



Vegetation dynamics in a corridor between protected areas after slash-and-burn cultivation in south-eastern Madagascar

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ABSTRACT

Slash-and-burn cultivation is a major cause of deforestation in Madagascar, and abandonment leads to the secondary vegetation dynamics, i.e. colonization by herbaceous vegetation, shrubs and trees. The study was conducted in south-eastern Madagascar in a steep transition zone along an altitudinal and a sharp precipitation gradient between a high altitude rainforest and a lowland dry tropical forest. The restoration of gaps created by abandoned fields in this narrow, winding corridor could be essential to maintain connectivity between two areas (areas 1 and 2) of Andohahela National Park. Prior to implementing restoration, baseline ecological information is needed on the reference ecosystem and vegetation resilience must be studied to identify restoration needs. This study aims to (1) assess whether cultivation practices (irrigated rice vs. cassava, maize and sweet potato) influence vegetation dynamics after abandonment; (2) study vegetation dynamics and soils over time since abandonment, and (3) compare secondary forest vegetation and soils with those of mature forest patches. Surveys of vegetation and soil were conducted in 26 secondary forest patches abandoned from 3 to >25 years (synchronic approach) and in 19 adjacent mature forest patches (controls). No relationship between age of abandonment and vegetation species richness, composition or structure was found, but clear differences were detected between secondary and mature forest patches. Secondary forests are not colonized by species from mature forests, but instead their vegetation dynamics appear to lead to the establishment of thorny thickets dominated by *Mimosa delicatula*, which is absent from the mature forest.

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1. Introduction

Contemporary global environmental changes, largely the result of human activities, include climate change and habitat fragmentation (Vitousek, 1994; Willis et al., 2008). Their combined actions are major threats to biodiversity and their consequences are potentially disastrous (Travis, 2003). Tropical forests, which contain a significant portion of global biodiversity, are cleared in rural areas for farming, industry or mining (Aide et al., 2000). The island of Madagascar, situated almost entirely within the tropics, is widely

recognized as one of the eight major biodiversity hotspots and as a global conservation priority (Myers et al., 2000). It has an exceptionally high level of endemism (ca. 90% at the species level; Phillipson et al., 2006) resulting from over 100 million years of evolution in tectonic isolation. The diversification of this biota has been driven in part by a wide range of climates and varied topography, and is reflected in vegetation ranging from perhumid forests to dry spiny dry bush land (Hannah et al., 2008), all of which are threatened by human activities. Forest cover decreased by almost 40% between 1950 and 2000 (Harper et al., 2007), and today primary vegetation covers less than 10% of the land area and is highly fragmented in most parts of the island. The main causes of deforestation are slash-and-burn cultivation and unsustainable exploitation for charcoal production, firewood and timber extraction (Casse et al., 2004).

Habitat destruction resulting from deforestation threatens the survival of species and reduces biodiversity. This process also creates forest fragments that are often too small to maintain viable

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populations, and it increases edge effects at the interface between intact and cleared habitat (Aide et al., 2000; Köhler et al., 2003; Urech et al., 2011). Fragmentation also impedes the dispersal of species (Andrén, 1994) and therefore reduces their potential for adaptation to future climate change (Travis, 2003; Hannah et al., 2008; Hoegh-Guldberg et al., 2008). Southern Madagascar, which is already the driest part of the island, will experience the greatest increase in temperatures (2.6 °C) as well as a decrease in precipitation in the coming decades, a prediction that will have significant biological implications in a landscapes that is heavily exploited and fragmented, and therefore more vulnerable to drought (Hannah et al., 2008).

One of the key elements in conservation efforts involves re-establishing connectivity between forest fragments and increasing their cover in order to improve landscape resilience. This could be accomplished in part by expanding the current protected areas network to ensure full inclusion of biodiversity and to mitigate against further disturbance (Aide et al., 2000; Lamb et al., 2005). Depending on the nature and degree of degradation, the process of secondary succession could offer an effective strategy for restoration of tropical forests (Aide et al., 2000). Forest patches that still contain moderate levels of biodiversity and a combination of residual trees, an abundant seed bank, and adequate biotic and abiotic conditions could facilitate re-colonization (Lamb et al., 2005). However, this process is often impeded because the landscape is overly fragmented and there are too many barriers to species dispersal and establishment (Zimmerman et al., 2000) for natural regeneration to take place fast enough to address conservation issues.

Changes in land use practices have also resulted in an increase in abandoned cleared lands, which present another opportunity for ecological restoration (Anderson, 1995; Aide et al., 2000). These areas can play an important role for conservation (Dobson et al., 1997; Young, 2000) by contributing to the reconnection of isolated patches of habitat and the creation of corridors and stepping stones, thus facilitating the dispersal of plant and animal species (Anderson, 1995).

In this context, an ecological restoration project is now being designed at Andohahela National Park located in south-eastern Madagascar. The target is located in a transition zone across a sharp ecotone between the two largest parcels of the park, one with humid forest and the other with dry forest and spiny bush. The project aims to restore the highly fragmented corridor linking these two parcels and retain the potential for migration in response to climate change.

