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Slow recovery of endangered xerophytic thickets vegetation after slash-and-burn cultivation in Madagascar

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10 Abstract

11 Xerophytic thickets (XT) in south-western Madagascar are threatened by deforestation, mainly due to
12 slash and burn cultivation. However, few studies have been conducted on how XT ecosystems operate.
13 This study characterizes XT plant biodiversity and analyses the post-cultivation regeneration process of
14 XT on the Belomotse plateau. Sixty 10 mx10 m plots were sampled according to soil type (calcisol and
15 lixisol) and age of abandonment (1-5, 6-10, 11-20, 21-40 years and >40 years as mature XT). Soil was
16 the main driver of XT floristic composition. Overstory floristic composition did not vary along
17 secondary succession stages. However, structure parameters (height and basal area) increased
18 significantly with age of abandonment, while diversity (species richness and evenness index) did not
19 increase with age of abandonment. Secondary succession in XT vegetation was assimilated to growth of
20 structural parameters. The slowness of the growth of shrub species found in post-cultivation XT plots
21 can explain this lack of change in diversity and floristic composition along secondary succession stages.
22 The reduction of pressure on XT by promoting alternative activities that provide income for local
23 communities (goat breeding and extension of arable areas along rivers delimiting XT) is proposed in
24 order to protect the endangered biodiversity of this region.

25

26 Key words: biodiversity, conservation, dry forests, rare species, regeneration, semi-arid ecosystems.

27

1. Introduction

Over three decades ago, Janzen (1988) noted that because dry forests are less prone to visible human degradation than humid forests, they may be neglected by scientific research and conservation projects. This observation remains largely true today. However, forty percent of worldwide tropical forests are located in semi-arid tropical zones, and thus represent a crucial conservation issue (Miles et al., 2006; Quesada et al., 2009). This is also true in Madagascar, where almost half of the forested area consists of dry forest ecosystems, which were until recently poorly studied (Waeber et al., 2015).

The island of Madagascar is recognized for the richness and originality of its biodiversity, associated with very high rates of endemism for both its flora and fauna (Ganzhorn et al., 2001). This biodiversity is distributed, albeit unequally, in both moist and dry forests, both of which are threatened by a wide range of human pressures (Myers et al., 2000, Goodman and Raherilalao, 2003, Waeber et al., 2015). Despite a bias in favour of wet forest species, about 11.5% of plant species and 14.2% of mammal species are specific to dry-forest, with nearly 62% of carnivore species, 41% of rodent species and 62% of primates found in dry forests (Waeber et al., 2015). These distribution patterns show that attempting to conserve biodiversity in Madagascar without considering dry forest ecosystems would be a serious mistake with regard to both generalist and specialized species. Many authors have pointed out the lack of research on these "neglected but under pressure" (Waeber et al., 2015) dry forests, despite the fact that these areas are recognized as priority areas for the implementation of conservation and restoration projects (Goodman and Raherilalao 2003, Ganzhorn et al., 2001). Thus, in order to limit the impact of deforestation and to contribute to planning for the conservation and sustainable use of the forest, it is essential to understand the role of human practices on biodiversity dynamics and on the resilience of dry ecosystems. In addition, it is essential to inventory the species of the various dry forest ecosystems that are still too poorly known, and to understand how the different species respond to disturbances induced by human practices (Goodman and Raherilalao, 2003; Waeber et al., 2015).

In Madagascar, slash-and-burn cultivation and wood charcoal production are the main disturbances which occur in such dry forest ecosystems (Casse et al., 2004; Blanc-Pamard et al., 2005). The few existing studies in western and south-western semi-arid areas showed that after the cessation of slash-and-burn cultivation, the recovery of the dry forest via natural regeneration from seed germination or

tree sprouting should occur (Leprun et al., 2009; Raharamalala et al., 2010; Randriambanona et al., 2015). These studies reported the same general pattern observed elsewhere (Quesada et al., 2009): an overall increase in plant diversity (species richness and evenness index) and structure indicators (canopy height, basal area and biomass) along secondary succession stages. However, repeated bush fires after plot abandonment in southwest Madagascar has led to the maintenance of tree savanna with open, mixed woody-herbaceous vegetation (Leprun et al., 2009), even though the cessation of fires has led to an increase in woody biomass and species richness over time (Randriambanona et al., 2015). Few studies in Madagascar have compared the original plant communities with those following human disturbances. In addition, no existing studies have described and analysed patterns of change in plant communities over time in xerophytic thicket (XT) vegetation.

Like other types of tropical dry forests, the vegetation of xerophytic thickets (XT) provides several goods and services, such as: (i) timber for building houses and pirogues, (ii) medicinal plants, (iii) food (tubers, honey and meat from hunted animals), (iv) fuelwood and woody charcoal, and (v) land for agricultural use or goat pastures (Randriamalala et al., 2016 and 2017). This multi-functionality of XT makes the conservation of its biodiversity difficult. Furthermore, XT are described as being less resilient to human disturbance than other dry and humid forests because forest recovery is slow and difficult due to the slow regrowth of shrub species (Gaspard et al., 2018). The weak resilience of XT to woody charcoal production has already been studied (Randriamalala et al., 2016 and 2017), but to date, only De Wilde et al. (2012) have studied post slash-and-burn cultivation regeneration of thicket vegetation, but in the wetter south-eastern part of Madagascar rather than the drier southwest.

