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

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23

24 **Abstract**

25 Today, exotic invasive alien species are considered to be one of the greatest threats to
26 biodiversity. However, not all exotic species cause negative consequences in the
27 ecosystems in which they settle. In some cases, artificial plantations of exotic species can
28 act as a catalyst for the regeneration of native species. In southern central Madagascar,
29 which has been affected by diverse disturbances (cyclones, logging, cultivation), *Pinus*
30 *patula* plantations have become environments conducive to the regeneration of native
31 species. This study aims to assess the level of understorey plant diversity in these
32 artificial plantations, describe the vegetation dynamics, and examine the effects of
33 agricultural practices and logging on vegetation diversity and structure. Floristic
34 inventories and biomass measurements were made on three types of vegetation that have
35 resulted from previous human-induced disturbance: (i) cassava crops established after
36 pine logging; (ii) fallows corresponding to cassava crops left fallow for 1 to 2 years; and
37 (iii) post-logging regrowth after pine logging 3 to 10 years previously. Botanical surveys
38 were conducted on 205 10x10 m² quadrats placed along 40 transects. A total of 125
39 species, 34 of which endemic, from 46 families were inventoried. The Shannon Weaver
40 index H' values were significantly different between post-logging regrowth
41 (H'=4.01±0.67), and cultivated fields (H'=1.46±0.23) and fallows (H'=3.31±0.78)
42 (p<0.001). Agricultural practices, such as tillage regime, number of crop-fallow cycles
43 (>2 cycles) and number of fire occurrences (>4 fires) had a greater impact on the
44 reconstitution of vegetation than environmental parameters such as slope and topographic
45 position. The Shannon-Weaver diversity index (H') and vegetation structure parameters
46 (tree density, biomass) were inversely correlated with the intensity of disturbance linked

47 to these agricultural practices. These results suggest that a low level of disturbance, such
48 as that resulting from *Pinus* tree logging, can act as a catalyst for the establishment of
49 native woodlands. Excessive disturbance from silvicultural and agricultural practices,
50 such as frequent burning, heavy tillage and high numbers of crop/fallow cycles, may
51 hinder, but does not block, the establishment of native woodlands.

52

53 **Key words**

54 Agriculture, Biodiversity, Disturbance, Exotic species, Logging, Restoration, Succession.

55

56 **1. Introduction**

57 The early 1990s were marked by the emergence of new practices and research into the
58 role of forest plantations as areas that could potentially act as catalysts for the
59 regeneration of native species (Parrotta, 1992; Lugo, 1992; Parrotta, 1995; Telila et al.,
60 2015). These studies show that under certain conditions, it is possible to restore both
61 animal and plant biodiversity in degraded landscapes thanks to regeneration processes of
62 native forest species that occur after the reforestation species, most often introduced, are
63 logged (Parrotta et al., 1997; Lamb et al., 2005). The results of these studies, conducted
64 in Puerto Rico, China, Uganda, and elsewhere, provide strong evidence of the positive
65 role of these plantations in the regeneration and implantation of native species, but they
66 emphasize the importance of taking local specificities into account at both the ecological
67 (landscape) and socioeconomic (land management) levels when considering how to apply
68 the lessons learned from this research (Lugo, 1992; Parrotta et al., 1997; Piironen et al.,
69 2015). In Madagascar, numerous plantations of *Pinus*, *Eucalyptus*, and *Acacia* were
70 established in the 1930s across the Central Highlands in degraded forest areas, on the
71 edges of existing forests, and on grasslands at times far from forests and without an
72 established forest history (Parrot, 1925; Carrière and Randriambanona,
73 2007; Randriambanona, 2010; Martin et al., 2012). While exotic species introduced with a
74 forest plantation can disturb ecosystems and ecological habitats by modifying their
75 structure and composition (Thébaud and Simberloff, 2001; Callaway and Ridenour,
76 2004), the areas planted are of undeniable interest for understanding the role of such
77 plantations in the regeneration of native forest species in degraded areas near natural
78 forests. These reforested areas in effect attract fruit-eating forest animals such as birds

79 and lemurs (Martin et al., 2009; 2012; Gérard et al., 2015) that can contribute to locally
80 increasing the dispersion of forest species seeds on these plantations, and therefore to the
81 regeneration of these areas lying outside the forests due to nucleation (Carrière et al.,
82 2002; Schlawin and Zahawi, 2008). The conditions of this regeneration of native or even
83 endemic species depend as much on the structure and composition of the plantations
84 (Sansevero et al., 2011), which affect animal movements, as the distance to the source of
85 seeds (Jesus et al., 2012) and the effect of disturbances (agricultural and logging
86 practices) conditioning the regeneration of pioneer species. Numerous authors deplore
87 forest managers' preference for fast growing introduced species, but they also point to a
88 lack of knowledge about the ecology of these plantations and the silvicultural practices
89 associated with native and introduced species to facilitate regeneration (Lugo 1997;
90 Lamb et al., 2005, Pareliussen et al., 2005).

91 Madagascar is no exception. Indeed, in this biodiversity “hotspot” (Myers, 1988), little
92 consideration has been given to the role of introduced forest species other than as a threat
93 to native biodiversity through their potentially invasive character (Binggeli, 2003; Kull et
94 al., 2007; Carrière et al., 2008). Nonetheless, these vigorous species (Perrier de la Bathie
95 1931) could play a role in restoring Malagasy ecosystems (Gérard et al., 2015).

96 In the southern central part of the island, Ranomafana National Park and the landscapes
97 around the commune of Androy present special features for the study of ecological
98 restoration possibilities. The particular feature of the pine plantations (*Pinus patula*
99 Schltdl. & Cham.) in this area (near the forest corridor linking Ranomafana and
100 Andringitra National Parks) lies in their placement on grassy areas abandoned by
101 agriculture rather than on lost or degraded forests (Randriambanona, 2010). The

102 proximity of natural and artificial plant formations and the heterogeneous landscape
103 where fluxes of birds contribute to seed dispersal (Martin et al., 2009 and 2012) create an
104 excellent site in which to understand the effect of these trees and their use (crops,
105 logging, vegetation burning) on natural regeneration. A better understanding of the forest
106 regeneration processes on these plantations is an important step for setting up forest
107 restoration measures in Madagascar. It would enable the valorisation of areas with few
108 species, such as grasslands, while also enabling the use or production of resources
109 required for human survival (Brunet et al., 2011; Gérard et al., 2015).