Prior to implementing the project, restoration needs must be identified by: (i) collecting baseline ecological information on the reference ecosystems; (ii) studying the resilience of the impacted areas to be restored; and (iii) identifying and testing appropriate restoration actions (Hobbs, 2007). As part of this process, the present study aims to characterize the dynamics of secondary vegetation that has become established in the corridor (i.e. colonization by herbaceous vegetation, shrubs and trees) in areas that were cultivated and are now abandoned. More specifically, this work aimed to: (1) assess whether cultivation practices (crop grown, i.e. irrigated rice or cassava, maize and sweet potato) influenced vegetation dynamics after abandonment; (2) study vegetation dynamics and soils over time, cultivation abandonment ranging from 3 to >25 years (up to 33 years) and (3) compare secondary forest vegetation and soils with those of mature forest patches.

2. Materials and methods

2.1. Study site

The present study was carried out near Andohahela National Park, on the steep western, leeward slope of the Anosy Mountains,

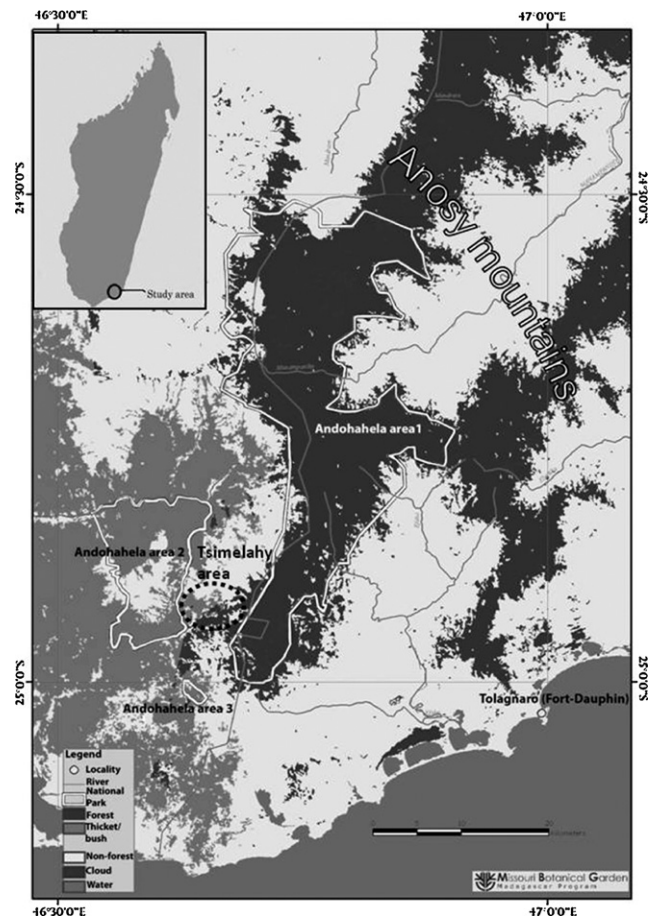


Fig. 1. Map of south-eastern Madagascar showing the 3 areas of Andohahela National Park and the location of the Tsimelahy area (ellipse with dotted lines) where the study was conducted. Rainforest is indicated in dark gray and lowland dry tropical forest in light gray.

in south-eastern Madagascar (24°30'S–25°02'S, 46°32'E–46°54'E). At higher elevation in the east, adjoining one of the park's three separate areas, the climate is tropical sub-humid with rainforest vegetation (area 1), whereas at lower elevation in the west, adjacent to another parcel, the climate is sub-arid with dry forest vegetation (areas 2 and 3). The study site is located between areas 1 and 2 characterized by a transition climate, and is occupied by extensive farmland and two highly fragmented forest corridors whose vegetation reflects the transition between rainforest and dry forests. The work reported here was carried out within the southern forest corridor of Tsimelahy (~2800 ha; 24°56'30.98"S, 46°38'02.64"E) located 40 km NW of the town of Tolagnaro (Fort Dauphin) (Fig. 1). The area has a mosaic of vegetation types that reflects recent land-use practices, including residual mature forest patches, farmland, and abandoned slash-and-burn fields where zebu cattle occasionally graze.

2.2. Choice of secondary forest patches

Twenty-six secondary forest patches were selected using stratified random sampling in order to provide a representative sample of abandoned fields in the corridor (see Appendix 1 in Supplementary Material). Information on the cultivation trajectory of each secondary forest patch, viz. the type of cultivation, time since clearing, time since abandonment, and reason for abandonment (decrease crop production, death of the owner, interest in other crops, etc.), was obtained by interviewing owners and/or local guides. All selected plots had undergone a single clearing followed

