; Tesfaye et al., 2004). The values of the diversity index gradually increase as the vegetation is reconstituted thanks to the establishment of pioneer species generated by the weed plant potential that adds itself to the soil seed bank (Lepart and Escarre, 1983; Randriamalala et al., 2015). This is enabled by the presence and fluxes of fruit-eating forest birds and bats in these cultivated areas, *Pinus* plantations and mature forests (Martin et al., 2009, 2012, Picot et al., 2007).

Likewise, the total plant biomass values of herbaceous regrowth where tillage and successive fires have destroyed woody plants are five times smaller than those of pre-forest regrowth, as other authors have shown as in Floret and Pontanier (1982). Cultivated fields and young herbaceous natural regrowth are dominated by a large number of anemochorous species (79% of species), while zoochorous plant species are more developed in post-logging woody regrowth (50% of species). Guariguata and Pinard (1998) reported that the wind can move seeds 100 m or more from the seed source. Cultivated fields thus are open spaces favouring the establishment of anemochorous pioneer species which are spread efficiently and which constitute the first stages of the plant succession (Carrière et al., 2002; González-Tagle et al., 2008). Longer-lived pioneer species, particularly those spread by frugivorous animals, then establish themselves thanks notably to the soil seed bank (Randriamalala et al., 2015).

The development of trees and shrubs in fallows and post-logging plots may attract seed dispersers (Martin et al., 2009, 2012) and favour the installation of zoochorous, and, to a lesser extent, barochorous species in such plots.

4.3. Native vegetation regeneration on *Pinus* plantations

The characterization of regrowth after disturbance (logging and agriculture) enabled a description of three vegetation types that are different in terms of diversity, structure and species composition. The changes observed over the course of the plant succession are floristic and physiognomic. The considerably reduced number of species of cassava plots (Log + C) follows agricultural practices and thus the procedures strongly influence the succession (Mitja and Puig, 1991; Carrière et al., 2002; Styger et al., 2009; Randriamalala et al., 2007). The fallows (Log + C + Ab) correspond to two-year old fallows that follow two crop cycles (this is the maximum number of crop cycles recorded during the investigation). The herbaceous cover is different and dominated by annual ruderal and heliophilous species cited previously which are typical of the area's post-agricultural regrowth (Randriamalala et al., 2007), but also by herbaceous pioneer species and shrubs that have just established themselves (*Anthospermum emir-nense*, *Oldelandia herbacea*, *Psiadia sabviaefolia*, *Helichrysum attenuatum*). These ruderal species were already present when the plot was cultivated in the form of weeds or in the soil seed bank (Randriamalala et al., 2015). These short-cycle species are then gradually replaced by pioneer but perennial species such as *Chassalia bojeri* and *Schefflera* sp. From a physiognomic and species composition perspective, the plant succession then evolves towards a young shrubs stage (Randriamalala et al., 2007). The third type, post-pinus logging (Log + Ab), corresponds to tree formations that develop over the 10 years following the logging of the *Pinus* plantation. These are complex vegetation types with several strata as is the case for post-agricultural regrowth of this age in Madagascar (Styger et al., 2009; Randriamalala et al., 2007). These three vegetation types, their composition and their physiognomy, correspond to different stages of post-agricultural vegetation successions such as described in the study area and elsewhere in Madagascar (Styger et al., 2009; Randriamalala et al., 2007). These apply to herbaceous formations (crop and herbaceous post-crop regrowth) up to shrubby and woody formations (pre-forest regrowth). If one interprets the variations observed around this schema according to land use modes, it is the intensity of agricultural use, and particularly the duration of crop (whence the crucial role of crop history) and tillage, which are the most unfavourable factors for the reconstitution of pre-forest vegetation (Randriamalala et al., 2012; Randrianarison et al., 2015) and thus condition the characteristics and future of plant successions in the area. In other words, the vegetation of these regeneration foci in the *Pinus* plantations subjected to recurrent disturbances, such as cropping and with a brief fallow period (Randriamalala et al., 2007, 2012), probably would evolve towards degraded, pseudo-steppes like herbaceous formations with few species. This type of vegetation dynamic is comparable to that observed by Pfund (2000), Styger et al. (2009) and Randriamalala et al. (2007) in forest fallows of the Malagasy highlands.

5. Conclusion

The results obtained made it possible to confirm the role of logged exotic species plantation foci in promoting the dispersion, installation and gradual regeneration of native, indeed endemic, forest species. The openings caused by disturbances enabled native species to install themselves within several years, develop, and result in species-rich formations. The important extent (in duration and intensity) of the disturbance caused by putting land under cultivation appears to be decisive in determining the status of post-disturbance and post-agricultural vegetation on these plantations. Weak anthropogenic pressure leads to more diverse and complex pre-forest regrowth similar in terms of structure and composition to secondary forests. This capacity of native species to regenerate in reforested areas could be used to promote the afforestation of species-poor grasslands and forest succession dynamics in the numerous former plantations of exotic species in

Madagascar (*Acacia* spp., *Eucalyptus* spp., *Pinus* spp.), but also to imagine new avenues for assisted forest regeneration in degraded Malagasy forest areas. This study also contributes to a better understanding of the conditions for maintaining biodiversity in the many post-logging and post-agricultural regrowth and rural landscapes on the edges of Malagasy forests.

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