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

119

120 **2. Materials and Methods**

121 **2.1 Study site**

122 The study was conducted close to the forest corridor linking Ranomafana and Andringitra
123 National Parks in the commune of Androy (21° 22' S, 47° 18' E; elevation 1100-
124 1200 m), 300 km south of Antananarivo. Average annual rainfall is 1,296 mm and the

125 average temperature is 19°C. The soils are ferralsols according to the FAO classification,
126 characterised by a lack of available phosphorus and exchangeable cations (Randriamalala
127 et al., 2007). The landscape on the forest edges is heterogeneous (Martin et al., 2009;
128 2012) and composed of highly diverse ecological habitats: (1) dense medium-altitude
129 rainforests dominated by *Tambourissa* and *Weinmannia* (Koechlin et al., 1974), more or
130 less disturbed and secondary depending on the distance to villages and the presence of
131 formerly cultivated site, (2) post-cultivation regrowth of varying ages and composition
132 known locally as *kapoka* and *kilanjy*, (3) plantations of *Pinus* spp., *Acacia dealbata* Link
133 and *Eucalyptus* spp., and (4) *Aristida similis* Steud. grasslands (Carrière and
134 Randriambanona, 2007; Randriamalala et al., 2007).

135

136 **2.2 The *Pinus* plantation studied**

137 This government-owned industrial pine plantation (2,300 ha) was set up between 1969
138 and 1972 to supply a wood pulp factory that ultimately was never constructed
139 (Randriambanona, 2010). No fertilizer was used when the trees were planted in holes (50
140 x 50 x 50 cm cubic holes dug with spades) on *A. similis* grasslands (CTFT, 1967). The
141 distance between the tropical forest of the Ranomafana-Andringitra corridor and the
142 *Pinus* plantations varied between 200 to 600 m. The main tree species used for these
143 plantations were *Pinus patula*. Following the selective logging of pines over the entire
144 plantation, post-logging regrowth began to appear starting from 1994 in different gaps,
145 and then gradually elsewhere on the entire plantation (Randriambanona, 2010). Cyclone
146 Honorine in 1986 and Géralda in 1994 caused additional disruption (windfall), before and
147 after the felling of trees, which cannot be quantified (personal observations). Like the

148 logging, this led to intermittent forest regeneration phases within the plantations. These
149 phenomena transformed the reforestation areas into forest or pre-forest regrowth plots
150 dotted with some scattered pine trees. Beginning in 2001, the local population started to
151 farm these post-logged regrowth areas by felling, clearing, drying and burning the
152 vegetation (*Pinus patula*, *Vernonia garnieriana* Klatt., *Macaranga alnifolia* Baker,
153 *Anthocleista madagascariensis* Baker) and then planting cassava. The plots were then
154 tilled using an *angady*, a traditional spade, using two methods: (i) partial tillage
155 immediately around the planting hole, called *kobokaka* (light tillage; <10 cm depth, about
156 1 m radius around cassava cutting, which is the only crop planted with *kobokaka*) and (ii)
157 ploughing (heavy tillage, 10–20 cm depth) (Randriamalala et al., 2012). After a two-year
158 cassava crop cycle, the plots were left to lie fallow 3 to 4 years (Randriambanona, 2010).
159 It is only after the crop cycle and during the fallow phase that post-farming natural
160 regrowth developed, taking the form of low grasslands at the time of the study.
161 Understory vegetation in the *Pinus* plantation site can be grouped into three vegetation
162 types resulting from silvicultural and agricultural practices which correspond to
163 increasing levels of disturbance: (i) cassava plots (*Pinus* logging + cassava cultivation;
164 Log+C), (ii) fallow, agricultural regrowth (*Pinus* logging + plot cultivation + plot
165 abandonment; Log+C+Ab) and (iii) post-logging regrowth (*Pinus* logging + plot
166 abandonment; Log+Ab).

167

168

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171 **2.3. Vegetation study**

172 The vegetation inventories were made on 205 (10m x10 m) plots spaced 50 m apart along
173 40 transects spaced 100 to 150 m apart and of varying lengths depending on the width of
174 the study area (Figure 1).

175 [Insert Fig. 1]

176 This approach made it possible to take transects within the three main vegetation types
177 present: cassava crops (Log+C), fallows (Log+C+Ab), and post-logging regrowth
178 (Log+Ab) that had not yet been cultivated. For each plot, the following site variables
179 were recorded: slope (in degrees), exposition, altitude and topographical position (Top:
180 valley bottom, mid-slope, high slope, crest). For each woody individual with a diameter
181 >5 cm, the following parameters were recorded: species, height (h), diameter at a height
182 of 1.30 m (DBH), life form (tree, shrub, grass, lianas) and main mode of seed dispersal
183 (anemochory, zoochory, barochory). The following parameters were calculated for each
184 plot:

185 - species richness (S), defined as the total number of species found per plot;

186 - Shannon-Weaver diversity index (Shannon and Weaver, 1949);

187 - evenness index, $R=H/H_{max}$, where H is the Shannon-Weaver index and H_{max} is the
188 maximum value of H in the community, if all of the plant species are equally frequent
189 (Pielou, 1966);

190 - tree density ($N \cdot ha^{-1}$);

191 - total biomass (TB) composed by above-ground biomass (AGB) and below-ground

192 biomass (BGB). The AGB ($Mg \cdot ha^{-1}$) was assessed using the full harvest method in 15

193 randomly chosen plots in each vegetation type. This method consisted of cutting close to

194 the ground all standing plant material in a 2 x 2 m² square (Pfund et al., 1997); four
195 squares per plot were measured. The weight of the fresh material was recorded in the
196 field and the dry matter content was determined after drying in an oven (85°C for 24 h).
197 BGB was measured by assessing fine root biomass (diameter <2 mm) with the coring
198 method (Böhm, 1979) in the same squares as the AGB using a sensor (XOK-37000,
199 Lindquist International) with an 80 mm inner diameter, with 9 samples taken on the 0-10,
200 10-20, 20-30, 30-40, 40-50, 50-75, 75-100, 100-125, 125-150 cm horizons. The roots
201 were cleaned of dirt using a double screen under a spray of water, then rinsed, manually
202 sorted and dried in an oven (85°C for 24 hours), and weighed.

203

204 **2.3. Agro-ecological variables**

205 To retrace the silvicultural and agricultural history of studied plots, questionnaires were
206 used among the populations and, for the cultivated plots, the farmers. The information
207 collected concerned the following silvicultural and agricultural variables: (i) number of
208 successive fires since first clearing (FN-1: 1 fire, FN-2: 2 fires, FN-3: 3 fires, FN-4: 4
209 fires); (ii) crop-fallow cycle number (CC-0: uncultivated, CC-1: one cycle, CC-2: two
210 cycles); (iii) duration since the first pine logging (DEF-3: 3 years, DEF-4: 4 years; DEF-
211 5: 5 years); (iv) fallow ages (FA-0: uncultivated and/or under cultivation, FA-1: fallow 1
212 year-old, FA-2: fallow 2 year-old), and (v) tillage regime (T-0: no-tillage, T-1: light
213 tillage, *kobokaka*, T-2: heavy tillage, soil ploughing). Environmental parameters such as
214 (vi) slope values (low <10°, middle, between 10-20° and high >20°) and (vi) topographic
215 positions (Top-1: valley bottom, Top-2: middle slope, Top-3: upper slope and Top-4:
216 crest).