Xerophytic thicket vegetation (XT), is located in the most arid part of south-western Madagascar stretching along the coast (Razanaka et al., 2015; Randriamalala et al., 2016). The area, called ‘southern domain’ is listed as one of the 200 most important ecological regions in the world (Elmqvist et al., 2007). It extends across the extreme south and south-western area, covering approximately five million hectares (Wells 2003; Gautier and Goodman, 2003), and is the oldest and most arid biome of Madagascar (Wells 2003; Gautier and Goodman, 2003). Many plant species, that have adapted to store moisture efficiently and minimize water loss, compose the low-growing open spiny forest dominated by *Didieraceae* and *Euphorbiaceae* species (Gautier and Goodman, 2003). This area accounts for the

84 highest known proportion of endemic plants in the island, reaching up to 90% of the 336 plant species
85 documented (Phillipson, 1996), while some authors have suggested that with further research, the
86 number of new species is likely to increase (Waeber et al., 2015). Spiny thicket is also classified as an
87 'endemic bird area' (Stattersfield et al., 1988), and is also home to nine endemic endangered lemur
88 species (IUCN, 2003). Due to the high level of plant and animal endemism and to potential and actual
89 threats to the spiny thicket, it is essential to improve our knowledge of this unique ecosystem.
90 The aim of this paper is to investigate the effects of slash-and-burn cultivation on plant communities
91 and plant species regeneration in XT in southwest Madagascar. The following question is addressed:
92 does XT recovery in terms of diversity (species richness and evenness) and structure (height, diameter
93 at breast height or DBH, tree and shrub density) occur after plot abandonment in the framework of
94 slash-and-burn cultivation? We compared the structure, diversity and species composition in four
95 successional stages (1-5; 6-10; 11-20; 21-40 years) after plot cultivation abandonment to the mature XT.
96 Two XT environments: calcisol and lixisol soils, which correspond to the main soil types in the region,
97 were considered.
98
99 2. Methods
100 2.1. Study site
101 The study site is located in and around the territory of Ankiliberengy village, in southwestern
102 Madagascar (Fig. 1). The climate is semi-arid, with an annual precipitation of 350 mm (Gaspard et al.,
103 2018). Over 67% of annual precipitation falls between December and February, and the remaining nine
104 months are mostly dry (Randriamalala et al., 2016). The two main soil types are calcisol (rocky
105 calcareous soil) and lixisol (yellow sand soils), which are both poor in organic matter and in nitrogen
106 (Milleville and Blanc-Pamard, 2001). The natural vegetation of the study site is composed of xerophytic
107 thickets (XT), characterised mainly by species from the *Didieraceae* and *Euphorbiaceae* families
108 (Cornet and Guillaumet, 1976).
109 The local population belongs mainly to the Tanalana and Masikoro ethnic groups. Small ruminant
110 breeding and the marketing of forest products (woody charcoal and fuelwood) are the most important
111 sources of income. Slash-and-burn cultivation is also practiced to provide staple food (Rabeniala et al.,

2013). It consists of slashing all trees and shrubs in a plot during the dry season in November-December, before the first rains, then letting them dry out for 2-10 days before burning them. The clearing concerns all of the woody individuals in the plot, but cut stumps are not removed and some of them may sprout later. Maize (*Zea mays* L.), peas which are leguminous plants (*lojy*, *hantake*: *Vigna* spp., *kabaro*, *Phaseolus lunatus* L.) and cucurbitaceous plants (melon: *voatango*, *Cucumic* sp. and *vamanga*, *Citrilus* sp.) are sown together after the first clearing, and then during the first two to three cropping periods. Plots on calcisol cannot be easily ploughed and they are definitely abandoned after cropping for 2-3 years, while plots on lixisol may be exploited more continuously with cassava (*Manihot esculenta* Crantz) and/or sweet potato (*Ipomoea batatas* (L.) Lam.) and sometimes with groundnuts (*Arachis hypogaea* L.) after manual soil ploughing (Pers Obs.). Plots on lixisol are temporarily abandoned when invasion by herbaceous weeds occurs, and/or when crop yields decline. After a 2-5 year periods of abandonment, the lixisol plots are burned and cassava and sweet potato crops are grown for 2-3 years. Repeated burning and soil ploughing on lixisol ends up destroying all of the remaining shrub sprouts and makes post-cultivation regeneration more difficult.

2.2. Vegetation study

Sixty 10 m x 10 m plots were sampled according to age of abandonment (1-5; 6-10; 11-20; 21-40 years, and >40 years as mature XT which have never been cleared for cultivation and have not been exploited for woody charcoal production), and soil type (calcisol and lixisol; Table 1). The area of the sample plots is larger than the dimensions of the shrubs (height and crown width), which do not exceed 3 m. No mature XT on lixisol in the study site had been spared from slashing for cultivation. Interviews with local guides, two young men (20-25 years) and one older one (60-65 years), provided an estimation of the age of abandonment and as accurate as possible a description of practices (slashing, crop succession and tillage regime) was made for each surveyed plot. A census of all shrubs and lianas in the 10 m x 10 m plot was carried out. Shrubs with a height ≥1.3 m belonged to overstory vegetation, and the other individuals and the surviving sprouts <1.3 m high belonged to understory vegetation. The line intercept method (Barabesi and Fattorini, 1998) was used to assess herbaceous plant cover along 10 m lines that were randomly drawn in the 10 m x 10 m plot. The presence or absence of herbaceous plants was

140 checked every 10 cm. The following diversity and structure indicators were calculated for each plot:
141 species richness, which is the total number of species in each plot; evenness of shrubby species
142 abundance (Pielou, 1966), described as J=H/Hmax, where H is the Shannon-Weaver index and Hmax is
143 the maximum value of H, if all of the plant species are equally frequent; liana species richness; shrub
144 density; mean total height and mean DBH: shrubs at the study site often present multiple trunks of
145 which the diameters were not all measured, only the largest DBH per individual was taken into account
146 ; diameter combined with the maximum height may be a good proxy of shrub species woody biomass
147 (Navar et al., 2004); and proportion of individuals from tree sprouts. All of these diversity and structure
148 indicators were calculated for both understory and overstory vegetation, except the (i) liana species
149 richness, which was associated with understory vegetation, (ii) the mean DBH and (iii) the mean height,
150 which was only calculated for overstory vegetation. Cover of herbaceous plants was also calculated as:
151 Ch=100 x N / (N + n), where N is the number of herbaceous plants intercepted and n the number of bare
152 soil intercepted along the 10 m line.
153
154 2.3. Statistical analysis
155 A series of co-inertia analyses (ADE-4; Dray et al., 2003) were used to study the relationship between
156 soil type and age of abandonment and species composition. The first concerned overstory vegetation
157 ([soil and age of abandonment, then age of abandonment only] x species composition). The second
158 concerned understory vegetation ([soil and age of abandonment, then age of abandonment only] x
159 species composition). Co-inertia analysis is a multivariate method for coupling tables that provides a
160 decomposition of the co-inertia criterion on a set of orthogonal vectors (Dray et al., 2003). The method
161 maximizes the square covariance between the projections of the two sets of variables on these vectors.
162 The significance of the correlation coefficients ρ calculated between the two sets of variables was tested
163 by a Monte Carlo permutation test with 1000 replications, and the canonical weights of each variable
164 along each co-inertia axis were calculated (ADE-4). Links between the two sets of variables were
165 identified by their canonical weight (CW) and their coordinate along the considered co-inertia axis.
166 Only variables with CW greater than the mean CW along the co-inertia axis were taken into account.
167 Another series of co-inertia analysis (ADE-4) were used to study the relationship between structure and