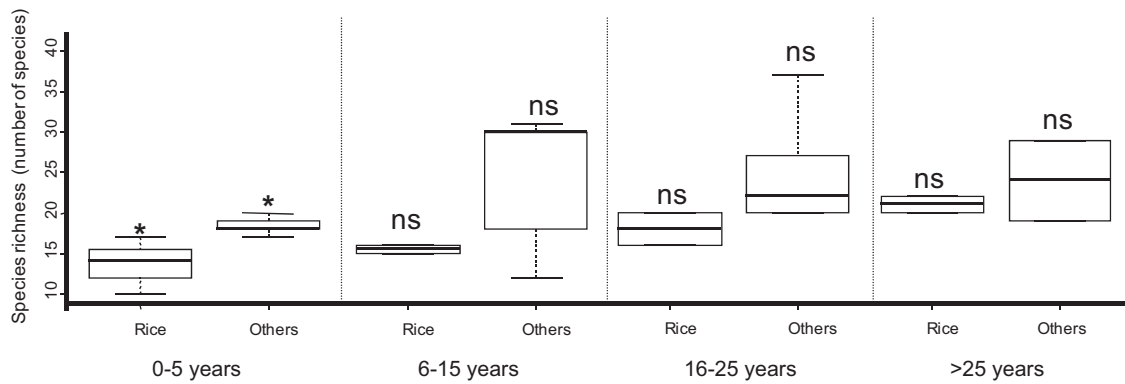


Fig. 2. Boxplots performed on species richness (upscaled to an area of 1600 m²) according to past cultivation and age since abandonment (Mann–Whitney $W=0.5$, $p < 0.05$). Boxes represent 25–75 percentiles, lines within boxes represent the median value, bars indicate the 90th and 10th percentiles, and points are outliers. * indicates a statistically significant difference ($p < 0.05$); ns = non significant.

by several cycles of cultivation without following before complete abandonment. Three complementary approaches were used, as follows:

- 1) In order to assess whether cultivation practices (i.e. crop grown) influenced vegetation dynamics after abandonment, vegetation surveys were carried out on two types of secondary forest patches: abandoned terraced irrigated rice paddies and abandoned fields used for other crops (principally cassava, maize and sweet potato, often cultivated together in a given field) (Table 1).
- 2) In order to study vegetation dynamics using a synchronic method, secondary forest patches of various ages, ranging from 3 to >25 years (up to 33 years) since abandonment, were selected (Table 1).
- 3) In order to compare secondary forest vegetation with that of mature forest, surveys were also conducted in patches of mature forest located adjacent to (i.e. <300 m from) the studied secondary forest patches. For some secondary forest patches situated relatively close to one another, a single mature forest patch was surveyed. A total of 19 mature forest patches were thus sampled; all together 45 forest patches were thus sampled: 26 secondary forest patches and 19 mature forest patches (see Appendix 1 in Supplementary Material).

2.3. Sampling procedures

2.3.1. Vegetation sampling

Between mid-February and mid-March 2009, for each forest patch, plant identifications and measurements were carried out in various sized plots, depending on the DBH (diameter at breast height, i.e. 1.30 m above ground) of the tree and shrub species present. Within each plot, all living individuals were identified, their DBH measured using a Vernier caliper, and their cover (m²) and height visually estimated. For multi-stemmed individuals (from re-sprouting or suckering), the number of stems was assessed and the diameter of the bigger stem was considered. Basal area was then calculated for all species using all DBH values for this species in a given plot. Individuals with a DBH ≥ 10 cm were recorded in

a single 40 m \times 40 m plot in each forest patch; plants with a DBH ≥ 5 cm but <10 cm were recorded in one 20 m \times 20 m plot, and individuals with a DBH between 1 and 4.9 cm were recorded in a single 10 m \times 10 m plot. Two plots of 2.5 m \times 5 m within each patch were used to record plants with a DBH <1 cm and height >1.30 m; each plant was identified and measured, and the cover of individuals with a height <1.30 m was estimated.

2.3.2. Soil sampling

One soil sample was taken from each of the 45 patches of secondary and mature forest in order to study physico-chemical properties. Each sample consisted of 5 pooled sub-samples randomly taken from within the 40 m \times 40 m plot, collected in the first five centimeters of soil (i.e. below the litter layer). The samples were dried and analyzed at the FOFIFA soil science laboratory in Antananarivo. The following parameters were measured: pH, Kjeldahl nitrogen (%), phosphorus (Bray II), carbon (%), the C/N ratio, exchangeable aluminum (mequiv./100 g), exchangeable potassium (mequiv./100 g), clay (%), silt (%) and sand (%).

2.4. Statistical analysis

To study the effect of past cultivation on species richness, basal area, tree density, number of stems per tree and soil parameters, Mann–Whitney tests were performed on data for each age class since abandonment. To investigate the possible effect of the age since abandonment on these same parameters and on average height in secondary and mature forest patches, Kruskal–Wallis tests were performed followed by Mann–Whitney tests with a Bonferroni p -value adjustment if a significant difference was found. The Sørensen similarity index was used as a qualitative measure of β diversity. This index was calculated to examine the floristic similarity among mature forest patches, then among secondary forest patches, and finally between mature and secondary forest patches. Differences in Sørensen similarity indices were assessed using Kruskal–Wallis tests followed by Mann–Whitney tests with a Bonferroni p -value adjustment if a significant difference was found.

Table 1

Numbers of secondary forest patches of various ages since abandonment according to cultivation practice (other = cassava, maize, sweet potato, often cultivated together in a field), $n = 26$.

	Age since abandonment (years)			
	0–5	6–15	15–25	>25
Number of forest patches originally cultivated with rice	3	2	2	2
Number of forest patches originally cultivated with other crops	5	5	5	2

Multivariate analyses were conducted to examine the complex relationships between species and their environment. PCAs (principal component analysis) were performed on species percentage cover for plots of different sizes in order to analyze the variation in composition and physiognomy of the vegetation independently for large trees (<10 cm in 40 m × 40 m plots), medium-sized trees (between 10 and 5 cm in 20 m × 20 m plots), small trees (between 4.9 and 1 cm in 10 m × 10 m plots) and shrubs (>1 cm in the two 2.5 m × 5 m plots). Then, co-inertia analysis was run on species presence/absence data for all patches and all plots to assess changes in species composition and environmental features and to identify possible successional patterns. Environmental characteristics taken into account include pH, N, P, C, C/N, aluminum, potassium, clay, silt, sand, percent cover of litter, bare soil, dead wood, moss and rock, slope, and orientation. A Monte-Carlo permutation test (1000 permutations) was used to verify the significance of the relationships.