217

218 **2.4 Data analysis**

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

232

233 **3. Results**

234 **3.1 Floristic composition**

235 One hundred and twenty-five species belonging to 91 genera and 46 families were
236 identified in the whole plots. The most represented families are the Asteraceae (19
237 species), followed by the Poaceae and the Rubiaceae with 14 species each. Thirty-four
238 species are endemic. In total, 30 tree species, 32 shrub species, 51 herbaceous species and
239 12 liana species were counted. The majority of woody species (trees and shrubs) were

240 native or endemic. The species associated with cassava crops (Log+C) are *Manihot* sp.
241 (Euphorbiaceae) and annual herbaceous belonging to the Asteraceae family, such as
242 *Bidens pilosa*, *Erigeron naudinii* (Bonnet) Humbert, those associated with fallows
243 (Log+C+Ab) are essentially *Pteridium aquilinum* (L.) Kuhn (Dennstaedtiaceae),
244 *Rhynchelytrum repens* (Willd.) C.E. Hubb. (Poaceae), and *Imperata cylindrica* (L.)
245 Rausch (Poaceae). Post-logging regrowth (Log+Ab) are essentially characterized by
246 woody species such as *V. garnieriana*, *Syzygium emirnense* (Baker) Labat and G.E.
247 Schatz (Myrtaceae), *Weinmannia rutenbergii*, *Tambourissa purpurea* (Drake)
248 (Monimiaceae), *Polycias ornifolia* Baker Harms (Araliaceae).
249 The dependence between the species and the variables considered is significant (p
250 <0.001, RV coefficient = 0.447). The first co-inertia axis (68% of the total co-inertia)
251 opposes: (i) plots that are characterized by a low frequency of fires (FN-2), with soil
252 never tilled (T-0), not cultivated (CC-0), and located at the crest of hills (Top-4), and (ii)
253 plots that underwent one (CC-1) or two crop cycles (CC-2); were lightly tilled (*kobokaka*;
254 T-1) or ploughed (T-2), frequently burned (FN-3 and FN-4) and located at the valley
255 bottom (Top-1) (Fig. 2).

256 [Insert Fig. 2]

257 The species associated with type (i) plots are mainly trees and shrubs such as *V.*
258 *garnieriana*, *Gaertnera macrostipula* Baker (Rubiaceae), *S. emirnense*, *W. bojeriana*,
259 *Myrica phyllireaefolia* Baker (Myricaceae), *Rytiginia* sp. (Rubiaceae), *Oncostemum*
260 *bojerianum* A. DC. (Myrsinaceae), *Vaccinium emirnense* (Ericaceae), *Allophyllus* sp.
261 (Sapindaceae), *T. purpurea*, *Anthocleista madagascariensis* Baker (Loganiaceae), *P.*
262 *ornifolia*. Some lianas are present: *Cissus lemurica* Desc (Vitaceae), *Ligodium*

263 *lanceolatum* Desv. (Schizaceae). The species associated with the second type of plots (ii)
264 are essentially annual herbaceous species belonging to the Asteraceae family (*Ageratum*
265 *conyzoides* L. and *Helichrysum attenuatum* Humb.), the Poaceae family: *Imperata*
266 *cylindrica* (L.) Rausch, *R. repens* and a fern species *Pteridium aquilinum*. They are
267 associated with a few shrub species: *Trema orientalis* L. (Ulmaceae), *Solanum*
268 *auriculatum* Aiton (Solanaceae).

269 The second axis (16%) opposes plots that were: (iii) logged, cultivated, and then left
270 fallow one year (FA-1) or two years (FA-2), to those (iv) uncultivated (FA-0) and
271 recently cleared (3 years, DEF-3). The species associated with type (iii) plots are Poaceae
272 such as *Paspalum* sp., *Panicum* sp, Asteraceae *Elephantopus scaber*, *Helichrysum*
273 *cordifolium*, Rubiaceae *Morinda* sp., *Oldelandia herbacea* D. C., *Danais fragrans*
274 (Comm. Ex. Lam) Pers., some Fabaceae (*Hyposestes* sp., *Crotalaria uncinella* Lamk) and
275 Rosaceae (*Rubus rosaefolius* J. E. Smith), as well as some shrubs such as *Dodonaea*
276 *viscosa* Jacquin (Sapindaceae), *Halleria ligustrifolia* Bak. (Scrophulariaceae) and
277 *Morinda* sp. (Rubiaceae). The species associated with type (iv) plots are cassava *Manihot*
278 sp. (Euphorbiaceae) and *B. pilosa* (Asteraceae). In the end, the co-inertia analysis linking
279 species and agro-ecological variables made it possible to distinguish three vegetation
280 types: (i) plots less disturbed since the pinus trees were planted, (ii) plots abandoned 1 or
281 2 years previously after having been cultivated and subjected to intense tillage and fires,
282 located on the lower slopes, and (iii) plots under cultivation that were cleared some time
283 ago (5 years). The effect of slope was not significant. Human practices represented by the
284 number of crop-fallow cycles, the number of successive fires, and the tillage regime had
285 the greatest impact on the distribution of species in the study site.

286

287 **3.2. Effects of silvicultural and agricultural practices and other ecological variables**
288 **on vegetation diversity and structure**

289 The dependence between vegetation diversity and structure and agro-ecological variables
290 considered is significant ($p < 0.001$, RV coefficient = 0.516). The first co-inertia axis
291 (97% of the total co-inertia) is characterized by Below-Ground Biomass (BGB), Total
292 Biomass (TB), Above-Ground Biomass (AGB), Tree Density (D), and Shannon Index
293 (H') (Fig. 3).

294 [Insert Fig. 3]

295 The same first co-inertia axis showed that frequent fires, crop-fallow cycles and soil
296 ploughing reduce biomass values and, to a lesser extent, the Shannon-Weaver index
297 values (H'), tree density (D) and total biomass (TB) (Fig. 3). In fact, there is a global and
298 negative dependency between (i) these structure and diversity parameters (H' , BGB,
299 AGB, TB and D) and agricultural and silvicultural variables (fire number, tillage regime,
300 crop-fallow number) (Fig. 4, 5, 6).

301 [Insert Fig. 4]

302 [Insert Fig. 5]

303 [Insert Fig. 6]

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

308 [Insert Table 1]

309 The species richness of cassava crops is thus significantly lower than that of the fallows
310 and post-logging regrowth groups ($p < 0.001$). Between the latter two groups, the
311 difference of mean species richness is not significant ($p > 0.05$). The highest tree density
312 ($6,843 \text{ N. ha}^{-1}$) was recorded in post-logging regrowth and the lowest value (297 N. ha^{-1})
313 in cassava crops. A significant difference was observed between the total biomass values
314 of post-logging regrowth ($28.6 \pm 5.67 \text{ Mg ha}^{-1}$) and fallows ($5.83 \pm 1.5 \text{ Mg ha}^{-1}$) ($p < 0.001$).
315

316 **3.3. Life forms and dispersal mode of vegetation types**

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

319 [Insert Table 2]

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

331 percentage in the cassava crop ($1.7\% \pm 5.3$) and reach $14.0\% \pm 9.7$ in post-logging
332 regrowth ($F=4.840$; $p<0.05$).