168 diversity of XT, and soil types and age of abandonment. The first concerned overstory vegetation
169 ([species richness, evenness index, shrub density, mean DBH and mean height] x [soil and age of
170 abandonment]). The second concerned understory vegetation ([species richness, evenness index, shrub
171 density, liana species richness and herbaceous plant cover] x [soil and age of abandonment]). For
172 overstory vegetation, one-way ANOVA with Tukey tests (SPSS 17; SPSS Inc., 2008) was used to
173 analyse variations of mean DBH, species richness and mean height by age of abandonment.
174
175 3. Results
176 3.1. Overstory species composition (≥1.3 m)
177 Co-inertia analysis linking (i) soil type and age of abandonment to (ii) species composition showed that
178 dependence between these two sets of variables is significant (p=0.019). The first co-inertia axis
179 explains 43% of total co-inertia. The correlation coefficient along this axis is ρ=0.87. This axis
180 separates species linked to calcisol from those linked to lixisol (Fig. 2). The second co-inertia axis
181 explained 21% of total co-inertia and the correlation coefficient along the axis is ρ=0.72. It opposes (i)
182 young XT (1-5 years) and mature XT to (ii) old XT (11-40 years). Main species linked to lixisol are
183 mainly represented by the following species: *Flacourtia ramontchi* L'Hér., *Gyrocarpus americanus*
184 Kubitzki, *Pyrostria tulearensis* Razafim., Lantz & B. Bremer, *Chadsia flammea* Bojer and *Dalbergia*
185 *xerophila* Bosser & R. Rabev. Main species linked to calcisol and mature XT on calcisol are: *Kalanchoe*
186 *grandidieri* Baillon, *Albizia tulearensis* Viguier, *Helmiopsiella madagascariensis* Arènes and
187 *Lepidagathis grandidieri* Benoist. Co-inertia analysis linking age of abandonment and overstory species
188 composition of XT on lixisol did not show a significant correlation (p=0.068). It was the same for co-
189 inertia analysis linking age of abandonment to overstory species composition of XT on calcisol
190 (p=0.189). No significant variation of species composition with age of abandonment was found in the
191 XT on the two soil types. Soil type is the main driver of XT overstory species composition.
192
193 3.2. Xerophytic thickets overstory (≥1.3 m height) diversity and structure

194 The range of mean species richness of overstory vegetation was 8.14-14.57 .100 m^{-2}; mean evenness
195 index, 0.75-0.91, mean shrub density, 24.83-51 individuals .100 m^{-2}; mean height, 1.81-2.30 m, and
196 mean DBH of overstory vegetation, 0.73-2.03 cm. Co-inertia analysis linking structure and diversity
197 parameters of overstory vegetation to soil type and age of abandonment showed a significant correlation
198 between these two sets of variables ($p<0.001$). The first co-inertia axis (85% of total co-inertia; $\rho=0.67$)
199 is characterised by mean DBH, species richness and mean height. This axis also separates 1-5 years XT
200 from 21-40 XT and mature XT (Fig. 3). These last XT are associated with higher mean DBH, species
201 richness and mean height. Structure and diversity of XT are mainly affected by age of abandonment.
202 Mean species richness of XT varied significantly with age of abandonment ($F=4.48$; $p<0.001$; Fig. 4a),
203 there were significant differences between mean species richness of 1-5 year XT on lixisol and those of
204 21-40 years and mature XT on calcisol (Fig. 4a). Furthermore, significant variations of mean species
205 richness with age of abandonment were found in XT on calcisol ($F=3.402$; $p=0.022$): mean species
206 richness of 6-10 years XT was significantly different from those of 21-40 year XT (Fig. 4a). However,
207 there were no significant variations of mean species richness of XT on lixisol ($F=2.53$; $p=0.081$). Mean
208 height and mean of mean DBH of largest trunks increased overall with age of abandonment in the two
209 soil types ($p\leq0.001$; Fig. 4b and c). Significant differences between mean of mean DBH and mean
210 height of young XT (1-5 years) and those of old XT (21-40 years) and mature XT were found ($p<0.05$;
211 Figs 4b and c). XT overstory dynamics over time are mainly summarised by growth of structural
212 parameters such as height and mean DBH of largest trunks.
213
214 3.3. Understory species composition (<1.3 m)
215 Co-inertia analysis linking (i) soil type and age of abandonment to (ii) species composition of
216 understory vegetation showed that dependence between these two sets of variables is significant
217 ($p=0.007$; Fig. 5). The first co-inertia axis (41% of total co-inertia) opposes XT on lixisol to XT on
218 calcisol. The second co-inertia axis (23% of total co-inertia) separates 1-5 year and 11-20 year XT to 6-
219 10 year and 21-40 year XT. Co-inertia analysis linking (i) age of abandonment to (ii) species
220 composition of XT on lixisol did not show any significant correlation ($p=0.749$): understory species
221 composition of XT on lixisol does not significantly vary with age of abandonment. Main species

