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## **Multiple values of isolated and clusters of Ficus tree species protected by Betsileo farmers in rural landscapes in Madagascar: implications for biodiversity conservation**

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# Biodiversity and Conservation

## Multiple values of isolated individuals of Ficus tree species protected by Betsileo farmers in rural landscapes in Madagascar. Implications for biodiversity conservation --Manuscript Draft--

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<b>Abstract:</b>	<p>In Madagascar, biodiversity, local livelihoods and agroecosystems are increasingly threatened. It is critical to understand and support local social-ecological systems that sustain livelihoods and value biodiversity. This study investigates why Betsileo communities in Ambendrana and Sahabe protect isolated individuals and clusters of Ficus species in their rural landscapes. Ficus trees have multiple values and sustain webs of ecological interactions that favor biodiversity. We show that spontaneous seedlings of Ficus are protected and that people also actively propagate Ficus by stem cuttings. Their multiple values and uses and the distribution patterns of each species, are linked to social-ecological dynamics and to the historical construction of local landscapes. Both past and present uses associated with each Ficus species define how they are protected. Different sets of practices associated with each species are governed by both material and symbolic considerations. Ficus reflexa, a boundary marker of zebu corrals, has a symbolic role in protecting humans and livestock and checks erosion; F. lutea is a marker of residences of ancient noble classes and F. tiliifolia is a remnant of swidden agriculture and a marker of the memory of ancestors, but its numbers are shrinking. Ficus trees are protected but there is no strict taboo against cutting them when they hinder crop production. Their potential role for biodiversity conservation is linked to these social-ecological dynamics. Based on these findings, we propose some rules of thumb for developing collaborative</p>	

	<p>approaches which consider synergies between local and scientific knowledge.</p>
<p><b>Response to Reviewers:</b></p>	<p>Responses to reviewer 1: Many thanks for your detailed comments and your thoughtful visions that have helped us clarify our statements. Please find below our responses:</p> <p>1. "you repeatedly talk about „noble", „poor" and „ordinary" social classes who have different access rights to different Ficus trees. I am aware that in many Malagasy societies caste systems are in place but many readers are not, so i would suggest that you explain this early in the introduction and also relate these groups ethnically, in power and its socio-cultural context". We have responded to this comment. Please see lines 92-127.</p> <p>2. "You don't really study anything about livelihoods, therefore, i would remove this from all parts of the manuscript, i.e. for sustaining „biodiversity and livelihoods", it is certainly not the case that this is always mutually beneficial. You would have had to give this a framework , i.e. „sustainable livelihoods" or similar but you do don't. As it is now , it is not clear what is meant. Livelihoods mean different things to economists, geographers and social scientists".</p> <p>In the introduction (lines 81-94), we explain the following : (1) that livelihoods are very strongly linked in Madagascar to biodiversity. We explain that human activities in Madagascar have driven deforestation. There is thus no ambiguity in our statements. We do not imply that biodiversity and livelihoods necessarily have positive effects on each other. When we say the following : « The current decline in the rule of law in Madagascar could greatly harm biodiversity and local livelihoods”, we clearly mean that local livelihoods are highly dependent upon biodiversity. We do not say that local livelihoods necessarily sustain biodiversity. The whole paper in fact aims at identifying specific connections between people and some elements of biodiversity, in this case Ficus species, that could potentially help sustain biodiversity while also sustaining livelihoods. The roles of Ficus as keystone species that can potentially enhance the conservation of biodiversity are fully recognized in literature that we mention.</p> <p>Furthermore, as ethnoecologists, and not “social scientists” ( ethnoecology combines ethnology and approaches in ecology), we do not consider that livelihoods are independent from ways people perceive, use, and manage Ficus species within their rural landscapes. In this particular case, these elements of biodiversity have impacts on soil (fertilization) and water, impacts on feeding habits of children (much work on food systems shows that children access foods that adults do not use and that this often neglected part of their diets contributes nutrients essential to their health), on culture and interpersonal relationships, and on people’s beliefs and religion. It is fully recognized that human well-being is linked to all these dimensions of livelihood (cf Sustainable Development Goals, also see Sterling et al. 2017). We therefore consider that our use of the term “livelihood” fits with the content of this paper and cannot be removed.</p> <p>Sterling, E. J., Filardi, C., Toomey, A., Sigouin, A., Betley, E., Gazit, N., ... Stege, K. (2017). sustainability indicators across scales. <i>Nature Ecology &amp; Evolution</i>, 1(December). <a href="https://doi.org/10.1038/s41559-017-0349-6">https://doi.org/10.1038/s41559-017-0349-6</a></p> <p>3. « the frameworks about „nature" and „biodiversity" are inconsistently used throughout the manuscript. Given the (partly) social science approach of this paper, this needs more clarity and I would expect this section to be a bit more critical. Nature is a social construct, according to most social scientists, whereas biodiversity is not, which is much narrower defined but also includes many other things beyond tree diversity »As ethnoecologists, we do not use « Nature » only as a social construct, but we use a precise definition (given on lines 96 – 100) and we explain how the concept of nature that we use relates to biodiversity. We do not wish to remove the word biodiversity from the paper, because it is clear that when we speak of a species of Ficus with a scientific name, its position in a landscape, and how people relate to it, we do consider it as an element of biodiversity to which people refer to very precisely, even though vernacular classifications may differ from scientific ones.</p> <p>Malagasy rituals, traditions and beliefs are around nature but NOT about biodiversity, this is an interpretation, and many anthropologists and social scientists will not agree with this statements. Either remove it or back it up with more discussion and references. Explained above and references added in the manuscript.</p>

4. We deleted when possible some of Carrière's citations.

5. We deleted the mention to diameters because we used tree crown structure to elaborate the tree category that we used to identify the population structure. We backed this approach with two new references.

6. We counted almost in an exhaustive way all trees of the three species we have considered and therefore this was not a sample. This is a descriptive approach of the status of what had been preserved in the two study sites. We have no comments therefore to make on sample size.

7. We added a short sentence on this subject. We consider that in the introduction part, we discussed what is known about these trends in Madagascar and have Added in that part more details about the failure of many NG projects. Our paper did not aim specifically to develop such elements that are contextual, not the subject of our research.

Other comments: 90: current decline in rule of law, rule of law is in fact slowly improving (compared to the post 2011 area: we have cited the Jones et al. 2019 paper which is the most recent and cannot assess the these trends of changes otherwise.

Regarding the Reviwer 2 propositions, we included almost all changes requested and are thankful for the help in refining the paper.

[Click here to view linked References](#)

1 **Full Title:**

2 Multiple values of isolated individuals of *Ficus* tree species protected by Betsileo farmers in  
3 rural landscapes in Madagascar. Implications for biodiversity conservation

4

5 **Short Title:**

6 Multiple values of *Ficus* trees in rural landscapes, Madagascar

7

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80 INTRODUCTION

81 Madagascar is widely recognized for the high rate of endemism and the richness of its  
82 biodiversity (Goodman and Benstead 2003; Ganzhorn et al. 2014). Most of the population of  
83 Madagascar (80 %) lives in rural areas, conducting agriculture and pastoralism, and relies on  
84 biodiversity for food, medicine, fuelwood, and timber (Waeber et al. 2015). Increasing threats  
85 to Madagascar's biodiversity critically affect the integrity of ecosystems, inside protected areas  
86 and in rural landscapes, affecting local livelihoods (Jones et al. 2019). Agriculture, charcoal  
87 production and zebu grazing in forest areas by local inhabitants have driven deforestation,  
88 resulting in loss of habitats and biodiversity (Waeber et al. 2015). However, corruption  
89 associated with new agribusiness and mining activities brings new threats from forces acting at  
90 national and global scales. The current decline in the rule of law in Madagascar could greatly  
91 harm biodiversity and local livelihoods (Jones et al. 2019).

92 In this paper, nature is used following the concept of Nature's Contributions to People  
93 (NCP) defined by Diaz et al (2018) whereby nature relates to living nature, i.e., the diversity  
94 of organisms and the ecological and evolutionary processes within ecosystems. "Nature" can  
95 have different cultural meanings for different societies. In this paper, we consider this living  
96 part of nature as equivalent to biodiversity.

97 In Madagascar, people are connected to the power of life and nature known as *Hasina*,  
98 through the mediation of ancestors, their burial places and particular species or elements of  
99 ecosystems (Harper 2003, Aumeeruddy-Thomas et al. 2018). Access to different parts of  
100 territories and resources follows specific rules and management practices framed upon  
101 reciprocity between people and elements of biodiversity (Diver et al. 2019). Within this  
102 context, some species, groups of species, or ecosystems such as portions of forests are seen as  
103 active agents that may interact with people or elements that participate in the identity of  
104 people. Indeed, from the perspective of some Malagasy groups, forests reflect not only natural

105 history, but social history. They are viewed as symbols of shared histories of collective  
106 empowerment, including resistance to outside control (Harper 2003). Social organization  
107 governing access to different types of elements of nature in Madagascar is based on social  
108 hierarchies and systems of power that have built up along history. In particular, the Merina<sup>1</sup>  
109 king Andrianampoinimerina ((1787-1810) , united Malagasy groups (e.g. Sakalava, Betsileo,  
110 Betsimisaraka and many others that previously were organized in the form of small  
111 independant kingdoms) to establish a state at the beginning of the 19<sup>th</sup> century. enforced a  
112 caste system including *andriana* (noble), *hova* (free) or *andevo* (slave). This system served  
113 the interests of the king's taxation system based on a reinforced link to the land and tombs  
114 that also facilitated the control of allegiance by all social groups to the Merina. The *andriana*  
115 status could be conferred for loyalty or service to the king, while *hova* took on varied  
116 meanings in different parts of the island but in all cases referred to people possessing lands  
117 and ancestors buried in these lands.