333

334 **Discussion**

335 **4.1. Disturbed *Pinus* plantations as forest regeneration foci**

336 The results of this study confirm for the first time in Madagascar that logged forest
337 plantations operate as regeneration foci (Parrotta et al., 1997; Holl et al., 2011; Zahawi et
338 al., 2013) as defined by nucleation theory (Corbin and Holl, 2012; Piironen et al., 2015),
339 which enable an afforestation process to begin. The species-poor *Pinus* plantations
340 disturbed by logging have enabled the dispersion, natural regrowth, and establishment of
341 native and even endemic forest species such as *T. purpurea*, *Evodia madagascariensis*
342 Baker, *V. garnieriana*, *Nuxia capitata*, *N. sphaerocephala* and *Aphloia theiformis* (MBG,
343 Tropicos Data Base) in areas that previously had been grasslands.

344 In this regrowth, mainly composed of trees, shrubs and lianas, the proportion of
345 herbaceous species is low compared to post-crop regrowth of the same age and the
346 absence of shrub species in cassava crops is mainly due to clearing, burning, tillage, and
347 weeding operations before crop farming (Randriamalala et al., 2007; 2012). The
348 regeneration and presence of tree species and shrubs in post-logging regrowth and
349 fallows is therefore more important than in cassava plots. This also may be due to the
350 competition imposed by herbaceous species (heliophilous), which establish rapidly in
351 cassava plots and can block for a time the regeneration of pioneer shrubs and tree species
352 (more sciaphilous) (Carrière et al. 2002; Randriamalala et al., 2007; 2012). Shrub canopy

353 closure reduced herbaceous cover and favoured the development of tree and shrub
354 species in fallows and post-logging plots (Table 2).

355 The botanical composition and levels of species diversity are similar to those observed in
356 post-cultivation forest regrowth originating from slash-and-burn agriculture and the
357 secondary forests in the study area (Goodman and Razafindratsita, 2001; Randriamalala
358 et al., 2007; 2012; Randrianarison et al., 2015). The species diversity of this regrowth (H'
359 = 3.31) is comparable to that observed ($H' = 3.54$) in the regrowth on *Pinus patula* and
360 *Cupressus lusitanica* plantations in Colombia (Cavelier and Tobler, 1998). This value is
361 in contrast superior to that obtained by Senbeta et al. (2002) in regrowth on a *Eucalyptus*
362 plantation in Ethiopia. In terms of tree density, the value obtained in this study ($D = 6843$
363 $N.ha^{-1}$) is higher than that obtained by Senbeta et al. (2002) and Yirdaw (2001) in the
364 same type of plantation in Ethiopia ($D = 2325$ to $4495 N.ha^{-1}$) (Table 3). The age of these
365 plantations may be the reason for this difference, with the plantations in Ethiopia being
366 younger (less than 30 years). Moreover, the *Pinus* plantations in the study area were
367 never maintained (weeding and cleaning), allowing woody species to develop and
368 multiply rapidly. The tree density obtained ($D=6843 N.ha^{-1}$) is in the same range as that
369 obtained by Lee et al. (2005) in Hong Kong ($9031 < D < 10000$). However, it is less than
370 that recorded on the *Acacia* plantations ($7273 < D < 11169$) established in the 1920s in the
371 same study area (Randriambanona, 2010). These comparisons do not enable a conclusion
372 to be drawn regarding the factors determining the tree density values (Table 3). The total
373 plant biomass values of this natural regrowth ($28.6 Mg ha^{-1}$) are similar to those of an
374 *Acacia* plantation (70 years old) in the same study area (Randriambanona, 2010).

375 However, they are greater than those of regrowth in four-year-old *Albizia lebeck*
376 plantations in Puerto Rico (7.71 Mg ha⁻¹) (Parrotta, 1992).

377 The results of this study show: (1) the capacity of these logged *Pinus* sites composed of
378 few species to attract both zoochorous and anemochorous plant species (Schlawin and
379 Zahawi, 2008; Zahawi et al., 2013; Traverset et al., 2014), (2) Malagasy forest plant
380 species can spread outside forests, and this despite a limited community of seed
381 dispersing animals (Goodman and Ganzhorn, 1997), and (3) the capacity of these forest
382 species to grow in more or less unfavourable conditions to start a diversified forest
383 succession dynamic. In effect, Parrat (1966) noted the negative features of the physical
384 and chemical characteristics of the soil (shallow soil with pseudo-concretions, deficient in
385 phosphorous and exchangeable bases) of the Androy *Pinus* plantation schemes studied
386 here. The diversity of forest species observed in this regrowth is partially related to their
387 proximity to seed sources such as the “mature” forest (less than one km), the existence of
388 shred forest, the presence of extensive post-agricultural forest regrowth rich in species
389 (Randriamalala et al., 2015), and the presence of numerous isolated trees and copses
390 which contribute to the spatial heterogeneity of the landscape and thus promote fluxes of
391 fruit-eating animals dispersing seeds (Fournier et al., 2001; Martin et al., 2009; 2012).

392 These heterogeneous landscapes composed of numerous and diverse wooded areas
393 (Martin et al., 2012) are important seed sources and are decisive in the evolution of the
394 vegetation beyond the young stages. Indeed, the frugivorous forest species present in the
395 landscape were found to occupy almost exclusively areas with trees because they remain
396 highly dependent on the arboreal structures distributed in the landscape, as has been
397 demonstrated in several studies elsewhere (De Clerck et al., 2010; Harvey et al., 2006;

398 Söderström et al., 2003). These structures, including *Pinus* plantation regrowth, may thus
399 also serve as stepping stones, refuges and complementary habitats for birds and other
400 species fluxes in the agricultural mosaic (Fischer and Lindenmayer, 2002; Harvey et al.,
401 2006; Manning et al., 2006). These fluxes are what largely determine the nucleation
402 observed (Yarranton and Morisson, 1974).

403

404 **4.2. The effect of silvicultural and agricultural practices on regrowth**

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

412 These results corroborate those obtained in the same study area by Randriamalala et al.
413 (2012) and by Randrianarison et al. (2015) in post-farming forest regrowth that follows
414 slash-and-burn agriculture in natural forests. Soil variables have only a slight influence
415 on the post-crop regeneration dynamics (Randriamalala et al., 2007). Likewise, Pfund
416 (2000) obtained the same results on the same type of tropical rain forest in Beforona
417 further north in Madagascar. These studies also indicated that environmental factors such
418 as slope, altitude, exposure, and topographical position had a weak influence on
419 regeneration dynamics.