222 characterising understory vegetation on lixisol are: *Uncarina stellulifera* Humbert, *Terminalia fatraea*
223 Candolle, *Ipomoea bolusiana* Schinz, *Aerva javanica* Jussieu and *Chadsia flammea* Bojer. Co-inertia
224 analysis linking (i) age of abandonment to (ii) species composition of XT on calcisol showed significant
225 dependence between the two sets of variables (p=0.043). The first co-inertia axis (46% of total co-
226 inertia) separates species linked to (i) 6-10 years XT from (ii) 21-40 year and mature XT (Fig. 5). The
227 second axis (25% of total co-inertia) opposes (i) species linked to 1-5 year XT to (ii) 21-40 year XT
228 (Fig. 5). Main species linked to understory vegetation of 1-5 year XT on calcisol are: *Neobeguea*
229 *mahafaliensis* J.-F. Leroy, *Solanum* sp., *Aerva javanica* (Burm. f.) Juss., *Vaughania interrupta* Du Puy,
230 Labat & Schrire and *Mimosa delicatula* Baill. Understory vegetation of 6-10 year XT on calcisol are
231 essentially characterised by: *Indigofera* sp., *Commiphora mahafaliensis* Capuron, *Secamonopsis*
232 *madagascariensis* Jum., *Flacourtia ramontchi* L'Hér. and *Tabernaemontana coffeoides* Bojer. Species
233 linked to understory vegetation of 21-40 year XT and mature XT on calcisol are essentially: *Albizia*
234 *tulearensis* R. Vig., *Commiphora marchandii* Engler, *Dalbergia xerophila* Bosser & R. Rabev.,
235 *Dichrostachys alluaudiana* Viguier, *Kalanchoe grandidieri* Baill. and *Operculicarya decaryi* H.
236 Perrier. Finally, species linked to only 21-40 year XT on calcisol are essentially: *Stereospermum*
237 *euphorioides* DC., *Allophylus decaryi* Danguy & Choux, *Koehneria madagascariensis* (Baker) S.A.
238 Graham, Tobe & Baas, *Tetrapterocarpon geayi* Humbert and *Celosia argentea* L. Understory species
239 composition of XT on calcisol changes with age of abandonment, which is not the case for XT on
240 lixisol.
241
242 3.4. Understory diversity and structure
243 Co-inertia linking (i) diversity and structure of understory vegetation to (ii) soil and age of abandonment
244 did not show a significant correlation (p=0.072). No significant variations of mean species richness
245 (8.14-15.27 100 m^{-2}), mean evenness index (0.67-0.87), mean liana species richness (3.33-4.60 100 m^{-2}),
246 mean shrub density (34.67-77.71 100m^{-2}), and mean herbaceous plant cover (10.67-34.86%) by soil
247 type and by age of abandonment were found. Diversity and structure of understory vegetation of XT
248 were not affected by soil type or by age of abandonment. 21-51% of individuals in the understory

vegetation and 70-88% of individuals in the overstory vegetation came from tree sprouting except in the mature forest, which has never been cultivated (Tab. 2), and the other individuals are germinated plants.

4. Discussion

4.1. Soil, main driver of species composition

Soil type is the main factor conditioning XT species composition. Results of the co-inertia analyses enabled a distinction to be made between two plant species communities: (i) those on calcisol and (ii) those on lixisol (Figs 4 and 5). This is in line with the findings of a previous study (Randriamalala et al., 2016) in XT vegetation under woody charcoal production and goat grazing, conducted about 50 km south-east of the study site. Differences in the water conservation of the two soil types may explain this phenomenon: shallow calcisols are associated with weak water retention, while deeper lixisols allow better water conservation in their deeper layers and maintain humidity for a longer period (Koechlin et al., 1997). This difference in water availability may have shaped the adaptations of different plant communities on these two types of soil (Koechlin et al., 1997): the plant community on calcisol is more resistant to drought than that on lixisol, where water availability is higher. More generally, soil characteristics are an important driver of species composition and vegetation distribution in semi-arid areas (Vargas-Rodriguez et al., 2005; Mills et al., 2009).

4.2. Low variations in species composition with age of abandonment

Species composition of overstory vegetation of XT on any soil type and those of understory vegetation on lixisol did not vary significantly with age of abandonment (Figs 3 and 5). Those results are partially in concordance with those of De Wilde et al. (2012), who found no relationship between age of abandonment and vegetation species richness, composition or structure in a dry forest of humid/semi-arid transition zone in the south-east of Madagascar. However, they detected differences between secondary and mature forest patches (in terms of diversity, structure and species composition). Furthermore, our results confirmed those of Lévesque et al. (2011) who did not observe any changes in species composition, 10 years after experimental tree cutting in a dry forest in Jamaica (Mean annual precipitation P=780 mm $year^{-1}$). However, our results go against those of Raharimalala et al. (2010),

who showed that variations of species composition of dry secondary regrowth vegetation in Morondava, Madagascar (P=767 mm year^{-1}) were mainly driven by the age of abandonment. Furthermore, Randriambanona et al. (2015) showed that species compositions of post-cultivation vegetation in semi-arid Mikea (about 100 km northwest of our study site; P=600-800 mm year^{-1}) vary with the age of plot abandonment when they are protected against recurrent cultivation bush fires.

The extreme aridity of the study site climate (P<400 mm year^{-1}) may explain the absence of variations in species composition of overstory vegetation with age of abandonment. Tree and shrub species in semi-arid areas grow slowly (Worbes, 1999; Gebrekirstos et al., 2008), especially those at the study site (Gaspard et al., 2018), and seed germination under conditions of absence or scarcity of water into the soil sub-surface is difficult (Khurana and Singh, 2001; McLaren and McDonald, 2003). Plants maximize their biomass production through photosynthesis during the wet season, when vegetation has leaves rather than spines (Borchert, 1999; Eamus and Prior, 2001), which is very short or may be absent at the study site (2-3 months a year). The vegetative origins (tree sprouts) of the majority of trees and shrubs of the overstory vegetation, and a large fraction of those of understory vegetation, and the weak variation of shrub density with age of abandonment, confirm this explanation.