To study possible differences in physicochemical properties between mature and secondary forest patches, Mann–Whitney tests were performed on soil data. All statistical tests were done using R software (The R Foundation for Statistical Computing, version 2.10.1) with packages *ade4* and *stat*.

3. Results

3.1. Succession on abandoned fields with different cultivation practices

Abandoned rice paddies tended to have lower mean species richness than abandoned areas where other crops were grown; this difference was only significant for the youngest secondary forest patches (0–5 years after abandonment) with 13 ± 3 and 18 ± 1 species on average, respectively ($W = 0.5$, $p < 0.05$, Fig. 2). There was no significant effect of past cultivation on variables reflecting vegetation structure (tree density, basal area, and number of stems per tree) or on soil variables except pH which was lower on abandoned rice paddies ($W = 22.5$, $p < 0.01$).

3.2. Structure of secondary and mature forests

The average basal area increased with the age since abandonment ($\chi^2 = 34.9$; $p < 0.001$; Fig. 3). The youngest secondary forest patches had a lower average basal area (0.90 ± 0.32 m²/ha; $p < 0.05$) than the older ones (6–15 years: 2.78 ± 1.04 m²/ha; 16–25 years: 4.86 ± 1.97 m²/ha and >25 years: 2.40 ± 0.52 m²/ha). Basal areas in all secondary forest patches (3.47 ± 1.44 m²/ha) were significantly lower than in mature forest patches (16.42 ± 3.05 m²/ha).

Average tree densities in secondary forest patches of various ages since abandonment were not significantly different from one another although they tended to increase (0.27 ± 0.17 trees/m²) but were significantly lower than in mature forest patches (1.15 ± 0.18 trees/m²; $\chi^2 = 27.5$; $p < 0.001$).

The average numbers of stems per tree in secondary forest patches did not vary significantly with age since abandonment although they tended to decrease (4.72 ± 0.87 stems/tree; Fig. 4); however they were significantly higher compared to the numbers observed in mature forest patches (1.79 ± 0.24 stems/tree; $\chi^2 = 27.5$; $p < 0.001$). Similarly, average tree height in secondary forest patches of various age since abandonment was not significantly different between one another although they tended to increase (3.9 ± 1 m; Fig. 5); however it was significantly lower than in mature forest patches (5.5 ± 0.7 m; $\chi^2 = 20.6$; $p < 0.001$).

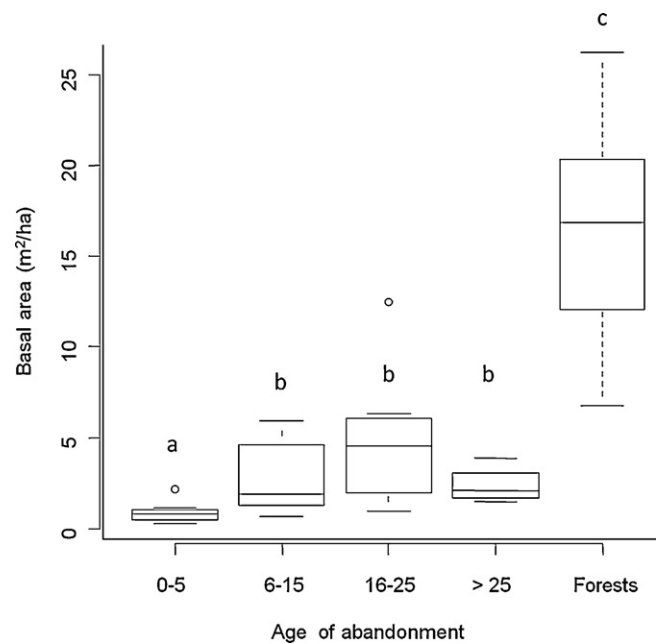


Fig. 3. Boxplots performed on the basal area (upscaled to an area of 1600 m²) (grouped in four classes of age since abandonment, 0–5 years: $n = 8$; 6–15 years: $n = 7$; 15–25 years: $n = 7$; >25 years: $n = 4$) and mature forest ($n = 19$) (Kruskal–Wallis $\chi^2 = 34.9$; $p < 0.001$). Boxes represent 25–75 percentiles, lines within boxes represent the median value, bars indicate the 90th and 10th percentiles, and points are outliers. Letters (a, b, c) indicate statistically significant differences ($p < 0.05$).