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

430 Likewise, the total plant biomass values of herbaceous regrowth where tillage and
431 successive fires have destroyed woody plants are five times smaller than those of pre-
432 forest regrowth, as other authors have shown as in Floret and Pontanier (1982).

433 Cultivated fields and young herbaceous natural regrowth are dominated by a large
434 number of anemochorous species (79% of species), while zoochorous plant species are
435 more developed in post-logging woody regrowth (50% of species). Guariguata and
436 Pinard (1998) reported that the wind can move seeds 100 metres or more from the seed
437 source. Cultivated fields thus are open spaces favouring the establishment of
438 anemochorous pioneer species which are spread efficiently and which constitute the first
439 stages of the plant succession (Carrière et al., 2002; González-Tagle et al., 2008). Longer-
440 lived pioneer species, particularly those spread by frugivorous animals, then establish
441 themselves thanks notably to the soil seed bank (Randriamalala et al., 2015).

442 The development of trees and shrubs in fallows and post-logging plots may attract seed
443 dispersers (Martin et al. 2010, 2012) and favour the installation of zoochorous, and, to a
444 lesser extent, barochorous species in such plots.

445

446 **4.3 Native vegetation regeneration on Pinus plantations**

447 The characterization of regrowth after disturbance (logging and agriculture) enabled a
448 description of three vegetation types that are different in terms of diversity, structure and
449 species composition. The changes observed over the course of the plant succession are
450 floristic and physiognomic. The considerably reduced number of species of cassava plots
451 (Log+C) follows agricultural practices and thus the procedures strongly influence the
452 succession (Mitja and Puig, 1991; Carrière et al., 2002; Styger et al., 2009; Randriamalala
453 et al., 2007). The fallows (Log+C+Ab) correspond to two-year old fallows that follow
454 two crop cycles (this is the maximum number of crop cycles recorded during the
455 investigation). The herbaceous cover is different and dominated by annual ruderal and
456 heliophilous species cited previously which are typical of the area's post-agricultural
457 regrowth (Randriamalala et al., 2007), but also by herbaceous pioneer species and shrubs
458 that have just established themselves (*Anthospermum emirnense*, *Oldelandia herbaceae*,
459 *Psiadia salviaefolia*, *Helichrysum attenuatum*). These ruderal species were already
460 present when the plot was cultivated in the form of weeds or in the soil seed bank
461 (Randriamalala et al., 2015). These short-cycle species are then gradually replaced by
462 pioneer but perennial species such as *Chassalia bojeri* and *Schefflera* sp. From a
463 physiognomic and species composition perspective, the plant succession then evolves
464 towards a young shrubs stage (Randriamalala et al., 2007). The third type, post-pinus

465 logging (Log+Ab), corresponds to tree formations that develop over the 10 years
466 following the logging of the *Pinus* plantation. These are complex vegetation types with
467 several strata as is the case for post-agricultural regrowth of this age in Madagascar
468 (Styger et al., 2009, Randriamalala et al., 2007). These three vegetation types, their
469 composition and their physiognomy, correspond to different stages of post-agricultural
470 vegetation successions such as described in the study area and elsewhere in Madagascar
471 (Styger et al., 2009; Randriamalala et al., 2007). These apply to herbaceous formations
472 (crop and herbaceous post-crop regrowth) up to shrubby and woody formations (pre-
473 forest regrowth). If one interprets the variations observed around this schema according
474 to land use modes, it is the intensity of agricultural use, and particularly the duration of
475 crop (whence the crucial role of crop history) and tillage, which are the most
476 unfavourable factors for the reconstitution of pre-forest vegetation (Randriamalala et al.,
477 2012; Randrianarison et al., 2015) and thus condition the characteristics and future of
478 plant successions in the area. In other words, the vegetation of these regeneration foci in
479 the *Pinus* plantations subjected to recurrent disturbances, such as cropping and with a
480 brief fallow period (Randriamalala et al., 2007; 2012), probably would evolve towards
481 degraded, pseudo-steppes like herbaceous formations with few species. This type of
482 vegetation dynamic is comparable to that observed by Pfund (2000), Styger et al. (2009)
483 and Randriamalala et al. (2007) in forest fallows of the Malagasy highlands.

484

485 **5. Conclusion**

486 The results obtained made it possible to confirm the role of logged exotic species
487 plantation foci in promoting the dispersion, installation and gradual regeneration of

488 native, indeed endemic, forest species. The openings caused by disturbances enabled
489 native species to install themselves within several years, develop, and result in species-
490 rich formations. The important extent (in duration and intensity) of the disturbance
491 caused by putting land under cultivation appears to be decisive in determining the status
492 of post-disturbance and post-agricultural vegetation on these plantations. Weak
493 anthropogenic pressure leads to more diverse and complex pre-forest regrowth similar in
494 terms of structure and composition to secondary forests. This capacity of native species to
495 regenerate in reforested areas could be used to promote the afforestation of species-poor
496 grasslands and forest succession dynamics in the numerous former plantations of exotic
497 species in Madagascar (*Acacia* spp., *Eucalyptus* spp. *Pinus* spp.), but also to imagine new
498 avenues for assisted forest regeneration in degraded Malagasy forest areas. This study
499 also contributes to a better understanding of the conditions for maintaining biodiversity in
500 the many post-logging and post-agricultural regrowth and rural landscapes on the edges
501 of Malagasy forests.