Species composition of understory vegetation of XT on calcisol varied with the age of abandonment (Fig 5). Germinating seeds from soil seed banks or from seed dispersal from species located in surrounding undisturbed XT on calcisol, helped by relative rapid development of overstory vegetation which provided shade, may explain these patterns of change in understory vegetation species composition on calcisol. In fact, weak agricultural disturbance of XT on calcisol (short crop duration and no use of soil ploughing) limited damage to soil seed banks (Randriamalala et al., 2015) and favoured tree and shrub sprouting, which may rapidly increase the woody plant cover. These tree and shrub sprouts can play a nurse plant role and favour seed germination and survival of seedlings from this germination. In fact, it was demonstrated that survival rates of seedlings in semi-arid areas are higher under the shade of thickets than those of seedlings in open space (no shade), because this is facilitated by nurse plants (Howard et al., 2012; Adie and Yeaton, 2013).

Secondary succession of XT on lixisol seems to be prevented for a longer period of time. Heavier agricultural disturbance of plots on lixisol may explain this slowness or lack of regeneration. In fact,

plots on calcisol are abandoned after being cultivated for 2-3 years, while plots on lixisol are often cultivated continuously after the first XT clearing (Rabeniala et al., 2013), which may be the main reason why mature undisturbed XT on such soil types do not still exist at the study site. Furthermore, soil ploughing for tuber crop and for peanuts is practiced on lixisol. The combination of long crop duration and soil tillage may destroy most of soil seed banks and tree and shrub sprouts on lixisol (Randriamalala et al., 2015), and partially prevent secondary succession. In fact, settlement of new species depends both on availability of seeds from soil seed banks and/or seed rain from the nearby forest matrix. However, these two seed sources are gravely impacted (soil seed banks) or non-existent (forest matrix for seed rain) for XT on lixisol. Furthermore, settlement of seedlings from seed germination is hindered by the slowness of development of the shrubby layer, which does not provide the necessary shade.

4.3. Weak variation of plant diversity indicator with age of abandonment

The mean evenness index did not significantly vary with age of abandonment, nor with soil type. However, mean species richness of overstory vegetation significantly varied with soil type, and to a lesser extent with age of abandonment (Figs 4): an overall but not significant increase of mean overstory species richness with age of abandonment occurred in the two soil types. However, the supply of new species due to this apparent species richness increase does not affect significantly the XT composition. These results go against what is generally observed in post-disturbance dynamics of dry forest, namely an overall increase in species richness along secondary succession stages (Kennard, 2002; Ruiz et al., 2005; Kinhal and Parthasarathy, 2008; Quesada et al., 2009). Furthermore, De Wilde et al. (2012) found a slight increase in species richness with age of abandonment of dry forest in a transition zone of dry and humid forest in southeastern Madagascar. In the same way, Raharimalala et al. (2010) found an increase in species richness with age of abandonment in a series of post-cultivation plots in Morondava, western Madagascar (P=767 mm $year^{-1}$).

This stagnation of the diversity of XT along age of abandonment may also be explained by the high mortality of seeds and seedlings from seed germination during the long dry season. In fact, species richness variation along secondary succession stages comes from a balance between (i) arrival of new

species by seed germination (seed bank or rain), and (ii) mortality of individuals belonging to the pre-existing species. The absence of significant species richness increase associated with (i) the lack of correlation between species composition and age of abandonment (at least for understory vegetation), and (ii) the abundance of individuals from tree and shrub sprouts, seem to show the absence of the arrival of new species and/or a weak survival of seedlings from seed germination, especially in XT on lixisol. Moreover, the relative importance of agricultural disturbance on lixisol (longer crop duration and soil ploughing) may destroy most seed banks in this soil (Randriamalala et al., 2015). Only remaining tree and shrub sprouts and the small surviving soil seed banks contribute to natural regeneration in XT on this substrata. Therefore gap dynamics, often used to describe the process of regeneration in tropical rainforests, cannot be used to describe regeneration in the XT ecological habitat, as was claimed for a dry forest in Jamaica (Lévesque et al., 2011).

4.4. XT structure recovery

Significant increases in mean height and mean DBH with age of abandonment were found in every soil type (Figs 4b and c). These results are close to those obtained by Madeira et al. (2009) in southern Brazil (P=828 mm $year^{-1}$), by Alvarez-Añorve et al. (2012) in Mexico (P=748 mm $year^{-1}$) and by Holm et al. (2012) in south-western Porto Rico (P=722 mm $year^{-1}$), who found an increase in basal area, mean DBH, mean height along successional gradients in dry forests. Mean tree and shrub density did not significantly vary with age of abandonment. These results are concordant with results of De Wilde et al. (2012) regarding the lack of correlation between mean tree and shrub density and the age of plot abandonment. Mean herbaceous plant cover did not vary significantly with age of abandonment, even if it seemed to increase with age of abandonment in XT on lixisol, and to decrease when age of abandonment increased in XT on calcisol. Persistence of herbaceous species in XT on lixisol may be explained by canopy opening (Laurance et al., 1998), which is the consequence of weak regeneration due to intensive cultivation (long crop duration and soil ploughing). In contrast, gradual canopy closure in XT on calcisol may reduce pioneer heliophilous herbaceous plant cover in such XT.