3.3. Secondary and mature forest composition

Although the number of species in each forest patch was relatively small, a total of 284 species in 64 families were recorded across all sites, 210 of which were found in mature forest patches and 181 in secondary forest patches (107 species occurred in

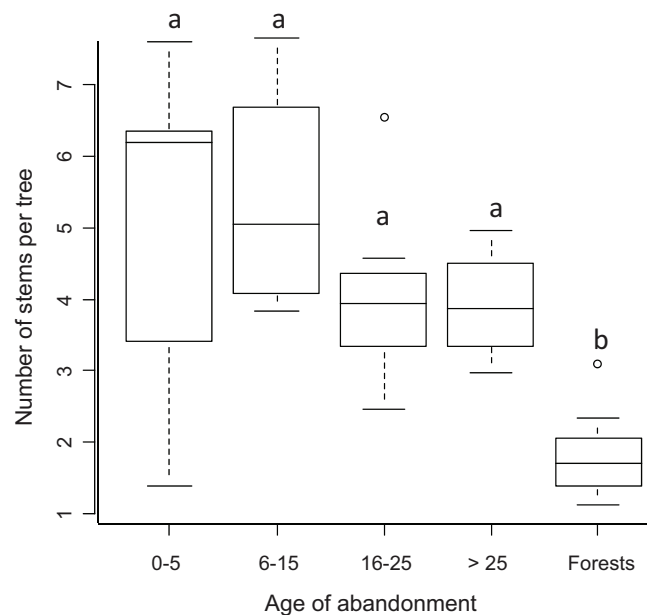


Fig. 4. Boxplots performed on the number of stems per tree (upscaled to an area of 1600 m²) grouped in four classes of age since abandonment (0–5 years: $n = 8$; 6–15 years: $n = 7$; 15–25 years: $n = 7$; >25 years: $n = 4$) and mature forest ($n = 19$) (Kruskal–Wallis $\chi^2 = 27.5$; $p < 0.001$). Boxes represent 25–75 percentiles, lines within boxes represent the median value, bars indicate the 90th and 10th percentiles, and points are outliers. Letters indicate a statistically significant difference ($p < 0.05$).

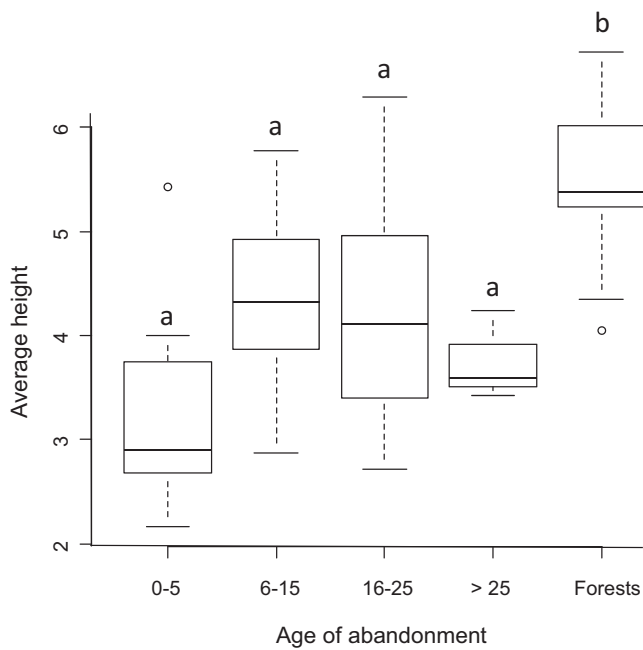


Fig. 5. Boxplots performed on tree height (upscaled to an area of 1600 m²) grouped in four classes of age since abandonment (0–5 years: $n=8$; 6–15 years: $n=7$; 15–25 years: $n=7$; >25 years: $n=4$) and mature forest ($n=19$) (Kruskal–Wallis $\chi^2=20.6$; $p<0.001$). Boxes represent 25–75 percentiles, lines within boxes represent the median value, bars indicate the 90th and 10th percentiles, and points are outliers. Letters (a, b) indicate statistically significant differences ($p<0.05$).

both, 103 species occurred only in mature forest patches and 74 only in secondary forest patches). Species richness in secondary forest patches increased with age since abandonment ($\chi^2=31.3$; $p<0.001$; Fig. 6). Secondary forest patches abandoned for 0–5 years and 6–15 years had a similar low level of richness (19 ± 3 species), whereas patches abandoned for more than 15 years had

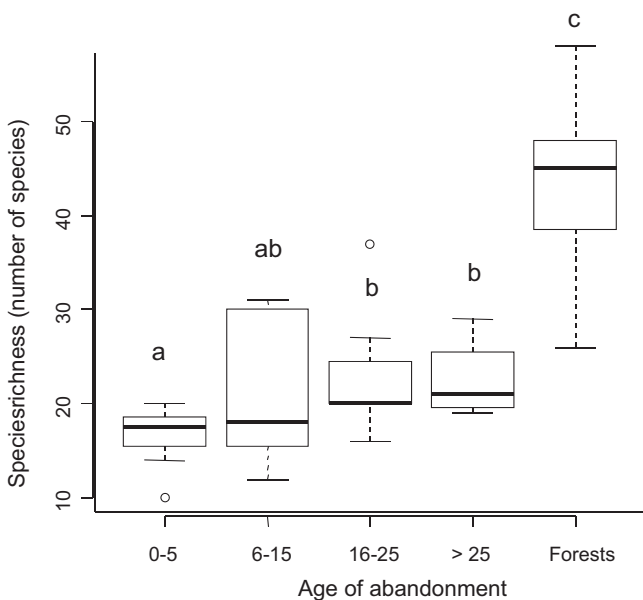


Fig. 6. Boxplots performed on species richness (upscaled to an area of 1600 m²) grouped in four classes of age since abandonment classes (0–5 years: $n=8$; 6–15 years: $n=7$; 15–25 years: $n=7$; >25 years: $n=4$) and mature forest ($n=19$) (Kruskal–Wallis $\chi^2=31.3$; $p<0.001$). Boxes represent 25–75 percentiles, lines within boxes represent the median value, bars indicate the 90th and 10th percentiles, and points are outliers. Letters (a, b, c) indicate statistically significant differences ($p<0.05$).

higher species richness (23 ± 3 species); the difference was significant between the 0–5 and >15 year classes. Species richness on secondary forest patches was significantly lower than on mature forest patches (respectively 22 ± 6 and 43 ± 8 species on average).