502

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512

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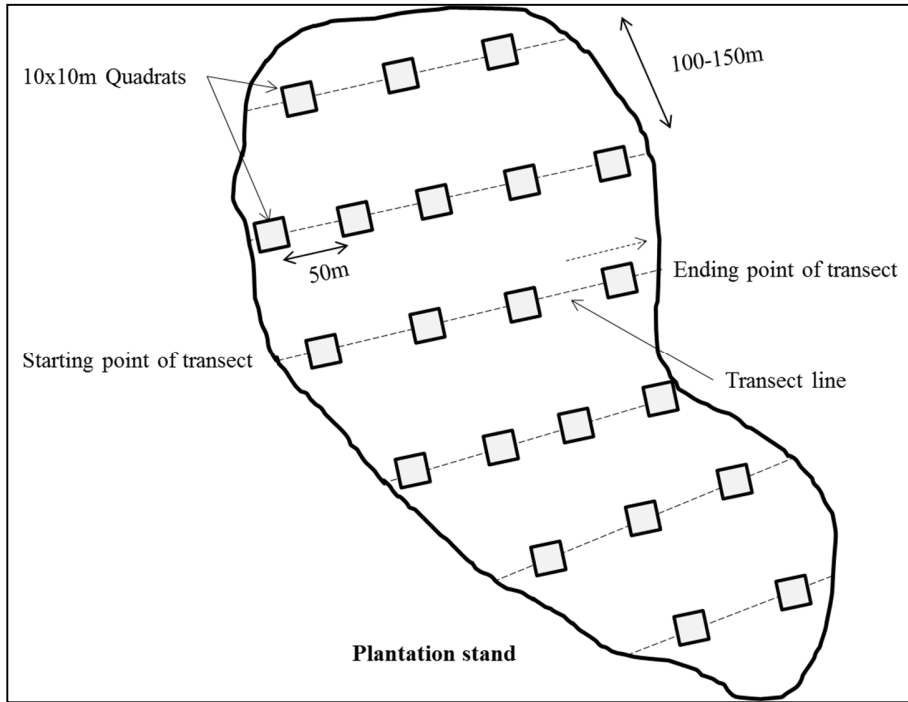
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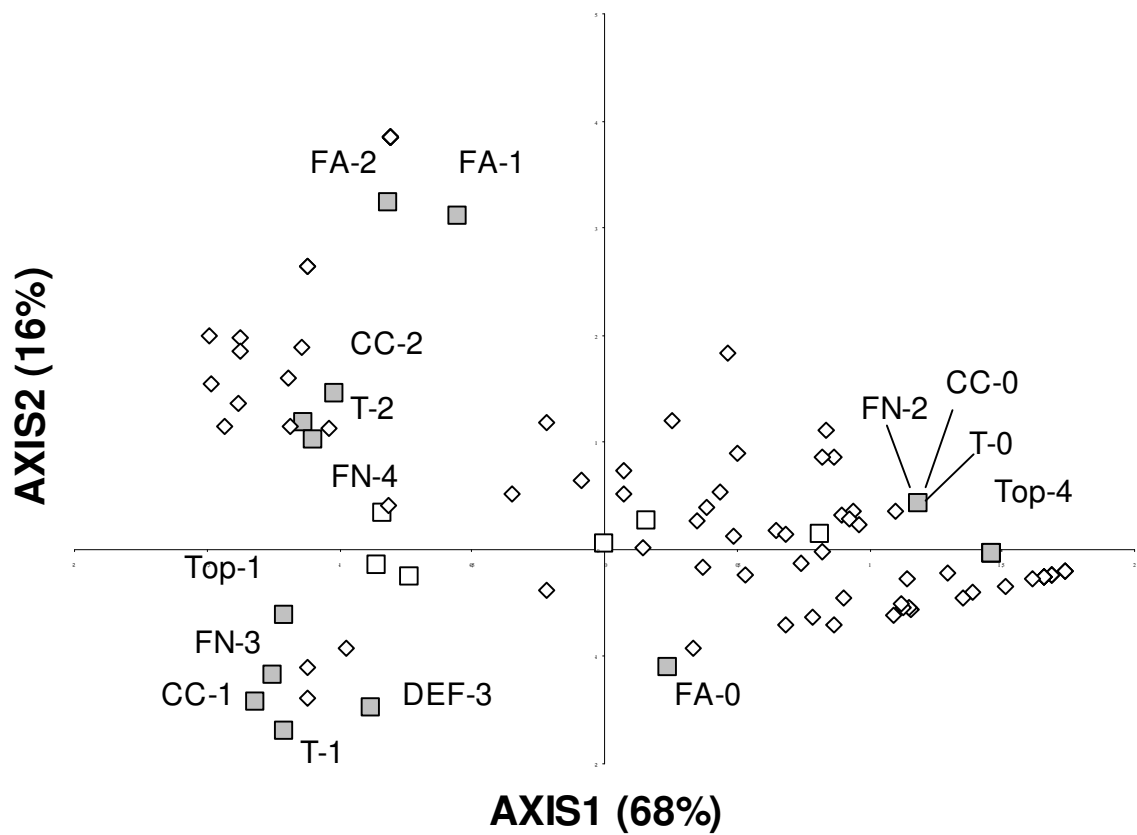
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Figure 1. Vegetation sampling.



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703 Figure 2. Co-inertia analysis: relation between agro-ecological variables and species

704 distribution. **CC**: crop-fallow cycle (0: No, 1: CC; 2: 2 CC); **FA**: fallow age (0 year; 1

705 year; 2 years); **FN**: Fire frequency since first clearing (2: ≤ 2 fires; 3: ≤ 4 fires; 4: ≥ 4 fires);

706 **T**: tillage regime (0: no tillage; 1: light tillage; 2: heavy tillage); **Top**: plot's

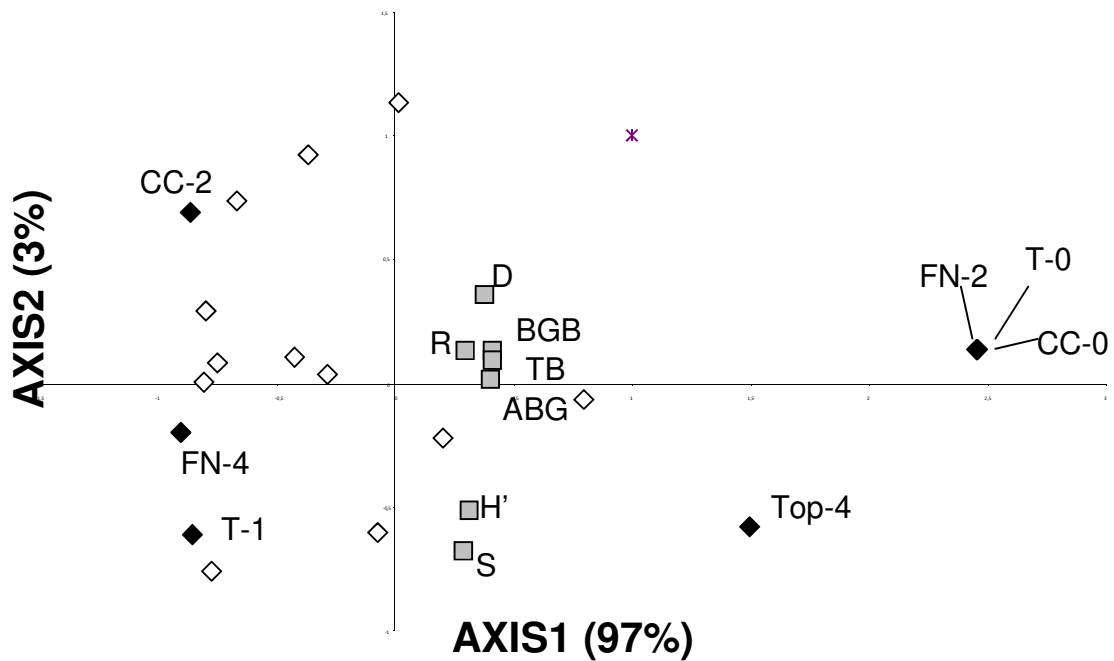
707 topographical localisation (1: bottom; 4: crest). Diamond: species; Grey squares: agro-

708 ecological variables that affect species distribution; White squares: other agro-ecological

709 variables.