118 Some *Ficus* species, such as *Ficus lutea*, are among these particular species that  
119 symbolized the power of the king Andrianampoinimerina and contributed to enforce his  
120 hegemony (Aumeeruddy-Thomas et al. 2018).

121 In the Highlands, the organization of landscapes is defined by diverse categories of  
122 spaces, which each bear a local term that designates jointly ecological aspects and associated  
123 practices (Blanc-Pamard 1986, Blanc-Pamard and Rakoto Ramiarantsoa 2007). Formal and  
124 informal social hierarchies, local institutions and practices (including rituals, such as zebu  
125 sacrifices in the case of Madagascar) and exchange networks define people's relationships  
126 within social-ecological systems (Berkes and Folke, 1998). Such complexity is rarely taken  
127 into account in conservation policies in Madagascar, which are historically based on zonation

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<sup>1</sup> The Merina is the dominant cultural group that lives in the northern part of the Highlands in Antananarivo and in the surroundings of what came to be the capital city of the country.

128 and restricted access shaped solely by biological considerations Marie et al. 2009, Diver et al.  
129 2019).

130 Indeed, conservation policies in Madagascar are based on protected areas from which  
131 people are excluded. These policies, initiated by the French colonial government, have  
132 continued to the present, with investment from numerous international conservation NGOs. The  
133 network of protected areas was expanded in 2003. Additions included the establishment of  
134 ecological corridors such as the Ambositra-Vondrozo forest strip connecting Ranomafana and  
135 Andringitra National Parks that was created in 2008. This corridor, which borders our study  
136 area, acquired an official status as a “New Protected Area” with restricted access (Blanc-Pamard  
137 and Rakoto Ramiarantsoa 2007; Rakoto et al. 2014).


138 As in the rest of the world, since the 1970’s there have been many efforts in Madagascar  
139 to develop approaches that integrate biological conservation and human development (Marie et  
140 al. 2009; Aumeeruddy-Thomas 2013). Numerous efforts were made in Madagascar by a large  
141 diversity of NGOs to integrate human development into conservation. However, it seems that  
142 the urgency for developing the conservation network, led by the global conservation agenda  
143 and its priorities, accorded little attention to local knowledge, practices and institutions  
144 including attachment to land (Marie et al. 2009). Globally, results of similar efforts elsewhere  
145 have generally been unsatisfactory (Ward et al. 2018). In Madagascar, GELOSE, a national law  
146 adopted in 1996, aimed to devolve the management and conservation of forests to local  
147 communities and stimulate economic development. Contractual agreements between the state  
148 and local community-based groups (CoBa) were drawn up, defining rules of access in a  
149 zonation system based mainly on conservation priorities. Social scientists pointed out that  
150 GELOSE redefined access to spaces in a way that did not take into account practices of the  
151 area’s rural population (Blanc-Pamard and Fauroux 2004). McConnell and Sweeney (2005)  
152 further explain: The policies “reify monolithic communities to which authority can be rapidly

153 devolved, when in fact these ‘local communities’ are difficult to define, much less successfully  
154 engage in conservation activities, especially after a long era of strong state control”. These  
155 experiences highlight the gap between global conservation endeavors and local social-  
156 ecological dynamics.

157         At the global level, new approaches take into account the importance and role of  
158 biodiversity outside protected areas, and address landscape and social dynamics (Mora et. al.  
159 2011). New types of conservation areas include IUCN categories V and VI, UNESCO  
160 Intangible Heritage sites, FAO Global International Agricultural Heritage Sites, and other  
161 types known as “other effective area-based conservation measures” or “OECM”  
162 (<https://www.iucn.org/commissions/world-commission-protected-areas/our-work/oecms>)  
163 among which different types of governance are recognized including by governments, private  
164 actors, indigenous peoples and local communities, and areas of shared governance.

165         Maintaining extensive anthropic landscapes featuring a mosaic of low-input  
166 agriculture has been characterized as a “land-sharing” strategy that conserves biodiversity  
167 while sustaining agricultural production (Perfecto and Vandermeer 2010). Such landscapes  
168 are often significant reservoirs of biodiversity (Kun et al. 2009; Kull et al. 2013). This  
169 biodiversity may be critical to ensure the resilience of ecosystem functions, particularly in the  
170 present context of rapid climate change (Manning et al. 2019, Renard & Tilman 2019).


171         Tees or clusters of trees (e.g. small woods, hedges) initially part of forest environments,  
172 or those planted as isolated trees or within clusters of trees, can help create or re-establish  
173 connectivity in **fragmented** agrarian landscapes. They offer resources to animals and  
174 accelerate plant successions (Carrière 2002; Manning et al. 2006; Eden et al. 2015). Species of  
175 *Ficus* (Moraceae) are particularly important in this regard. Trees of this pantropical genus,  
176 which numbers about 800 species, are hubs in vast webs of interactions. These include the  
177 specialized insect pollinators, parasites and parasitoids of *Ficus*. They also include mammals

178 and birds that eat fruits and disperse seeds not only of *Ficus* but also many other plants  
179 (Shanahan et al. 2001; Harrison and Shanahan 2005; Kjellberg et al. 2005). When *Ficus* grow  
180 as isolated trees, they act as stepping-stones for forest animals in open habitats (Martin et al.  
181 2009). They also function as nuclei accelerating plant succession, as the frugivorous animals  
182 that visit them disperse seeds of forest plants in their droppings. These seeds germinate and  
183 establish, forming small patches of vegetation around these focal trees (Carrière 2002).   
184 Madagascar and elsewhere, *Ficus* trees are also associated with multiple social values that  
185 connect people to territories and nature (William and William 2013, Eden et al. 2015; Rafidison  
186 et al. 2016; Aumeeruddy-Thomas et al. 2017, 2018). Madagascar has 25 native *Ficus* species  
187 belonging to four subgenera, of which 15 species are endemic and four are shared with the  
188 African continent (Dalecky et al. 2003; Rafidison et al. 2011). Taxonomic and ecological  
189 information on *Ficus* species of Madagascar is given in Table 1. Three *Ficus* species represent  
190 33% of the isolated trees (sample size 45) in Betsileo rural landscapes; they attract numerous  
191 bird species as well as bats (Martin et al. 2009). Some species, such as *F. tiliifolia*, are highly  
192 attractive to frugivorous animals (Goodman and Ganzhorn 1997). *Ficus* have a cultural value  
193 for the Betsileo, and are protected for this reason, but a full understanding of their multiple  
194 values and their contributions to social-ecological dynamics is still lacking (Moreau 2002;  
195 Martin et al. 2009).

## 196 OBJECTIVE

197 Our objective is to understand social-ecological dynamics that affect the distribution,  
198 uses and values at the landscape level of *Ficus* species that are protected by Betsileo  
199 communities in two rural landscapes. We use our findings to discuss the importance of  
200 collaborative approaches that consider local social-ecological dynamics that can improve  
201 biodiversity management and human livelihoods.

202 We focus on farmers' local knowledge and historical, cultural and practical reasons that  
203 explain why farmers plant and/or protect *Ficus* trees in their agrarian landscape. We use an  
204 ethnobotanical approach to assess the uses, multiple values and distribution of *Ficus* spp. within  
205 the territories of two Betsileo villages that border the Ambositra-Vondrozo forested corridor.  
206 Our specific aims are to:

- 207 (1) Identify the relationships between their distributions and uses, within the history of   
208 the construction of their rural landscape by the Betsileo in two sites;
- 209 (2) Identify past and present socio-political, economic, practical and symbolic values  
210 attributed to *Ficus* species by two Betsileo communities and consequences of these  
211 values for their management;
- 212 (3) Propose rules of thumb for designing collaborative approaches based on our  
213 understanding of local social-ecological systems and the roles of key elements such  
214 as *Ficus* species.

215

## 216 STUDY SITE, MATERIALS AND METHODS

217 Our study area is located on the eastern side of the Malagasy Highlands. It is bounded  
218 to the west by a mountain ridge that stretches north to south along Madagascar. A forest strip  
219 known as the Ambositra-Vondrozo corridor, characterized by a dense mid-altitude humid forest  
220 (Goodman & Razafidratsita 2001), covers the portion of forest adjoining our study area and  
221 joins Ranomafana and Andringitra National Parks. Tanala people, who are distinct from the  
222 Betsileo, inhabit the humid eastern slopes of this escarpment.

223 Betsileo cultural groups inhabit our study area, which is characterized by rugged relief  
224 comprising hills, slopes, valleys and flat marshy areas. Farms comprise hill and downslope  
225 marshy lands, the latter often exploited for paddy rice cultivation. Irrigated terraced lands are

226 also used for paddy rice. Slopes are used to grow rain-fed maize, cassava and beans. Permanent  
227 agriculture has replaced swidden agriculture (*tavy*), which may still occur on forest fringes. To  
228 the east, the rural landscape is a mosaic of secondary forest of varying age resulting from past  
229 swidden cultivation, intermingled with sedentarized paddy rice and upland cultivated areas. To  
230 the west, the agricultural landscape becomes increasingly open, with plantations of eucalyptus  
231 or pine found only on hilltops. Lying in continuity with the Malagasy Highlands, this rural  
232 landscape is bounded on the west by a series of high cliffs (Fig 1). The climate is tropical with  
233 a dry season (April – September) and a rainy season (November – March); altitude varies  
234 between 1100 and 1300 m a.s.l.

235 The mosaic of cultivated and non-cultivated habitats, including fragments of native  
236 forest, plantations of non-native species (e.g. *Eucalyptus*), hamlets and villages is highly  
237 heterogeneous, thus favoring some types of biodiversity associated with anthropogenic rural  
238 landscapes (Kull et al. 2013).