The floristic composition of secondary forest patches differed significantly from that of mature forest patches (β diversity = 0.13 ± 0.10 ; $\chi^2=298$; $p<0.001$). The latter were more similar among themselves than were the secondary forest patches (respectively β diversity = 0.35 ± 0.12 and β diversity = 0.20 ± 0.11 ; $p<0.001$). The PCAs run on large trees (40 m \times 40 m plots) and on medium-sized trees (20 m \times 20 m plots) showed that the composition of mature forest and secondary forest patches was different. On axis 1 (14% and 24.4%, respectively) mature forest patches were correlated with the presence of *Vepris calcicola* and on axis 2 (11.8% and 11.9%, respectively) secondary forest patches were characterized by *Mimosa delicatula*, an endemic thorny Fabaceae, and *Mangifera indica*. This means that the species composition of large trees (>10 cm) and medium-sized trees (between 5 and 10 cm diameter) was different in the mature forest and secondary forest patches. The PCAs run on small trees (10 m \times 10 m plots) and on shrubs (2.5 m \times 5 m plots) showed similar patterns. For small trees (10 m \times 10 m plots), secondary forest patches were again correlated with *M. delicatula* (axis 1: 14.7%) and mature forest patches with tree species at earlier stages of development (axis 2: 10.7%). For shrubs (2.5 m \times 5 m plots), secondary forest patches were characterized by *M. delicatula* (axis 1: 12.8%) and species found in disturbed areas, such as *Stachytarpheta jamaicensis*, *Catharanthus roseus* and *Psiadia altissima*. On axis 2 (10.6%) mature forest patches were characterized by many shrubs of the genus *Croton*.

Axis 1 (40.3%) of the co-inertia analysis opposed mature forest patches to secondary forest patches (Monte-Carlo permutation = 0.36; $p<0.05$; Fig. 7). Mature forest patches were correlated with several species, such as *Baudouinia fluggeiformis*, *Capurodendron mandrarensis*, *Commiphora humberitii*, *Coptosperma bernierianum*, *Diospyros danguyana* *Diospyros humberitiana*, *Erblichia integrifolia*, *Euphorbia leucodendron*, *Strychnos decaryi* and *V. calcicola*, and also with several soil variables, mainly C, litter, N, deadwood and Al. On the positive side of the axis, secondary forest patches were correlated with species such as *C. roseus*, *Crotalaria fiherenensis*, *Cynodon dactylon*, *Evolvulus elsinoides*, *Gagnebina commersoniana*, *Heteropogon contortus*, *M. indica*, *M. delicatula*, *Neostapfiella humberitiana*, *Ocimum americanum*, *P. altissima*, *Sida acuta*, *Sida rhombifolia*, *S. jamaicensis* and *Tamarindus indica*, and also with pH and bare soil. Axis 2 (12.9%) distinguished among different mature forest patches, some of which were correlated with species such as *Erythroxylum buxifolium*, *Leucaena leucocephala*, *Phyllarthron bernierianum*, and *Vaughania perrieri* and also with higher K more silt and north orientation. These were opposed to other mature forest patches that were correlated with species such as *Albizia gummifera*, *Alchornea* sp., *Brexia montana*, *Calantica cerasifolia*, *Crateva humblotii*, *Croton* sp., *Diospyros cupulifera*, *Diospyros quercina*, *Diospyros tropophylla*, *Doratoxylum stipulatum*, *Dracaena reflexa*, *Ecolium syringyfolium*, *Elaeodendron humberitii*, *Erythroxylum corymbosum*, *Plagioscyphus* sp. and *Psychotria aegialodes*, and with sand and P.

3.4. Soil characteristics

Mature forest soils had significantly higher levels of Al^{3+} (0.07 ± 0.02 mequiv./100 g, $W=71.5$, $p<0.001$), C ($3.6\pm 0.9\%$, $W=36$, $p<0.001$) and N ($0.3\pm 0.09\%$, $W=79$, $p<0.001$) than secondary forest patches (Al^{3+} 0.04 ± 0.02 , C 2.1 ± 0.5 , N 0.2 ± 0.005 , MO 3.6 ± 0.9). The C/N ratio was also higher in mature forests (12.4 ± 1.4 vs. 11.3 ± 2.4 , $W=151.5$, $p<0.05$). Secondary forest soils were less acidic (6.3 ± 0.2 vs. 5.9 ± 0.2 , $W=451.5$, $p<0.001$) and