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714 Figure 3. Co-inertia analysis: relation between agro-ecological variables and vegetation

715 diversity and structure. **CC**: crop-fallow cycle (0: No CC; 2: 2 CC); **FN**: Fire frequency

716 since first clearing (2: ≤ 2 fires; 3: ≤ 4 fires; 4: ≥ 4 fires); **T**: tillage regime (0: No tillage; 1:

717 light tillage; 2: heavy tillage); **Top**: plot's topographical localisation (1: Valley bottom; 4:

718 crest). Black diamonds: agro-ecological variables that affect vegetation diversity and

719 structure; White diamonds: agro-ecological variables; Grey squares: vegetation diversity

720 and structure variables: **S**: species richness, **H'**: Shannon-Weaver index, **R**: Evenness

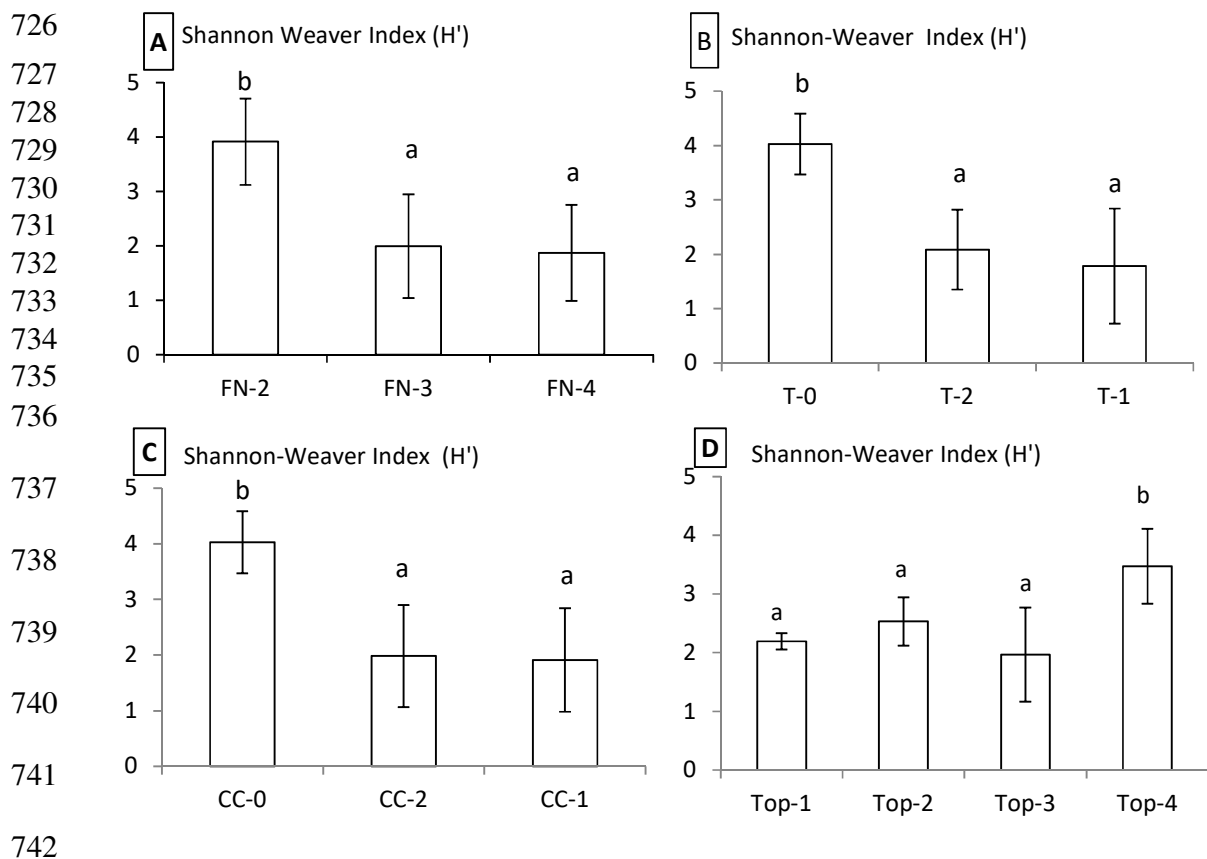
721 index, **D**: Tree density, **BGB** Below-Ground Biomass, **AGB** Above-Ground Biomass;

722 **TB**: Total Biomass.

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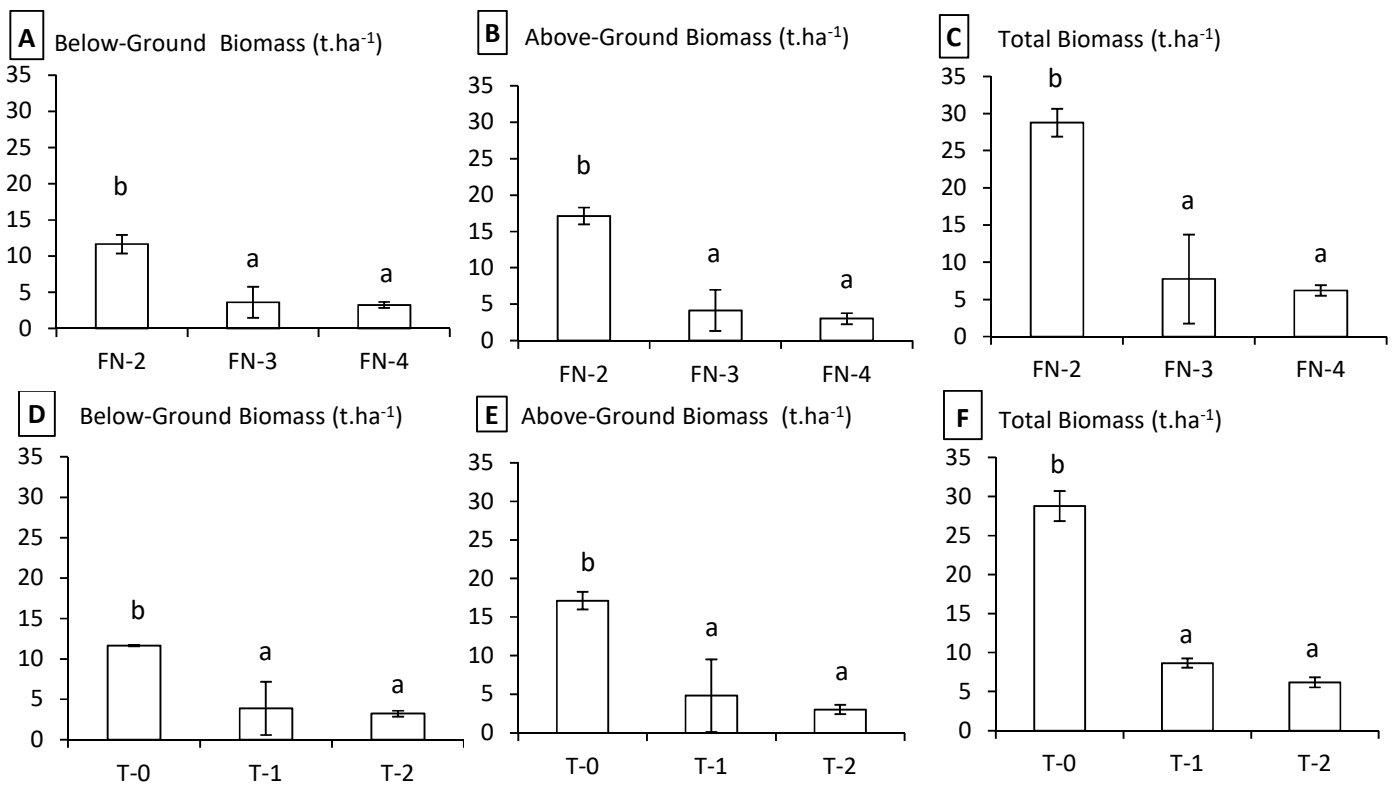
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743 Figure 4. Effect of cropping history and environmental variables on Shannon-Weaver
 744 index. **FN**: Fire frequency since first clearing (2: ≤ 2 fires; 3: ≤ 4 fires; 4: ≥ 4 fires); **CC**:
 745 crop-fallow cycle (0: No CC; 2: 2 CC); **T**: tillage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