239 We investigated the territories, comprising customary agrarian and forest lands, of two  
240 distinct Betsileo villages, Ambendrana (Site 1; Lalangina district, *Fokontany* (municipality)  
241 Iambara) and Sahabe (Site 2; Ambalavao district, *Fokontany* (municipality)  
242 Andohanimananatanana), separated by approximately 60 km (Fig 1).

243 Previous works in human geography (Moreau 2002; Blanc-Pamard and Rakoto  
244 Ramiarantsoa 2007) and in ecology and ethnobotany (e.g. Carriere et al. 2005; Martin et al.  
245 2009) in these sites provide context for our work. Further context is provided by studies of  
246 distribution patterns of *Ficus* species in the forest corridor and the two national parks (Kjellberg  
247 et al 2010, Rafidison et al. 2011). Choice of these two sites for this study allowed investigating  
248 how social values accorded to *Ficus* species interact with their ecology.

249 Our two study sites belonged historically to distinct Betsileo chiefdoms until the  
250 unification of the country by the Merina in the 19<sup>th</sup> century. The Betsileo cultural group the  
251 largest cultural group that inhabit the southern part of the Highlands (Harper 2003). The  
252 Betsileo originate from an admixture of groups of migrants who successively colonized the  
253 highlands. Their language includes linguistic elements of different cultural groups (Antemorro,  
254 Tanala, Merina) (Dubois 1938). They transformed the forest with swidden agriculture (*tavy*),  
255 cultivating mostly rainfed rice (Dubois 1938). The advent of irrigated rice cultivation among  
256 the Betsileo during the late 17<sup>th</sup> and early 18<sup>th</sup> centuries has been attributed to internal changes  
257 associated with a demographic increase, participation in trade of slaves and weapons, and  
258 contacts with the Merina (Kottak 1977). The Betsileo were comprised of distinct small  
259 chiefdoms, each with its specific frontiers, territories and hierarchical system (Kottak 1977;  
260 Raherisoanjato 1984). Ambendrana (Site 1) was part of the Lalangina chiefdom (Kottak 1977),  
261 and Sahabe (Site 2) belonged to the Arindrano chiefdom (Giambrone 1973; Kottak 1977). After  
262 unifying the country during the 19<sup>th</sup> century, the Merina reinforced drainage and irrigation to  
263 favor paddy rice cultivation and collected taxes. The French colonial government ruled  
264 Madagascar from 1896 to 1960.

265 Details on *Ficus* species found in the study area (Table 1) show aspects of their ecology,  
266 their life forms, fruit size and geographical distribution. We analyzed the uses and values of all  
267 the nine *Ficus* species found in our sites, and looked in detail only at the distribution of the three  
268 most common species, *Ficus lutea*, *F. reflexa* and *F. tiliifolia*. These species are found mainly  
269 in eastern and southeastern Madagascar at altitudes below 1700 m (Dalecky et al. 2003;  
270 Rafidison et al. 2011).

271 We conducted ethnobotanical studies during successive periods of 15 days totaling six  
272 months in the two sites. Open-ended interviews were conducted with 64 (Ambendrana) and 90  
273 persons (Sahabe), children, adults and elders of both sexes from farmer families (Table 2).

274 Among all persons interviewed, the elders *ray aman-dreny*, (literally “father and mother”  
275 representing customary heads), and *ombiasy* (traditional healers), and lineage heads (adults or  
276 elders), had extensive knowledge of local history and social practices. Local *ombiasy* use *Ficus*  
277 species, among other plants, to mediate, through dreams and visions, interactions between  
278 humans, ancestors and intangible entities of nature (Beaujard 2009). Lineage heads and elders  
279 accompanied us to locate *Ficus* individuals and provided ethno-historical information on  
280 present-day practices and oral memory of past uses and practices. We recorded local names,  
281 sayings and stories relating to plants and places. All interviews were in Betsileo and were  
282 transcribed literally. Following the terms of our research permit  
283 (No°:193/08/MEFT/SG/DGEF/DSAP/SSE-01/07/08), all informants were informed that their  
284 responses would be used for scientific purposes and all gave their consent. Heads of these  
285 villages and major informants were invited to Antananarivo in 2016 and contributed as authors  
286 to a paper presenting preliminary results (Rafidison et al. 2016).

287 We determined the distribution of individuals of the three most common *Ficus* species  
288 across the two rural landscapes according to their position relative to distinct land-use units  
289 distinguished by local people. Land-use units were defined as social-ecological facets, building  
290 on the concept of ecological facet used by Blanc-Pamard (1986). We define a social-ecological  
291 facet as a locally recognized spatial entity characterized by homogeneous ecological and use  
292 characteristics. All social-ecological facets are designated by distinctive names in Betsileo.  
293 These names are interpreted locally to represent types of land associated with a particular set  
294 of practices. They include land-use units as well as elements such as tombs, megaliths, rivers,  
295 rivulets and paths that are markers of agrarian and forest territories (Table 3). We  
296 complemented the list of facets recorded by Blanc-Pamard and Ralaivita (2004) in Ambendrana  
297 and identified those of Sahabe.

298           The distribution of individuals of the three most common *Ficus* species in 31 different  
299 hills, each generally associated with one farm (18 in Ambendrana and 13 in Sahabe), was  
300 recorded with the help of owners of the land and other inhabitants. They provided  
301 ethnobotanical data during field surveys on all *Ficus* species. We identified all *Ficus* individuals  
302 to the species level and characterized the social-ecological facets in which the three most  
303 common species occurred and noted GPS coordinates. All elements of the landscape, such as  
304 houses, planted or spontaneous vegetation, rivers and cliffs were noted, and schematic drawings  
305 were made in order to obtain a visual record of the spatial relationships between the different  
306 elements of the rural landscape. An example of these schematic drawings is given in Fig 2.  
307 Almost all *Ficus* individuals of the most common species found in the territories of the two  
308 villages were noted. Given the social importance of *Ficus*, local experts were able collectively  
309 to locate exhaustively all individuals of each *Ficus* species, except for those found in  
310 inaccessible areas such as cliffs. For example, for *Ficus reflexa*, all individuals planted around  
311 zebu corrals were counted. Similar exhaustive censuses were conducted on all three most  
312 common *Ficus* species.

313           We aimed at understanding population dynamics of *F. tiliifolia* (the only species out of  
314 the three chosen for a detailed study that was not planted or very rarely), to identify whether  
315 this species could maintain itself without human interventions. We classified *F. tiliifolia*  
316 individuals into three categories on the basis of their architecture, following Hallé et al. (1978),  
317 and functional categories of ‘trees of the past’ or old (trees with complex branching patterns,  
318 large round to flat crowns), ‘trees of the present’ or mature (trees with simple branching patterns  
319 and a pyramidal crown) and trees of the future or young (saplings with few lateral branches)  
320 (Oldeman and van Rijk 1991). These functional categories are supported by studies on tree  
321 architecture that consider repetitions and reiterations as elements of trees’ ontologies



322 (Barthélémy and Caraglio 2007). Furthermore, we **cross checked** the trees' relative age with the  
323 help of elders' local expert knowledge.

324 .

## 325 **RESULTS**

326 We conducted ethnobotanical surveys of uses and practices related to the nine *Ficus* species  
327 found in these two sites with 154 informants. Distribution patterns were documented in detail  
328 for the three most abundant species. In the two sites, we recorded a total of 195 isolated trees  
329 of *Ficus tiliifolia*, 138 individuals of *Ficus reflexa*, isolated or in clusters in small woods or **liv**  
330 hedges located around zebu corrals, and 29 individuals of *Ficus lutea*, isolated or mixed with  
331 *F. reflexa* around zebu corrals.

### 332 **Naming and symbolic and material uses of *Ficus* species**

333 All *Ficus* species are known locally, bear names shared by all inhabitants and have one or  
334 several associated symbolic and material uses; sets of uses differ among species (Table 4).

#### 335 *Naming*

336 Names are symbols generally linked to significant meanings that are linked either to a  
337 characteristic (motivated) or are arbitrary (non-motivated). All nine *Ficus* species bear  
338 motivated names. The Betsileo have no generic taxon name that corresponds to the genus  
339 *Ficus*. But once people realized our interest for *Ficus* species, they showed without hesitation  
340 all *Ficus* species growing in their territory and only *Ficus*, even those we did not know initially.  
341 Some names are based on a system of correspondence or analogy with the human body and  
342 other names refer to the social significance accorded to the tree, its morphology, the type of  
343 fruits it bears, the uses of its leaves and potentially the tree's links to other cultural groups,  
344 especially the Merina.

345 Each species bears a distinct motivated name except for two pairs of species that bear each  
346 the same motivated name (*F. politoria* and *F. brachyclada*; *F. botryoides* and *F. trichoclada*).

347 The first two, like many species of the section *Sycidium*, have scabrous leaves that can be  
348 used as sandpaper and are named *kivozo* or *ampaly* (literally, “scabrous”). The second pair,  
349 named *fompoha*, have young tree stages that are similar morphologically and are closely  
350 related species in section *Sycomorus*. *Fompoha* (literally “to blow”) relates to the small cloud  
351 of tiny insects that come out of the ostiole (opening at the apex of all figs, through which fig  
352 wasps penetrate to pollinate the flowers inside, and through which their offspring emerge  
353 when the fruit matures) when one blows on a mature fig. Children readily demonstrated to us  
354 how they blow on *F. botryoides* fruits to make the fruit more palatable.