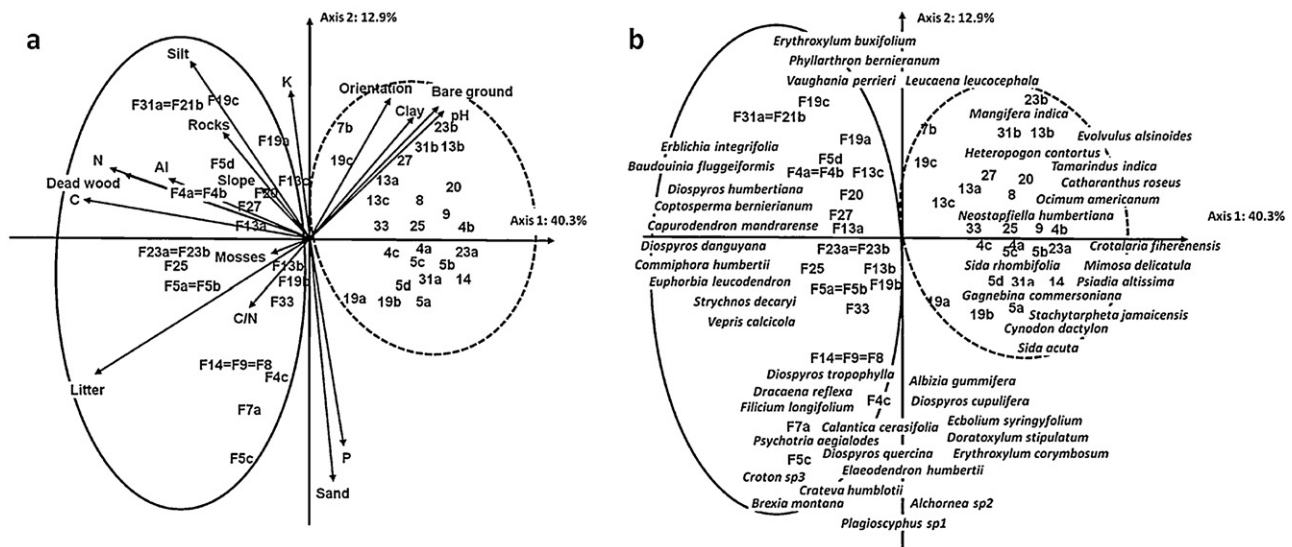


Fig. 7. (a) Environmental variables and sites, and (b) species and sites representations of co-inertia performed on the matrix of species in presence/absence (45 points \times 284 species) and the environmental variable matrix (45 points \times 17 variables) for secondary and mature forest patches. Only species that contribute most to the axes are indicated. The ellipses formed by solid lined group mature forest patches; those with dotted lines group secondary forest patches.

had less silt ($22.3 \pm 3.2\%$ vs. $24.7 \pm 2.9\%$, $W = 133.5$, $p < 0.01$). The P, K, clay and sand contents were similar in the two types of forest (P 10.6 ± 6.3 , K 0.7 ± 0.2 , clay 23.2 ± 3.1 , sand 53.4 ± 4).

4. Discussion

4.1. Soil characteristics

Mature forest has more litter and dead wood than secondary forest, and carbon and nitrogen contents are thus significantly higher, whereas secondary forest has less litter and more bare ground. Although the soils of secondary forest are less rich in carbon and nitrogen than those of mature forest, they remain relatively rich for tropical soils (FOFIFA soil science laboratory; Raharimalala et al., 2010).

4.2. Secondary and mature forest structure

Vegetation structure of secondary vegetation does not change with time since abandonment—up to 33 years in our study—but differs significantly from that of the mature forest. Despite a higher number of stems per tree in the secondary forest, basal area is much lower than in mature forest. This can be explained by higher tree density and tree size in mature forest, which is dominated by large trees, whereas secondary forest is dominated by forbs and bushy shrubs. Howorth and Pendry (2006), who worked on post-cultivation secondary succession for 35 years, observed that structural complexity (basal area, density, and height) increases during succession, with the oldest secondary forests having a physiognomy comparable to that of mature forest. Other authors (such as Lebrija-Trejos et al., 2008) have found that canopy height recovered up to 75% of the mean for mature forest in 13 years and that basal area had a slower recovery rate, reaching 60–89% of that of mature forest after 40 years. While both forest types are probably subjected to various kinds of disturbance (e.g. some zebu grazing, wood extraction for cooking and local house construction), the observed differences may be the result of succession having been slowed by preferential harvest in the secondary forest patches (Urech et al., 2011).

4.3. Richness and composition of secondary and mature forest

Species richness increases slightly with the age since abandonment, an observation that corroborates many other studies showing this characteristic successional process over various time frames (20 years: González-Iturbe et al., 2002; 23 years: Randriamalala et al., 2007a; 35 years: Howorth and Pendry, 2006; 50 years: Lee et al., 2002). By contrast, other authors have observed either no difference in the number of species at various ages since abandonment (Fukushima et al., 2008) or higher richness at intermediate successional stages (Aiba et al., 2001; Kalacska et al., 2004; Raharimalala et al., 2010), which is consistent with the intermediate disturbance hypothesis (Connell, 1978) because these stages may contain both pioneer species and species found in mature forest.

While species richness in later successional stages is similar following both types of cultivation (abandoned terraced irrigated rice paddies and abandoned fields used for other crops), as reported by Fukushima et al. (2008), species richness is lower early after abandonment (0–5 years) in abandoned rice paddies than in abandoned plots where other crops were grown. This may be due to slower colonization by pioneer species after the soil seed bank is destroyed by standing water in rice paddies (Randriamalala et al., 2007a). It may also be due to less favorable soil conditions for seedling development since zebu cattle are used to trample and loosen soil in paddies prior to planting and irrigation, and paddies are subjected to several crop cycles per year.