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

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791 Figure 6. Effect of cropping history and environmental variable on tree density. **FN**: Fire

792 frequency since first clearing (2: ≤ 2 fires; 3: ≤ 4 fires; 4: ≥ 4 fires); **CC**: crop-fallow cycle

793 (0: no CC; 2: 2 CC); **T**: tillage regime (0: no tillage; 1: light tillage; 2: heavy tillage);

794 **Top**: plot's topographical localisation (1: valley bottom; 4: crest). Vertical bars stand for

795 S.E.

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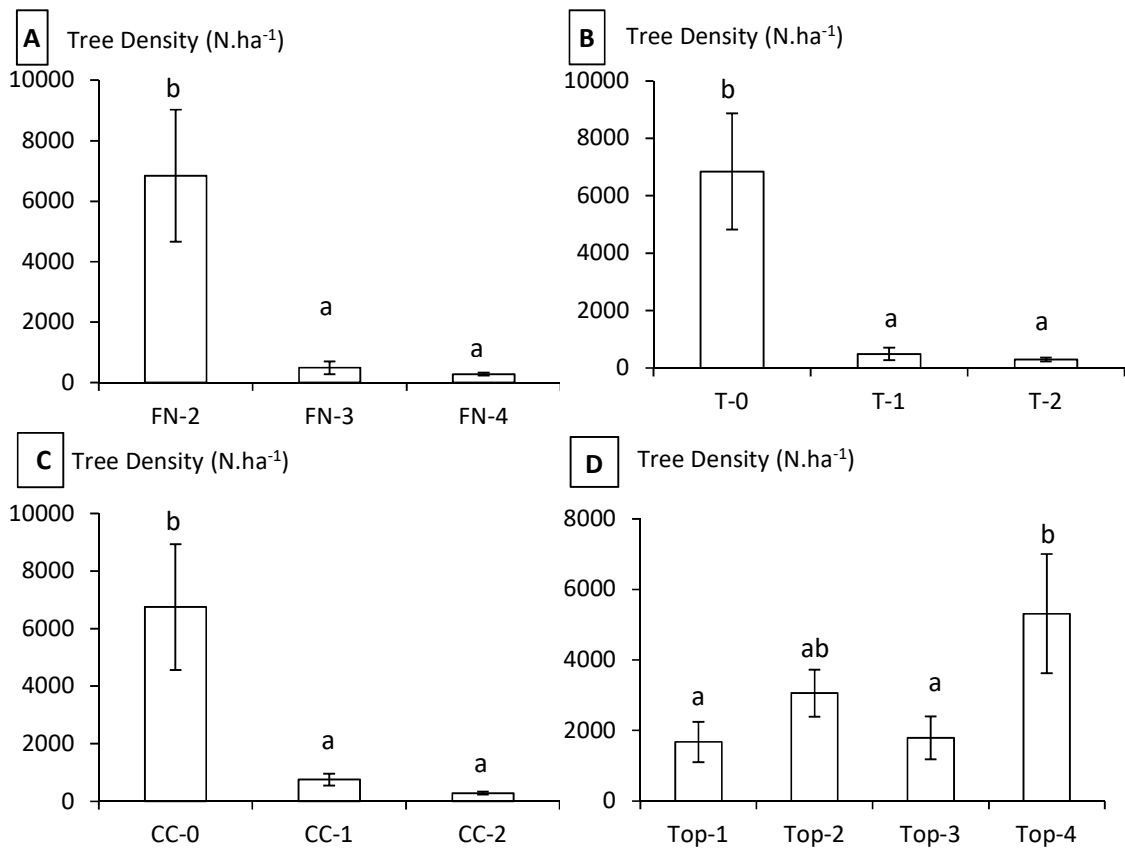


Table 1: Diversity index, densities and biomass of vegetation groups (means \pm S.E). The means identified with the same letter are the lines representing statistically homogeneous groups at a 5% probability level according to the Newman-Keuls test. Log: Pine Logging; C: Cultivation, Ab: Abandonment

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

Table 2: Life forms and species mode dispersion in percentage (means \pm 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	Cassava crops (Log+C)	Fallows (Log+C+Ab)	Post-logging regrowth (Log+Ab)	<i>P-value</i>
Trees	00.0 \pm 0.0a	15.6 \pm 6.5a	35.0 \pm 12.2b	< 0.0001
Shubs	00.0 \pm 0.0a	27.3 \pm 8.1b	23.7 \pm 9.9b	< 0.0001
Grass	97.5 \pm 7.9c	52.1 \pm 11.8b	28.6 \pm 19.6a	< 0.0001
Lianas	2.5 \pm 1.9a	5.0 \pm 4.1a	12.7 \pm 7.7b	< 0.0051
Anemochorous	79.3 \pm 6.8c	60.9 \pm 12.7b	35.7 \pm 11.9a	< 0.0001
Zoochorous	19.0 \pm 5.2a	34.0 \pm 10.5b	50.3 \pm 9.1c	< 0.0001
Barochorous	1.7 \pm 5.3a	5.1 \pm 5.3a	14.0 \pm 9.7b	< 0.002

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)	7273-11169	
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- 2700m	<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	Yidraw (2001)
	1200 mm	<i>Cupressus lusitánica</i> (14-16)	8218	
	19°C-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°C-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°C-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			Shibayama et al. (2006)
	3600-6000 mm	<i>Pinus caribaea</i> (22-28)	358-2828	
	25°C			