355 The name *amonta* (literally, “abundance”) is given to *Ficus lutea*, because it is associated  
356 with noble Betsileo classes (*hova*). Seedlings are protected for this reason. “*Avelao hitsiry ny*  
357 *amonta dia ny taranaka sy ny harena mba hamontafonta*” (Leaving the seedling of *amonta* to  
358 grow will make local descendants also rich). Although seedlings are allowed to establish  
359 anywhere, poor people are forbidden from planting this tree near their houses.

360 The name *nonoka*, applied to *F. reflexa*, means a feeding breast or the act of sucking milk  
361 (Table 4). The abundant white latex produced when the tree is wounded is associated with  
362 human milk and by analogy, leaves are used by breast-feeding women to increase milk  
363 production.

364 *Voara* (*F. tiliifolia*), (literally “fruit of *ara*”, the term *ara* meaning literally, “what is linked  
365 to” presumably to all people) is said to be the “*reninkazo*” (literally mother tree) and is a symbol  
366 of fecundity. People relate this name to the tree’s height and its abundant fruits, appreciated by  
367 children and zebus, its uses for making clothes and as a medicine for women giving birth. *Voara*  
368 is perceived as a tree that attracts and maintains water in the soil. By analogy, cutting a *voara*  
369 is a negative act that may lead to the drying up of children’s tears or of a mother’s milk. Two  
370 varieties of *Voara* are named according to the distinctive traits of their fruits, such as sweetness  
371 (*Voaramalefaka*) or an atypical shape of the fruit (*Voarabekobo*, meaning “with a thick lip”).

372 *Ficus trichopoda* is named *aviavy* meaning in Betsileo “arriving”, the same name is used by  
373 the Merina for *Ficus polita* in Antananarivo. *Tsaramady*, used by the Betsileo for *F. polita*,  
374 means literally “the good one”.

### 375 *Uses*

376 Uses of fig trees may vary according to the socio-ecological facets in which they grow. These  
377 uses, both symbolic and material, are dependent on whether the trees grow naturally or have  
378 been planted. Meanings and roles of the different *Ficus* species also vary depending on their  
379 historical connections with the Betsileo. For instance, the social significance of *F. tiliifolia* is  
380 strongly influenced by the past use of its bark as a textile, a use that was renewed during the  
381 turmoil of the 1940s for making blankets or coats which had a high economic value; a coat  
382 could be exchanged for a zebu. *Ficus* also figure in representations of political relationships of  
383 the Betsileo with other cultural groups in Madagascar. For example, a little ditty of the Merina  
384 is known by the Betsileo : “*Isa ny amontana, roa, ni aviavy, telo fangady*” (literally: “one is  
385 *amontana* king, two is *aviavy* and three is the Malagasy spade”) which was diffused in  
386 Madagascar by the Merina as a device for children to learn to count. *Amontana* (*F. lutea*), and  
387 *aviavy* (*F. polita*) symbolize the Merina kings’ residential areas and power. The name *Amonta*  
388 is used by Betsileo, but it is only planted by *hova* (nobles) who presumably have paid allegiance  
389 to the Merina. *Aviavy* is used by the Betsileo to name *F. trichopoda*.

### 390 *Material and symbolic medicinal uses*

391 All *Ficus* species have medicinal uses for the Betsileo and all are used today to treat diverse  
392 diseases (diarrhea, cough, fever, worm infections) and to treat wounds and a range of  
393 complaints related to women’s health. Some uses are shared between two or more species. The  
394 latex of *F. lutea*, *F. tiliifolia* and *F. reflexa* is used to heal wounds. Healing practices used by  
395 *ombiasy* (healers) make use of all *Ficus* species found in the area. Ancestors’ spirits, called

396 upon by the *ombiasy*, are said to systematically designate *Ficus* products as important remedies.  
397 The *ombiasy* receive this information through dreams or during possession rituals.

#### 398 Other material and symbolic uses

399 All *Ficus* species have technical uses that confer to them an economic value. Some species  
400 are widely recognized by the Betsileo to be consumed by animals such as birds, bats and lemurs,  
401 but some are known to be particularly attractive (*F. reflexa* and *F. lutea*). This knowledge is  
402 used when Betsileo hunt bats. The latex of *F. reflexa* and *F. trichopoda* is used as birdlime.

403 Fruits of *F. tiliifolia*, *F. lutea*, *F. reflexa* and *F. botryoides* are eaten by people, mainly by  
404 children. The fruits of *F. tiliifolia* were traded before new fruit species were introduced into the  
405 area.

406 The bark of both *F. politoria* and *F. pachyclada* is used for making strings and ropes, while  
407 the bark of *F. tiliifolia* and *F. botryoides* was used for making textiles and is symbolically  
408 associated with past lives of ancestors. Other technical uses are numerous, including planting  
409 of stem cuttings to prevent erosion through making living hedges (*F. reflexa* and *F. botryoides*)  
410 and use of dry leaves as fertilizer (*F. tiliifolia*) (Table 4). All these species are used as land  
411 markers but the species most frequently used for marking ancestors' tombs are *F. reflexa* and  
412 *F. lutea*.

#### 413 **Tree management practices: an ethnohistorical construction of Betsileo landscapes**

414 All *Ficus* species have symbolic and material uses that together determine when and  
415 where they will be protected or not. Symbolic uses of a given species can vary depending on  
416 the social-ecological facets in which individual trees grow. Indeed, any *Ficus* tree that grows  
417 from self-sown seedlings near social-ecological facets such as tombs, steles, abandoned ancient  
418 villages or elements of landscapes such as large rocks, are systematically protected. Indeed,  
419 their seeds are perceived to have been brought into these places by ancestors or other intangible

420 creatures. Fig trees are therefore a cultural element of the landscape and not solely an element  
421 of natural regeneration.

422         When growing in the middle of a field, where they may hinder agricultural production,  
423 spontaneously establishing fig trees of all species can be cut, despite a number of sayings and  
424 beliefs that encourage their protection. There is no strict *fady* (taboo) that protects *Ficus* species  
425 from being destroyed. *Ombiasy* also indicate to local inhabitants how to plant particular *Ficus*  
426 species. The *ombiasy* empower the tree through magical practices by adding a charm to trees  
427 planted on the border of zebu corrals to protect the latter against evil spirits or robbery, a  
428 practice named “*tafotombala*” (literally: “that brings wealth”).

#### 429         ***Reading the landscape: ethno-historical indicators***

430         Records of oral memory of the Betsileo, together with their local knowledge of landscape  
431 elements, show that their indicators of the composition of their rural landscapes are social-  
432 ecological facets, encompassing material (e.g., ecological and topographic aspects, types of  
433 agricultural practices or human habitats) and symbolic aspects (e.g. burial places, other markers  
434 of the memory of ancestors). Naming of social-ecological facets is precise (Table 3). They can  
435 be grouped into five large categories: vegetation types, agricultural land-use types,  
436 topographical elements, extraordinary or specific abiotic facets, and historical and sacred facets.

437         Based on these indicators, we identified three overlapping ethno-historical zones along an  
438 east-west axis in site 1-Ambedrana (Zone A-eastern forest; zone B-protected hill-tops; Zone C-  
439 15 roofs area) (Fig 3). The “15 roofs period” refers to the period, during the 19<sup>th</sup> century, when  
440 Merina administrators developed larger villages for the Betsileo, associated with markets closer  
441 to the lowlands. In Zone C-15 roofs area, the landscape is shaped both by activities conducted  
442 before the unification of Madagascar by the Merina and those developed with the establishment  
443 of a new village center during the Merina period, and contemporary periods. Details of the

444 landscape composition including traces of past activities, vegetation types, agricultural  
445 practices and *Ficus* distribution are given in the online resources (Online resource 1).

446 In Sahabe, pasture lands occupy larger areas than in Ambendrana; forest remnants are  
447 few and pasture and cultivated lands form the major part of the rural landscape. Small areas of  
448 forest fallows, associated with past *tavy* practices, are still found within Sahabe's open rural  
449 landscape. We characterized the rural landscape in Sahabe as a Zone C-15 roofs area for the  
450 purpose of comparison with a similar ethnohistorical area in Ambendrana. No east-west axis is  
451 visible, in contrast to Ambendrana (Fig 4). We do not have an explanation for the absence of a  
452 Zone B-protected hilltop in this site. We visited areas near forest fringes where none of the three  
453 *Ficus* species most common in our two sites were found.

#### 454 ***Management practices and distribution patterns of Ficus trees***

455 Two groups of *Ficus* species can be differentiated according to how individuals establish within  
456 the rural landscape. Species of the first group regenerate exclusively through self-sown  
457 seedlings (*F. tiliifolia*, *F. politoria* and *F. brachyclada*). Species of the second group reproduce  
458 by seedlings but are also actively propagated by large pole-like cuttings (*F. reflexa*, *F. lutea*, *F.*  
459 *botryoides*, *F. trichoclada*, *F. polita* and *F. trichopoda*). We recorded *in situ* only individuals  
460 of *F. trichopoda* that were propagated by cuttings (six individuals in site 1 and site 2 in Zone  
461 C-15 roofs area far from the forest), but local experts explain that seedlings exist, are rare and  
462 are protected (Table 2). *Ficus trichopoda* is found growing in the forest only on the eastern side  
463 of the mountain ridge.

#### 464 *Regeneration only by seeds: example of F. tiliifolia*

465 *Ficus tiliifolia* is abundant (70 individuals) in Zone A-eastern forest in Ambedrana but  
466 absent in Sahabe. In Zone B-protected hill-tops (this zone is inexistent in Sahabe), *F. tiliifolia*  
467 is less abundant (21 individuals) in Ambendrana than in Zone C-15 roofs area, with 65  
468 individuals in Ambendrana and 39 in Sahabe.