4.5. Implications for XT conservation and management

Following slash-and-burn cultivation, the resilience of XT is low; this ecosystem regenerates slowly after clearing and cultivation. Similarly, selective wood harvesting, such as that used for charcoal production, is not sustainable in XTs, and has a major impact on XT diversity and biomass recovery (Randriamalala et al., 2017). As a consequence, the establishment of a strict conservation policy for protected areas, as suggested by Gardner et al. (2016), could be a suitable solution. However, such an approach (reinforcing of protection policies) cannot be a long-term solution for the sustainable conservation of XT because its implementation would involve sustainable financial means that do not yet exist. Furthermore, the effectiveness of existing protected areas against deforestation and forest degradation is uncertain (Eklund et al., 2016; Gardner et al., 2018), so it would be more appropriate to improve the effectiveness of existing protected areas than to extend their area. Slash-and-burn cultivation, timber and firewood extraction for commercial purposes and woody charcoal production are the main pressures on this XT vegetation. Such pressure comes from the combination of (i) the presence of poor local communities, living in and around these XTs, and (ii) a heavy and growing demand for woody charcoal, firewood and timber from the town of Toliara, less than 30 km away to the south west. The sustainable management of these XTs will necessarily require the alleviation of these pressures by reducing the natural resource dependence of local communities through alternative income generating activities (Andrianarisoa et al., 2014; Gardner et al., 2018). Such alternative economic activities should (i) generate higher revenues than forest exploitation (woody charcoal and commercialisation of timber and firewood), and (ii) provide income for the purchase of basic necessities and food. In fact, activities linked to forest exploitation, especially, charcoal production, is not a desirable activity but a safety net when times are difficult, so other activities, economically more profitable and physically easier, may considerably reduce the interest of local communities in forest exploitation activities. However, to be adopted, such activities should be adapted to the arid climatic conditions, and be socially accepted. Goat breeding fulfils these two conditions (Andrianarisoa et al., 2013, Randriamalala et al., 2016). This activity is in fact the main source of income for households in these areas because goats and livestock in general (oxen and sheep) are better adapted to conditions of drought than most agricultural activities (Hanke, 2016). Thus, livestock sales almost entirely finance household expenditures (food and other) when agricultural production is lacking due to drier periods (Hanke, 2016).

389 An improvement in goat breeding methods could significantly increase the income of goat herders
390 (Andrianarisoa et al., 2014). The control of livestock reproduction using the technique of 'flushing'
391 enables an increase in birth frequency (1 vs 1.5-2 per year; Andrianarisoa et al., 2014), and the
392 reproduction performance of goat herds (fecundity and fertility, Andrianarisoa et al., 2014). The income
393 comes from the regular sale of the surplus animals produced; the oldest females and the adult males
394 could be sold because the herd recruitment is ensured by the birth of new kids. Furthermore, such
395 breeding techniques would avoid overgrazing, which is the main source of the detrimental impact of
396 small ruminants on vegetation in semi-arid regions (Rosa García et al., 2012). Goat grazing on XT, with
397 a stocking rate of one head per hectare, does not leave a significant footprint on the regeneration and
398 diversity of this vegetation (Randriamalala et al., 2016). Under these conditions, goat breeding may be a
399 sustainable way to exploit XT vegetation, and an efficient means to alleviate poverty and malnutrition at
400 the study site.
401 Another way to reduce the pressure on the XT is the rehabilitation and/or the building of small hydro-
402 agricultural infrastructure (small dams or canals), in order to increase the cultivated areas along the
403 main rivers (Onilahy and Fiherenana) bordering the XT zone (Fig. 1). Huge alluvial plains are located
404 along these two rivers (Masezamana et al., 2013). However, most of them are not cultivated because of
405 irrigation problems. These limitations induce massive population migration to the Belomotse Plateau,
406 where XT are overexploited (Rabeniala et al., 2013).
407
408 5. Conclusion
409 XT recovery is slow and limited to an increase in structure parameters. No changes in species
410 composition along age of abandonment occurred, except in understory vegetation of XT on calcisol.
411 Soil was the main driver of XT floristic composition. Secondary succession in XT vegetation was
412 assimilated to growth of structural parameters. Reduction of pressure on XT by the promotion of
413 traditional activities such as goat breeding and the rehabilitation of hydro-agricultural infrastructure
414 along rivers delimiting the study site XT may be the best way to conserve this valuable vegetation. XT
415 restoration is also necessary to maintain this vegetation. Such restoration may be passive and rely on
416 natural regeneration processes (assisted regeneration and nucleation), or be active and consist of native

417 species plantations. Both of these restoration approaches require a better understanding of how XT
418 ecosystems operate, particularly with regard to: (i) potential of regeneration (seed rain, seed bank and
419 tree sprout and their relative importance on XT regeneration), (ii) availability and effectiveness of seed
420 dispersers, (iii) viability, biology and ecology of dominant and abundant XT species, and (iv) their
421 interaction with rainfall variability. Data and knowledge on these four points currently are scarce and
422 must be obtained in order to design effective restoration strategies.
423
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429
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588 Table 1. Sampling design

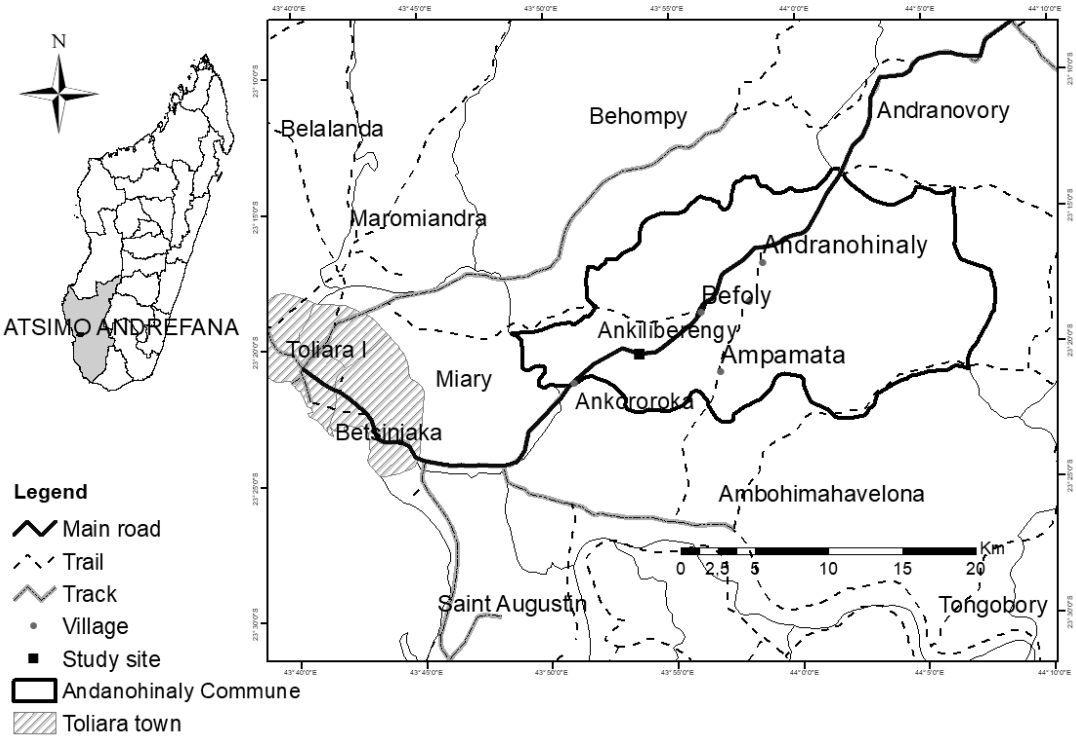
Soil type	Age of abandonment (years)	N
Calcisol	1-5	6
	6-10	7
	11-20	7
	21-40	7
	Mature XT (>40)	5
Lixisol	1-5	7
	6-10	7
	11-20	7
	21-40	7