At our study site, species richness is higher in mature forest (210 species) than in secondary forest (181 species). This is not always the case, as species richness in disturbed forests can be equal to or higher than in undisturbed forests (Lewis, 2009). In our study many mature forest species are totally absent from secondary forest. In any case, Lewis (2009) concluded that richness metrics by themselves are not sufficient to represent anthropogenic changes in community organization, and he suggested that community structure and composition must be examined more thoroughly.

Species composition differs very clearly between mature and secondary forests at all life stages. Mature forests are mainly characterized by tree species linked to dry to sub-arid thickets and deciduous forests, with *V. calcicola* being a dominant

(Perrier de la Bâthie, 1950). Several tree species (*V. calcicola*, *C. bernierianum* and *Diospyros* species) characteristic of mature forests generally in Madagascar were found in all diameter classes within the mature forest plots we examined. These species thus appear to be present at all stages of tree development and indicate dynamic understory vegetation in mature forests. Patches of mature forest differed from one another in plant composition. Patches located higher on the altitudinal gradient and thus closer to the humid forest area 1 of Andohahela National Park are characterized by species such as *A. gummifera* and *D. reflexa* that are typical of more humid environmental conditions (Schatz, 2001).

By contrast, secondary forest patches are fairly similar to one another in species composition. They include herbaceous species growing in open field (*C. dactylon*, *H. contortus*, and *N. humbertiana*), wind-dispersed species, and cosmopolitan species found in disturbed environments. The latter species are adapted to the conditions found in the secondary forest at our study site primarily dominated by grasses, forbs and small shrubs, including *S. jamaicensis*, a common species throughout the corridor where we worked. This introduced Verbenaceae, widely distributed in tropical America and naturalized in Madagascar, is known to be toxic to livestock (Standley, 1920), and its high abundance in our plots could therefore reflect its unpalatability. Other characteristic species of secondary forest patches, such as *C. roseus* (Catalogue of the Vascular Plants of Madagascar, 2011a), *P. altissima* (Humbert, 1960) and *O. americanum* (Hedge et al., 1998), are common species in disturbed habitats. The pioneer species *P. altissima*, a small shrub endemic to Madagascar, and *S. rhombifolia*, have been reported to establish quickly from seeds in early successional stages after clearing, mainly because they are anemochorous (Randriamalala et al., 2007b, 2012; Styger et al., 2007). *M. delicatula*, a thorny shrub (Catalogue of the Vascular Plants of Madagascar, 2011b) that is perhaps the most characteristic element in secondary forest, occurs in all stages of the dynamics, and individuals can grow to be quite large in size (to ca. 8 m tall). The ubiquity and frequency of this species can be explained at least in part by its thorny nature, which reduces or prevents consumption by cattle in favor of more palatable species. The mango (*M. indica*) and the tamarind tree (*T. indica*), two of the very few large tree species characteristic of secondary forest, are planted in fields and pastures as a fruit tree (Kull et al., 2012) and to provide shade for both people and livestock, and thus remain long after abandonment. It has been suggested that they may play a key role in attracting animal dispersers and stimulating zoochorous seed dispersal (Carrière et al., 2002; Martin et al., 2009, 2012). Some other species with fleshy or pulpy fruits, such as members of the genus *Diospyros*, occur in mature forests and are primarily dispersed by animals (Schatz, 2001), but these are absent from secondary forest and are rare elsewhere in the corridor, suggesting that dispersers are few in number and/or diversity.

Several biotic and abiotic factors may influence the dispersal, establishment and development of forest species (Holl et al., 2000). In the area where our study was conducted, a number of factors may have impacted forest regeneration in secondary forest patches, including landscape fragmentation, low disperser abundance, soil compaction by cattle (Martínez and Zinck, 2004; Álvarez-Yépiz et al., 2008), the effects of grazing, the presence of *M. delicatula* (which probably lowers animal movement in older thickets that are impenetrable), and abiotic conditions related to an open canopy in younger patches (Holl, 1999; Zimmerman et al., 2000). The successful colonization of *M. delicatula* could inhibit the germination of light-demanding pioneer species, impeding establishment of the next stage of the succession and/or promoting the growth of shade-tolerant species characteristic of later stages but whose diaspores do not seem to be dispersed.

5. Conclusion

While dynamic processes could be expected to operate in secondary forest, no strong relation between species richness, structure, composition and age since abandonment was found at our study site. However, there were clear differences in all these parameters between secondary and mature forests. Secondary forests are dominated by *M. delicatula*, which is absent from mature forests, and secondary forest patches are not being colonized by species characteristic of mature forest. Our results suggest that the dynamics operating today in secondary forests are not leading toward mature forest but rather to the establishment of a thorny thicket dominated by *M. delicatula*.

Although the time span of the study is relatively short (max. 33 years since abandonment), ecological restoration appears to be a potential suitable tool for strengthening the tenuous connection that remains between the forested areas of Andohahela National Park. Further data need to be gathered on the seed bank and seed rain in both mature and secondary forest as part of a broad ecological restoration study in order to determine the most effective levels for intervention and thereby develop an operational procedure that can be implemented to ensure continued forest connectivity across this remarkable ecotone.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agee.2012.06.016>.

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