469 In Ambendrana, *F. tiliifolia* individuals are located at the edges between different  
470 social-ecological facets, marking transitions between two types of landscape elements. Such  
471 positions are occupied by 57 % of 70 individuals in Zone A-eastern forest, 81 % of 21  
472 individuals in Zone B-protected hill-tops, and 59 % of 65 individuals in Zone C-15-roofs area  
473 In Sahabe, individuals located between two social-ecological facets, in Zone C-15 roofs area  
474 represent 41% of 39 individuals and are totally absent near the eastern forest fringes (Online  
475 resource 2).

476 The abundance of *F. tiliifolia* between two social-ecological facets indicates that they  
477 have been cut within each facet, e.g., during *tavy* clearing activities. The photo shown in Fig 5  
478 portrays an individual originating from the forest that has persisted on the edge of a paddy field.  
479 Such trees were incorporated into agricultural lands progressively as fields became permanent.  
480 According to local knowledge, all *Ficus tiliifolia* found across the landscape were trees  
481 maintained mostly by forefathers due to their multiple values. *F. tiliifolia* very rarely  
482 regenerates now in agricultural lands. It is still generally protected as a part of the heritage but  
483 in some cases, when the tree affects crop productions, individual tree may be cut. It is otherwise  
484 maintained for its qualities for fertilizing soils and for maintaining soil water, when it does not  
485 hinder agricultural production (Table 4). Analysis of the population structure of *F. tiliifolia* in  
486 the two study sites shows that old trees are predominant (91%) with only one individual  
487 representing the young stages (Fig 6).

488 *Ficus species that both regenerate by seeds and are propagated by stem cuttings:*  
489 *examples of Ficus reflexa and Ficus lutea*

490 *Ficus reflexa* is rare in Zone A- eastern forest areas in both Ambendrana (three  
491 individuals) and in forest fringes of Sahabe (five individuals). In Zone B- protected hilltops, *F*  
492 *reflexa* is absent in Ambendrana. It is most abundant in site C-15 roofs area in both sites, with  
493 44 individuals in Ambendrana and 89 in Sahabe.

494 In both sites, *F. reflexa* is mainly located at interfaces between two social-ecological  
495 facets (71 % of 44 individuals at Ambendrana; 93 % of all individuals at Sahabe). They are  
496 associated with *vatobe* (steles) and *vatolahy* (very large ancient megaliths), *fasana* (sacred  
497 woods), *alagasy* (forest), and *tanimboakazo* (orchards), places where they establish as  
498 seedlings and are then protected. *Valanomby* (zebu corrals), *tanana haolo* (abandoned  
499 villages), *cour* (courtyards), and *valamparihy* (mud walls along rice fields) are typically facets  
500 where individuals of this species are planted as pole cuttings. Some individuals are associated  
501 with tombs, thickets, pasturelands and threshing areas or grow spontaneously as hemi-  
502 epiphytes on old forest trees bordering fields or as lithophytes on rocks (Online resource 3)

503 *Ficus lutea* is rare in Ambendrana (five individuals) and found only in zone C-15 roofs  
504 area. Several plants from self-sown seedlings were found nearby on the cliffs (not counted). In  
505 Sahabe, this species is more abundant (24 individuals). In this site, most individuals are located  
506 at edges between two social-ecological facets (71 % of 24 individuals). They grow from  
507 spontaneous seedlings, which are always protected. They are also planted by large stem  
508 cuttings, but only members of noble classes are allowed to plant them, never ordinary people.  
509 They are absent in Zone A-eastern forest and Zone B-hill tops. Some individuals are also found  
510 on the humid eastern slopes (Tanala side) of the mountain ridge (V. Rafidison & F. Kjellberg,  
511 unpublished data) (Online Resource 4).

512 According to local knowledge in both sites, plants of *F. lutea* growing in Zone C-15 roofs  
513 area originate from seeds brought by birds and bats that visit the cliffs or orchards. Individuals  
514 found in abandoned villages (*tanana haola*) in courtyards of noble people or *rayamandra* and  
515 in old herbaceous fallows (*songonala*), originate from the planting of large stem cuttings.  
516 According to ethno-historical accounts, they were planted by noble Betsileo classes, as a  
517 symbol of their power over land and a sign of their connection to the Merina kingdom.  
518 Individuals growing spontaneously on tombs are strictly protected. Some individuals are found

519 regenerating naturally at the foot of the cliffs both in Ambendrana (few) and Sahabe (numerous,  
520 not counted).

## 521 DISCUSSION

522 Of the 24 *Ficus* species identified in the forest corridor that joins Ranomafana and  
523 Andringitra National Park (Rafidison et al 2015), nine are present and protected as isolated trees  
524 or as clusters in **liv** edges or in small woods in the adjoining rural landscapes of Ambendrana  
525 and Sahabe. Martin et al. (2009), show that 33 % of isolated individuals (sample size, 48) of  
526 tree species are represented by three *Ficus* species (*F. lutea*, *tiliifolia* and *trichopoda*).

527 The protection of the nine *Ficus* species is driven by their multiple uses and varies  
528 depending on their distribution in social-ecological facets. Ethnohistorical accounts show  
529 temporal continuity of some of the practices associated with these species, and also document  
530 changes over time. Distinct sets of uses (past, present, symbolic and material), are associated  
531 with each species. Multiple relational, economic and ecological values link uses and the  
532 distribution of *Ficus* trees in the landscape following social-ecological dynamics. Distribution  
533 patterns of the three species show that they are predominantly protected as “frontier” elements  
534 between social-ecological facets. Local people explain the greater numbers of these trees at the  
535 edges of agricultural lands by the fact that they are cut within agricultural areas when they  
536 hinder production, but are left in other places to fertilize soil and maintain soil water supply.  
537 Our analysis of the protection of *Ficus* trees also shows links between symbolic, material and  
538 economic dimensions. For example, when found near zebu corrals, *Ficus* trees play symbolic  
539 roles through charms to protect zebus and humans, but also have an important role in preventing  
540 soil erosion, thereby maintaining the sunken basins cut into the soil that serve as zebu corrals.  
541 No strict taboo (*fady*) enforces their protection, but some sayings encourage people to protect  
542 them. However, a *fady* or strict rule forbids the active plantation of *Ficus lutea* and *F.*

543 *trichopoda*, especially by ordinary people, although plants of these species that originate from  
544 self-sown seeds can be protected. Plants that establish naturally from seeds are considered by  
545 local people to have been planted by ancestors and other intangible creatures, and are highly  
546 valued, especially when they grow in social-ecological facets such as burial areas, steles or  
547 other landscape features such as rocks and cliffs. Out of the nine species, seven are actively  
548 planted by stem cuttings (Table 4) following decisions about where they should be planted and  
549 choice of social-ecological facet(s). Regarding the species that regenerate exclusively by  
550 seedlings (rare), their degree of protection remains unclear because they are rare.

### 551 **Vernacular and scientific taxonomy**

552 Our results show that identification and a comprehensive naming system of *Ficus* species  
553 is shared by all inhabitants from elders to children in both sites. This enhances the capacity of  
554 the Betsileo as a cultural group to share knowledge and rules pertaining to management  
555 practices, a mechanism known from many traditional societies (e.g. Friedberg 1986, Ellen  
556 1996). How Betsileo identify *Ficus* species and how scientists identify them are quite similar.  
557 Although they do not use a generic category encompassing all *Ficus*, the Betsileo identify *Ficus*  
558 species by observing similarities and differences among them in morphological and other traits  
559 of leaves, fruits, bark and latex. Differences in growth habits, such as those between hemi-  
560 epiphytes or lithophytes (able to germinate and grow on rocks) and those that grow only as  
561 standing trees, are also considered. Aspects of their phenology, such as the asynchronous  
562 production of leaves of some *Ficus* species, are also taken into account. The traits used to  
563 identify different species are often those associated with the uses of each species. For instance,  
564 the two species found locally whose leaves are scabrous are both named *ampaly*, meaning  
565 scabrous (Table 4), and are among the few pairs of species that bear the same name. They are  
566 in fact sister species in the section *Sycidium* of the genus (Table 1, 4).

567 The Betsileo eat the fruits of *Ficus tiliifolia*, *F. botryoides* and *F. trichoclada*. These related  
568 species all belong to the section *Sycomorus* of the genus (Table 1). The large and conspicuous  
569 crops of figs produced by these species are well-known by scientists to attract mammals  
570 (Shanahan et al. 2001; Harrison and Shanahan 2005). Fruits of many species of section  
571 *Sycomorus* are widely eaten by humans, for example in Africa (Burrows and Burrows 2003).  
572 *Ficus botryoides* and *F. trichoclada* bear the same local name (*fompoha*) and share the same  
573 uses, and indeed are sister species in the phylogeny of *Ficus*. Both are cauliflorous (bearing  
574 fruits on the trunk). Both grow in riverine forests and have very similar leaves (F. Kjellberg,  
575 unpublished data). *Ficus sycomorus*, the type species of section *Sycomorus*, which produces  
576 prolific amounts of fruits, is protected and its fruits are eaten near Tulear in western Madagascar  
577 (V. Rafidison, unpublished data). This species is widely utilized throughout Africa for its fruits,  
578 including in Egypt, beyond its natural distribution area, where it was domesticated by the  
579 ancient Egyptians (Burrows and Burrows 2003).

580 Other *Ficus* whose fruits are eaten are *F. lutea*, *F. trichopoda*, *F. polita* and *F. reflexa*.  
581 These species belong to section *Galoglychia*. The fruits of the first three species are consumed  
582 by humans because of their large size. In the area of Antananarivo, for example, the unripe  
583 fruits of *F. polita* are traded and consumed for their well-known benefits for the throat  
584 (Aumeeruddy-Thomas et al 2018).