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Table 2. Origins of tree and shrub in the XT

Soil types	Age of abandonment (years)	Proportion of individuals from tree sprouts (%)	
		Overstory	Understory
Calcisol	1-5	71	45
	6-10	74	35
	11-20	88	51
	21-40	77	51
	Mature XT(>40)	4	6
Lixisol	1-5	70	50
	6-10	75	33
	11-20	79	33
	21-40	76	21

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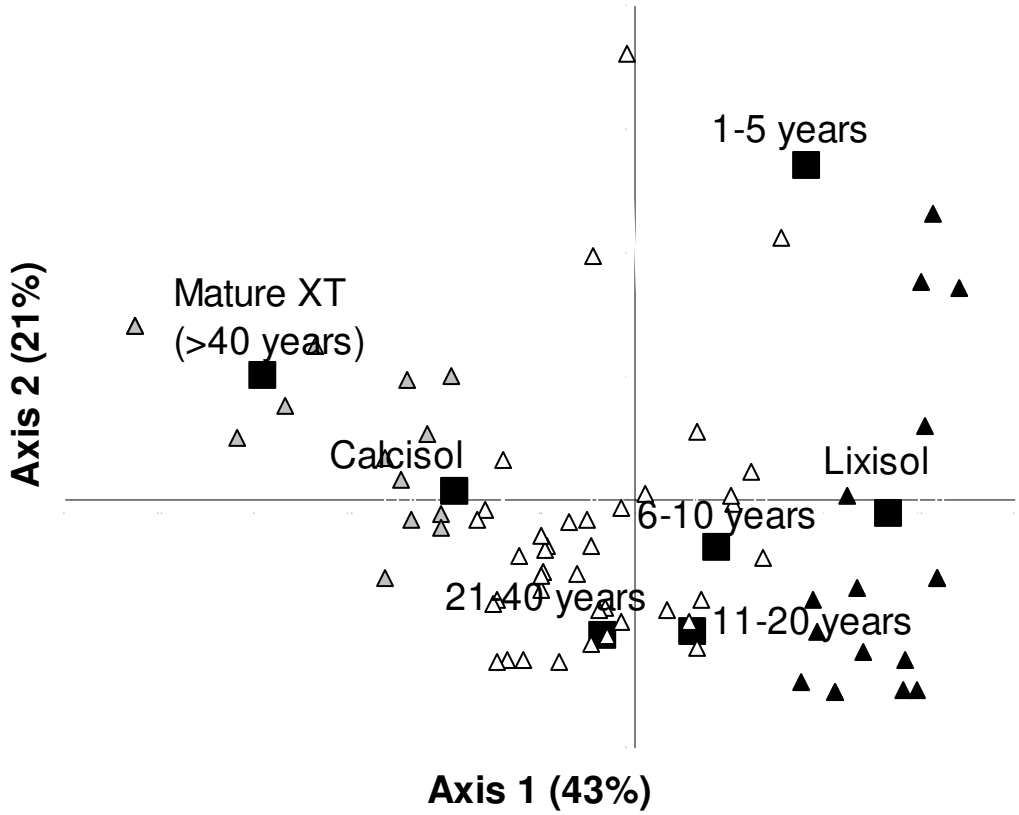
606 Fig 1. Study site.

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615 Fig. 2. Co-inertia analysis linking (i) overstory species composition to (ii) soil type and age of
616 abandonment. Black triangle: species linked to lixisol and 1-5 years XT; grey triangle: species linked to
617 mature XT and to calcisol; white triangle: other species