585 A most fascinating characteristic of species of section *Galoglychia* is their hemi-epiphytic  
586 and hemi-epilithic growth form. This characteristic, associated by the Betsileo with the idea  
587 that the seeds are “planted” by intangible creatures, is the reason why people protect them  
588 especially on sacred social-ecological facets, such as rocky steles or megaliths, and in small  
589 isolated woodland patches (*songonata*) within the open landscape. These woodland patches  
590 derive from nucleation processes as explained above (Martin et al. 2009; Rafidison, 2013). Such  
591 vegetation dynamics are also known for ‘orphan’ trees protected in swidden agriculture in

592 Africa (Carrière 2002) and in Asia (Eden et al. 2015). These small woods within open Betsileo  
593 landscapes acquire a sacred value, being associated with tombs or steles and *Ficus* species.

594 Most of the uses of *Ficus* documented in the Betsileo sites, such as their use to improve  
595 milk production by breast-feeding women, or by cattle, or their use as **live** hedges for protecting  
596 people or cattle, are similar to those of the same species elsewhere in Madagascar or of other  
597 *Ficus* species in Africa (e.g. Burrows & Burrows 2003), Asia (Kunwari and Bussman 2006)  
598 and the Pacific (Walter and Sam 1999).

### 599 **Continuities between past and present uses, symbolic and material**

600 Continuity between past and present-day uses is a key driver of the protection of isolated  
601 *Ficus* trees, or clusters of them, found in Betsileo rural landscapes. Human memory associated  
602 with transmission of local knowledge by forefathers, and ways people view this transmission  
603 as part of their identity, are key to linking people to biodiversity (including agrobiodiversity),  
604 places and landscapes (Nazarea 1999). Roles of trees in building territories and relationships to  
605 nature have been highlighted in many societies. Their perennial dimensions, multiple economic  
606 uses, and perceived symbolic analogies linking humans to trees are characteristics that favor  
607 their presence in many local territories. Their protection is further enhanced by diverse beliefs  
608 in their roles as mediators, or as hosts of intangible entities that may have positive or negative  
609 impacts on human well-being (Aumeeruddy and Bakels 1993; Rival 1998; Aumeeruddy-  
610 Thomas et al. 2018).

611 Trees, in this case *Ficus* **species** as perennial species, are transgenerational markers of local  
612 social-ecological systems and landscapes and link the present to cultural memory. Their role in  
613 the memory of the Betsileo can be compared to that of other permanent features such as  
614 topographic elements (hills, mountains, cliffs or rocks). Links between their symbolic and  
615 practical uses and the trees' ecology, their spontaneous regeneration by seeds in specific

616 habitats, or their propagation by stem cuttings, are jointly used for their management, as shown  
617 also for *F. carica* in the Mediterranean region (Aumeeruddy-Thomas and Hmimsa 2019).


618 Isolated or clustered individuals of *Ficus* within open agricultural landscapes participate in  
619 the construction of these rural landscapes, as markers of local history and as testimony to local  
620 attachment to the land and its resources. This attachment contributes to reinforcing local  
621 governance of social-ecological systems. During times of turmoil faced at the national level  
622 when threats on biodiversity, agroecosystems and local livelihoods are increasing, looking at  
623 ways local knowledge is linked to remarkable trees from cultural, economic and ecological  
624 perspectives, may help identify sustainable solutions to reinforce local social-ecological  
625 systems and livelihoods. Understanding such systems requires building bridges between local  
626 knowledge and scientific knowledge. A study conducted by Marie et al. (2009) on local  
627 practices related to an endangered group of tree species in Madagascar, the seven endemic  
628 baobab species (*Adansonia* spp.), shows that conservation narratives about threats relating to  
629 Malagasy baobab often attribute these threats to human activities, but neglect consideration of  
630 how baobabs are part of local agroecosystems and are often protected, if not cultivated, by local  
631 farmers.

### 632 **Reciprocal relations, tree agency and interconnected multiple valuing systems**

633 Trees are at the heart of exchanges between humans, other living beings (biodiversity) and  
634 intangible entities (Aumeeruddy-Thomas and Michon 2018). The roles of isolated or clustered  
635 *Ficus* individuals as mediators between people and ancestors and other intangible entities, as  
636 well as between people, their landscape history and their identity, and between people and the  
637 animals they hunt or that are perceived as disseminators of seeds (e.g., birds and bats), makes  
638 these trees active hubs. The Betsileo do not conceive of *Ficus* trees as simply passive elements,  
639 but as recipients of social actions built upon reciprocal relations between the Betsileo and the

640 power of nature, designated in Madagascar as *hasina* or sacred power, which is likened to God  
641 and which can be transmitted by people or plants, as shown for *F. lutea* in Antananarivo  
642 (Aumeeruddy-Thomas et al. 2018). To the Betsileo, trees have a level of agency, because they  
643 directly affect people's lives by bringing happiness or protection, or by purifying people of their  
644 deeds. They therefore also affect social organization and decisions, and in that respect form part  
645 of the hybrid communities that link humans to other living beings, as is true for many other  
646 indigenous peoples and local communities across the planet (Stepanoff and Vigne 2019). Diver  
647 et al. (2019) argue that in Madagascar, taking into account reciprocal relations between humans  
648 and biodiversity is crucial to improve conservation approaches. In particular, their study shows  
649 that local rules of access to resources and places reinforce reciprocal relations. In our study  
650 sites, the distribution of *Ficus* species across the landscape does not follow haphazard patterns,  
651 and associations of different *Ficus* species with different socio-ecological facets, i.e., specific  
652 places having strong meanings, leads to formulation of rules that guide access to and  
653 management of these places and the *Ficus* they include. These rules have to be considered in  
654 collaborative approaches for biodiversity conservation if local livelihoods are to be sustained.

655 Past and present uses of biodiversity, transmission of knowledge and local formal and  
656 informal rules guiding access and management approaches to resources contribute to enhance  
657 relational values that link people to landscapes (Chan et al. 2016). This needs full consideration  
658 if conservation efforts are truly to engage with indigenous peoples and local communities (Diaz  
659 et al. 2018).

660 In addition to their strong social or relational value, *Ficus* trees also have an ecological  
661 value as ecosystem engineers in sacred woodland patches in open agricultural areas in Betsileo  
662 rural landscapes. Their economic value is related to their roles in checking erosion and other  
663 multiple material uses. An interconnected multiple  luing system characterizes the use of  
664 isolated and clustered of *Ficus* trees in the Betsileo rural landscapes. As discussed by Pascual

665 et al. (2017), multiple valuing systems are crucial to understand and sustain to attain sustainable  
666 development objectives.

### 667 **Tree management and propagation practices and distribution**

668 Naming and uses are similar or confounded between the Betsileo and the Merina cultural  
669 groups who live in the region of Antananarivo, where we conducted a previous study. In that  
670 study we focused on *F. lutea* in the sacred hills of Antananarivo, and we showed that the Merina  
671 used many symbols to portray their supremacy, among them *F. lutea*. Trees of this species  
672 were planted by stem cuttings in new places they had ‘acquired’ during their unification of  
673 Madagascar as a state (Aumeeruddy-Thomas et al. 2018). Similar practices have been described  
674 in continental Africa, where *Ficus* trees were planted in front of conquerors’ houses or on their  
675 tombs to mark their acquisition of a new territory (Dury 1991). The use of the name *amonta* for  
676 *F. lutea* by the Betsileo is very similar to its Merina name *amontana*. Both in Antananarivo and  
677 in the Betsileo sites, *F. lutea* is associated with similar sets of symbolic values. All this suggests  
678 a strong Merina influence. In the rural landscape, *F. lutea* is mainly planted from stem cuttings  
679 by noble classes. It regenerates from seed only in the cliffs area (Zone C), where ancient *hova*  
680 (Betsileo nobles) lived (Moreau 2002). The absence of *F. lutea* in Zone A- Eastern forest  
681 (except in the humid Tanala side located on the eastern slope of the mountain ridge) suggests  
682 that it may have been brought into the Betsileo region by the Merina. The same pattern applies  
683 to *F. trichopoda*, which in the Betsileo study sites occurs only (except for rare seedlings) as  
684 planted individuals propagated from stem cuttings. This species bears the same name as *F.*  
685 *polita* in Antananarivo (*aviavy*). This pattern also applies to *F. reflexa*, which bears the same  
686 name (*nonoka*) in Betsileo and Merina. The above species are considered to have the power to  
687 protect humans and zebus, to purify people, or to bring happiness (but also death). These beliefs  
688 all portray the supernatural power accorded to them and a strong influence of the powerful  
689 Merina.

690 ***Potential and constraints of Ficus tree protection***

691 The diverse distribution patterns of *F. tiliifolia*, *F. reflexa* and *F. lutea* show very distinct  
692 dynamics that are taken into account in efforts of local people to protect them.

693 1. *Ficus tiliifolia*

694 While *F. tiliifolia* is accorded a positive value in agriculture for its role in fertilizing  
695 soils, it can also negatively affect agricultural production. The tree is deciduous (i.e., leaves of  
696 an individual are shed synchronously) but individual trees differ in when leaves are shed. Some  
697 individuals shed leaves at a time when the falling leaves can harm young rice seedlings. Farmers  
698 may decide to cut such trees. Martin et al. (2009) suggested that protection of *Ficus* species by  
699 the Betsileo was linked to respect for ancestors' practices, and roles of taboos (*fady*). The  
700 present study corroborates these findings and revises ideas about taboos. Taboos are often  
701 considered instrumental in reinforcing conservation but they can be lifted (Fernandez–  
702 Llamazares et al. 2018). Ethnobotanical and ethnohistorical approaches taken in our study show  
703 that several factors—historical, symbolic, but also economic—contribute to explaining why,  
704 what and where *Ficus* trees are protected in Betsileo rural landscapes. Patterns of protection are  
705 not linked to any strict taboo. Although people respect the practices of ancestors and refer to  
706 this in the first place, the Betsileo give numerous other reasons to explain why they have  
707 protected *F. tiliifolia* trees. Four major and interlinked reasons are given: (1) the numerous  
708 practical uses of this species, e.g. fertilizing soils and improving soil water content; (2)  
709 analogies between people and trees ; (3) its role as food for children and cattle; (4) its role as  
710 an identity marker for Betsileo people. In Sahabe, where *F. tiliifolia* is rare, people pay less  
711 attention to this tree than in Ambendrana. A possible explanation is that Sahabe is located at a  
712 higher altitude and the climate is colder and less suitable for this species. Furthermore, the rural  
713 landscape in Sahabe shows a larger extension of herbaceous grasslands associated with a higher

714 level of pastoral activities (Fig 4). As explained by Kottak (1977), the Arindrano chiefdom was  
715 probably more based on pastoralism than the Lalaina kingdom. Virtually restricted to forest  
716 environments, *F. tiliifolia* could not survive in the savannah-type environments of Sahabe (just  
717 as its population is now shrinking in the open areas created by sedentarized agriculture in  
718 Ambendrana).

## 719 2. *Ficus reflexa*

720 *Ficus reflexa* is protected owing to its multiple uses. It is abundant in a large area of plains  
721 and near the cliffs, areas that were occupied by the Betsileo before periods of insecurity in the  
722 17th and 18th centuries, and then occupied by the Merina in the 19th century, the area defined  
723 in this study as Zone C-15 roofs area. The distribution of *F. reflexa* in this zone is thus the result  
724 of historical accumulations of trees of this species planted by people, reflected in its abundance  
725 in abandoned villages (*tanana haola*) and in zebu corrals, both abandoned ones and those  
726 presently used.

## 727 3. *Ficus lutea*

728 *Ficus lutea* is also protected in Zone C-15 roofs area, but is less actively planted due to its  
729 association with noble classes. It is therefore much less common than *F. reflexa*, although it has  
730 multiple uses.

## 731 **Implications for conservation and potential collaborative approaches**

732 Conservation efforts increasingly consider anthropogenic landscapes made of the co-existence  
733 of agroecosystems and other elements such as forests, pastures, fallow land, that contribute to  
734 connectivity and habitat diversity (Perfecto and Vandermeer 2010; Manning et al 2019).  
735 Isolated and clustered *Ficus* individuals are key elements of Betsileo rural landscapes. Given  
736 the multiple economic, relational and ecological values associated with them, *Ficus* trees can

737 contribute both to biodiversity conservation and to support social-ecological systems built on  
738 local knowledge. “Community-based” approaches that were developed previously in  
739 Madagascar—and more widely across the planet—have not led to the expected results, (Ward  
740 et al. 2014, Blanc-Pamard and Fouroux 2004). This suggests that multiple-evidence and  
741 collaborative approaches that build on synergies between local and scientific knowledge to  
742 understand multiple valuing systems should be further implemented (Pascual et al. 2017, Tengo  
743 et al. 2014). Practical collaborative conservation work requires long-term involvement of  
744 scientists, conservation managers and local communities (e.g. Lama et al. 2001; Diver et al.  
745 2019). Our engagement in collaborative approaches started with the co-writing of a paper with  
746 local experts (Rafidison et al. 2016). Based on our experience, and on findings by other authors  
747 about the roles played by trees in open agricultural landscapes in Madagascar (e.g. Marie et al.  
748 2009), we suggest a few rules of thumb for developing collaborative approaches that conserve  
749 biodiversity and sustain local social-ecological systems. The following steps are some  
750 approaches that we suggest:

- 751 - Characterizing rural landscapes and their complexities based on i) local knowledge and  
752 other tools (e.g. remote sensing, ecological analysis, naturalists’ knowledge of  
753 biodiversity) and ii) a fine comprehension of social-ecological facets, distribution of  
754 practices and changes in practices in the landscape, over time;
- 755 - Identifying key elements such as *Ficus* trees through multiple evidence-based  
756 approaches based on local knowledge and joint investigations of ecological,  
757 ethnobotanical and anthropological aspects;
- 758 - Defining together through focus-group discussions with elders, men, women, and  
759 children, the key roles of specific species as indicators of well-being and their diverse  
760 values for people and how they affect other groups of species. Discussing potential plans  
761 for supporting the protection of such species, with due recognition of values, of who is

762 entitled to plant each species, and how and where (in which specific social-ecological  
763 facets) each can be propagated;

764 - Avoiding inventing “local” institutions that are not truly appropriated by local people,  
765 and building a joint understanding of collective visions and rules of access to  
766 resources.

767 - Constraints in such approaches lie in the different values accorded to biodiversity by  
768 conservation managers, scientists and local communities and the necessity to identify  
769 parts of their interest that can be shared as a first step for developing learning  
770 processes.

## 771 CONCLUSION

772 The roles of trees in live hedges, in small woodland patches or as isolated elements in rural  
773 landscapes are known, especially in agroforestry systems. However, the multiple social,  
774 historical and political roles of trees in open landscapes have rarely been discussed in relation  
775 to collaborative conservation approaches that consider local social-ecological dynamics. This  
776 case study provides an understanding of how the Betsileo people associate multiple relational,  
777 economic and ecological values with *Ficus* trees at the landscape level. The ecological role of  
778 *Ficus* trees as stepping-stones are known to enhance connectivity and facilitate re-forestation  
779 in fragmented rural landscapes. They may be considered for their potential to improve the  
780 management of biodiversity and for their multiple local values. Propagation techniques applied  
781 to each species, and the places where trees of each species are allowed to grow, are linked to  
782 interconnected cultural, ecological, historical and economic contexts. This study suggests  
783 avenues regarding approaches to understanding the multiple values of trees in open rural  
784 landscapes and their potential roles for supporting conservation of local social-ecological  
785 systems outside protected areas.

786

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801

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Section	Espèces	Mating System	Life form	Maximum height (m)	Placement of inflorescences	Maximum diameter of fruits (cm)	Habitat	Altitude (m)	Distribution
Sycidium	<i>F. pachyclada</i> Baker	d	Tree	25 (35)	C	1,5 D	Forest, often along rivers, marshes and seacoast	50-1090 (1150)	M (C to E)
	<i>F. politoria</i> Lamarck (synonym, <i>F. soroceoides</i> )	d	Shrub or treelet	8	C	1 F	Understory, abundant in patches, often in riverine forest	0-1700 (2500-2800)	M (E, C, N)
Sycomorus	<i>F. tiliifolia</i> Baker	m	Tree	20 (25)	C, A	1,5-5 F	Forest, sometimes planted	0-1700	M (all parts of the island islands) and Co
	<i>F. botryoides</i> Baker	m	Tree	25	C, A	2 (3,8) F	Forest, along rivers	0-1600	M (E, C, N)
	<i>F. trichoclada</i> Baker	m	Tree	15	C, A	3 (4) F	Along streams	100-1500	M
Galoglychia	<i>F. lutea</i> Vahl (synonym <i>F. baronii</i> )	m	Hemi-epiphytic	23	A	2,5 (3,5) F	In forest, often along rivers, marshes, and seacoast	0-1500	M, Co, Se, CA
	<i>F. trichopoda</i> Baker	m	Shrub or tree	10 (20)	A	2 F	Savanna woodland, in marshy places	500-1100	M (W, planted in Center), CA
	<i>F. reflexa</i> Thunberg	m	Hemi-epiphytic	10 (30)	A	1,2 D	In various types of forest	0-1700	M (all parts of the island), Me. other subspecies in Se (incl. AL), Co

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<i>F. polita</i> Vahl	m	Hemi-epiphytic	15(40)	C	4F	Evergreen (humid and gallery) forest	600-700	M (all island?),CA
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Source: Dalecky et al. 2003, revised 2010 by F. Kjellberg, V. Rafidison. and Y. Aumeeruddy-Thomas

*d*: dioecious; *m*: monoecious; *R*: ramiflorous; *C*: cauliflorous; *A*: axillary

D: dry, F: fresh

M (E, C, N, W, S): Madagascar (east, center, north, west, south), Co: Comoro islands; Se: Seychelles; CA: Continental Africa; Me: Mascarenes; Al: Aldabra

<b>Site</b>	<b>Ambendrana</b>	<b>Sahabe</b>
Men	45	59
Women	19	31
Total	64	90
<b>Precision on informants ages</b>		
Children < 12years	11	12
Youngsters 12-18 years	1	4
Young parent 20-40 years	29	52
Old persons	23	22

<b>Type</b>	<b>Terminology</b>	<b>Signification</b>
Natural or anthropogenic vegetation types	<i>Tapoka</i>	Marshy areas not yet transformed into paddy fields
	<i>Alagasy</i>	Literally, “malagasy forest”, stands for non-disturbed forests
	<i>Alakininina</i>	Eucalypt forest
	<i>Atikifafa</i>	Literally, “within the herbaceous savanna”, an area that was never cultivated but has been burned for pasture lands
	<i>Kapoka</i> ( <i>Ambendrana</i> )	Post- agricultural regrowth or forest or bushy vegetation fallows
	<i>Popoka</i> ( <i>Sahabe</i> )	
	<i>Kilanjy</i>	Worn out land with a fallow of herbaceous for an undetermined period
	<i>Kirihitra</i> <i>Songonala</i>	Bushy vegetation Literally “forest tuft” meaning an isolated small wood.
Agricultural land use	<i>Dobo</i>	Fish pond
	<i>Kipahy</i>	Cultivated terraces, most often irrigated paddy fields
	<i>Lalankely</i>	Path
	<i>Tanimboankazo</i>	Literally “land of fruit trees” meaning orchards
	<i>Tanimboly</i> <i>Tsihintany</i>	Literally “cultivated land”: the field Literally, « land mat » : threshing ground
	<i>Valamparihy</i> <i>Valanomby</i>	Mud walls protecting rice fields Zebu stockyard
Topographic element	<i>Amorotambina</i>	The lower border of hill slopes generally located just above paddy fields
	<i>Lohasaha</i>	The head of the field or valley
	<i>Tambina</i>	The lower part of hill slopes
Extraordinary or specific natural element	<i>Hara</i> ( <i>Harambato</i> )	Rocky cliffs
	<i>Renirano</i>	Literally “the mother of the wate”r : a river
	<i>Riandrano</i>	A rivulet
	<i>Vatobe</i>	Big rock
Historical site	<i>Aritsa</i>	Sacred wood where utensils and garments that have been used during burial ceremonies are thrown away
	<i>Fasana</i>	Tombs

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*Tanana Haolo  
or Valamaty  
Vatolahy*

Literally, abandoned hamlet or dead hamlet.