618

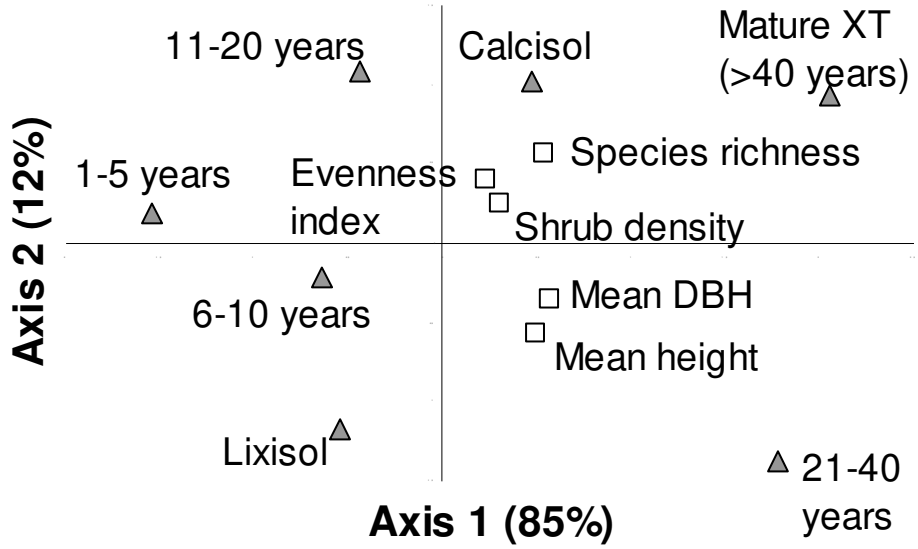
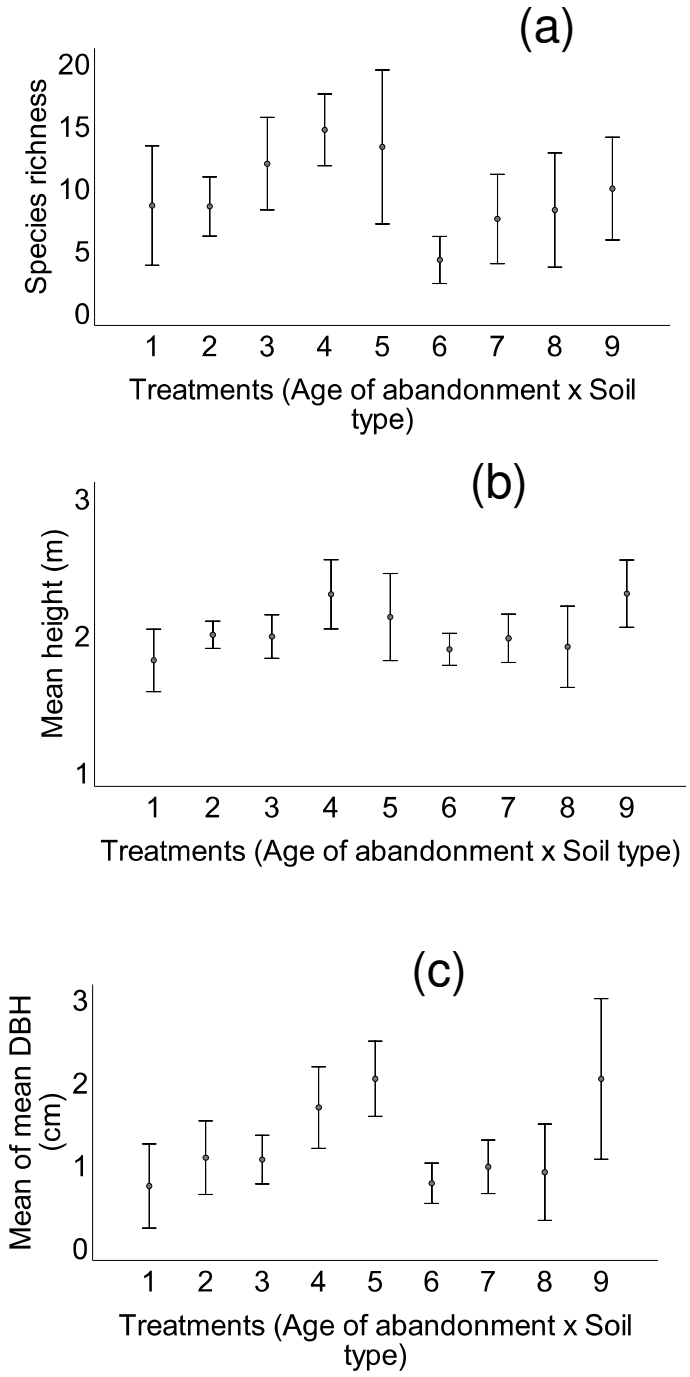


Fig. 3. Co-inertia linking (i) overstory vegetation diversity and structure parameters to (ii) soil type and age of abandonment.

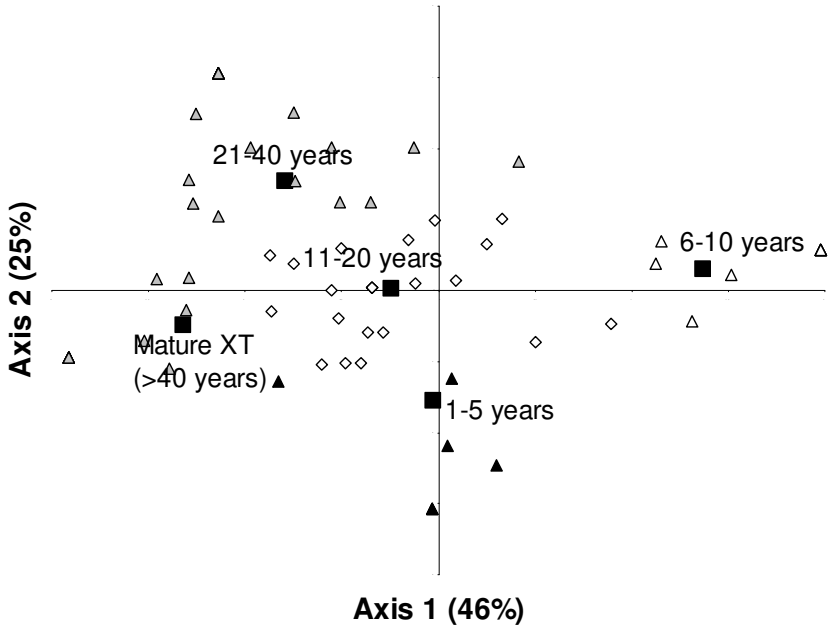


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627 Fig. 4. Evolution of mean species richness (a), mean height (b) and mean of mean DBH (c) in the two
628 soil types. 1: 1-5 years XT on calcisol; 2: 6-10 years XT on calcisol; 3: 11-20 years XT on calcisol; 4:
629 21-40 years XT on calcisol; 5: mature XT on calcisol; 6: 1-5 years XT on lixisol; 7: 6-10 years XT on
630 lixisol; 8: 11-20 years XT on lixisol; 9: 21-40 years XT on calcisol; Vertical bar: standard error
631 ($p<0.05$).

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637 Fig. 5. Co-inertia analysis linking (i) understory species composition to (ii) soil type and age of
638 abandonments of XT on calcisol. Black triangle: Species linked to 1-5 years XT; Grey triangle: Species
639 linked to 21-40 years and mature XT; White triangle: Species linked to 6-10 years XT; White diamond:
640 Other species (common species found in any successional stage).

641