Literally, Male stone Stela or megalith which can reach 1 to three meter high and which has a commemorative function..

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<i>Latin name</i>	<i>Betsileo name</i>	<i>Literal translation of Betsileo name</i>	<i>Uses (S) Symbolic ; (M) Material</i>	<i>Reproduction and propagation</i>	<i>Specificities related to protection</i>
<i>F. pachyclada</i> Baker	<i>kivozy,</i> <i>mapaly</i>	- scabrous	bark used for making ropes (M) firewood (M) leaves heal toothache and stomach pain (M, S)	natural reproduction by seed - rare	not found protected elsewhere than near burial areas, near cliffs
<i>F. politoria</i> Lamarck ( <i>Syn. F. soroceoides</i> )	<i>kivozy</i> <i>ampaly</i>	- scabrous	bark used for making ropes (M) fuelwood (M) leaves heals toothache and stomach pain (M, S)	natural reproduction by seed	grows in forest fallows
<i>F. tiliifolia</i> Baker	<i>ara</i> <i>voara,</i>	according to/ linked to fruit of Ara	tree linked to ancestors (S) ; presence linked to divinities and intangible creatures (S) fallen leaves fertilize soils (M) roots maintain water in the soil (M/ S) bark used for making a cloth named <i>ato</i> (M,-) Previously a coat made with <i>fato</i> could be exchanged against a zebu (M/S) the fruit is eaten. Two varieties known : <i>voara bekoba</i> and <i>voaramalefaka</i> (M) leaves have medicinal uses : heal stomach ache, skin disease, facilitates birth (M,S)	natural reproduction by seed, seedlings sometimes transplanted	local sayings encourage people not to cut this tree because this would have negative impacts on soil water, and would dry up children's tears and the milk of breast-feeding women.  protection also due to respect for ancestors and multiple uses.

			<p>tree is a marker of territories (M)</p> <p>tree important in open areas for its shade (M)</p> <p>wood for previous domestic uses : for making dishes, spoons, and preparing baskets and container for feeding livestock and chickens (M)</p> <p>latex used as birdlime to catch small birds, especially the fody (<i>Foudia madagascariensis</i>) or to repair holes in jugs and buckets (M)</p> <p>Tree, symbol of fertility (S)</p>		
<i>F.botryoides</i> Baker	<i>fompoha</i>	blow	<p>fruit eaten (M)</p> <p>leaves and fruits stimulate milk production by breast-feeding women (S/M)</p> <p>bark used in the past to make clothes and baskets (M/S)</p> <p>tree used to prevent soil erosion (M)</p>	natural reproduction by seed and planted by cuttings	protected due to its multiple uses
<i>F. trichoclada</i> Baker	<i>fompoha</i>	blow	<p>fruit eaten (M)</p> <p>leaves and fruits stimulate milk production by breast-feeding women (S/M)</p> <p>bark used in the past to make clothes and baskets (M/S)</p> <p>tree used to prevent soil erosion (M)</p>	natural reproduction by seed and planted by cuttings	protected due to its multiple uses

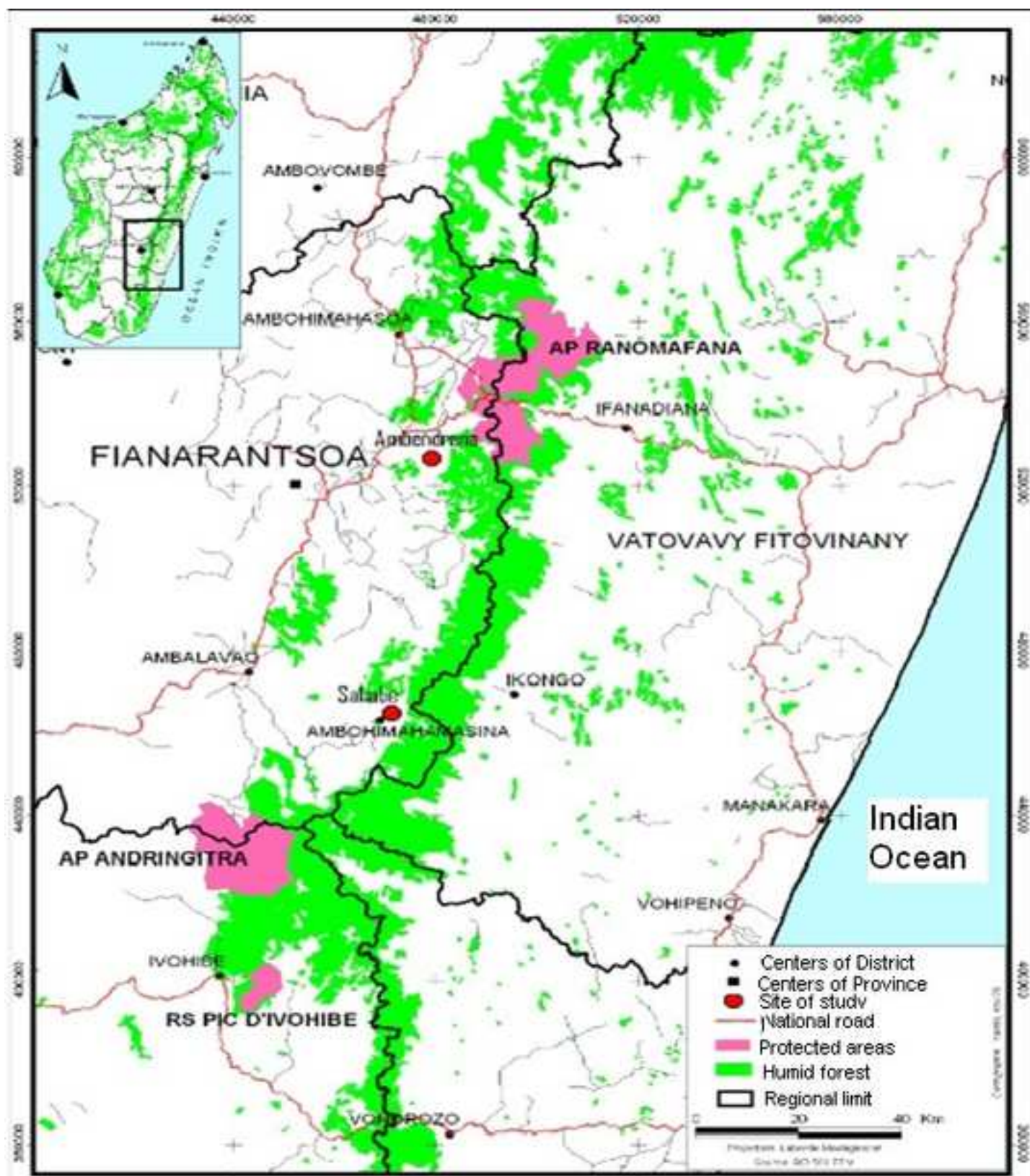
<p><i>F. lutea</i> Vahl (syn. <i>F. baronii</i>)</p>	<p><i>amontana</i>, <i>amonta</i></p>	<p>abundance</p>	<p>Tree, symbol of noble classes, richness and magnificence</p> <p>Bard used in the past to produce a thread to make mats (M/S)</p> <p>fruit eaten (M),</p> <p>leaves used for making tea (M)</p> <p>latex used as chewing gum and as birdlime (M)</p> <p>leaves fertilize soils (M)</p> <p>tree useful for shade in open areas (M)</p> <p>the tree is planted as wind break (M)</p> <p>leaves and fruits used as fodder for livestock (M)</p>	<p>natural reproduction by seed and planted by cuttings</p>	<p>protected if seedlings grow, and planted, but only by noble classes</p>
<p><i>F. trichopoda</i> Baker</p>	<p><i>aviavy</i></p>	<p>coming, arriving</p>	<p>tree brings happiness when growing naturally (S)</p> <p>tree has negative impacts if planted (S)</p> <p>rare seedlings are protected (M/ S)</p> <p>fruits can be eaten (M)</p> <p>tree mediator between humans and ancestors (S)</p> <p>wood used as a purifier if a <i>fady</i> (taboo) is not followed (S)</p>	<p>natural reproduction by seed and planted by cuttings</p>	<p>this tree is never planted, but rare seedlings are protected due to the benefits the tree brings.</p>

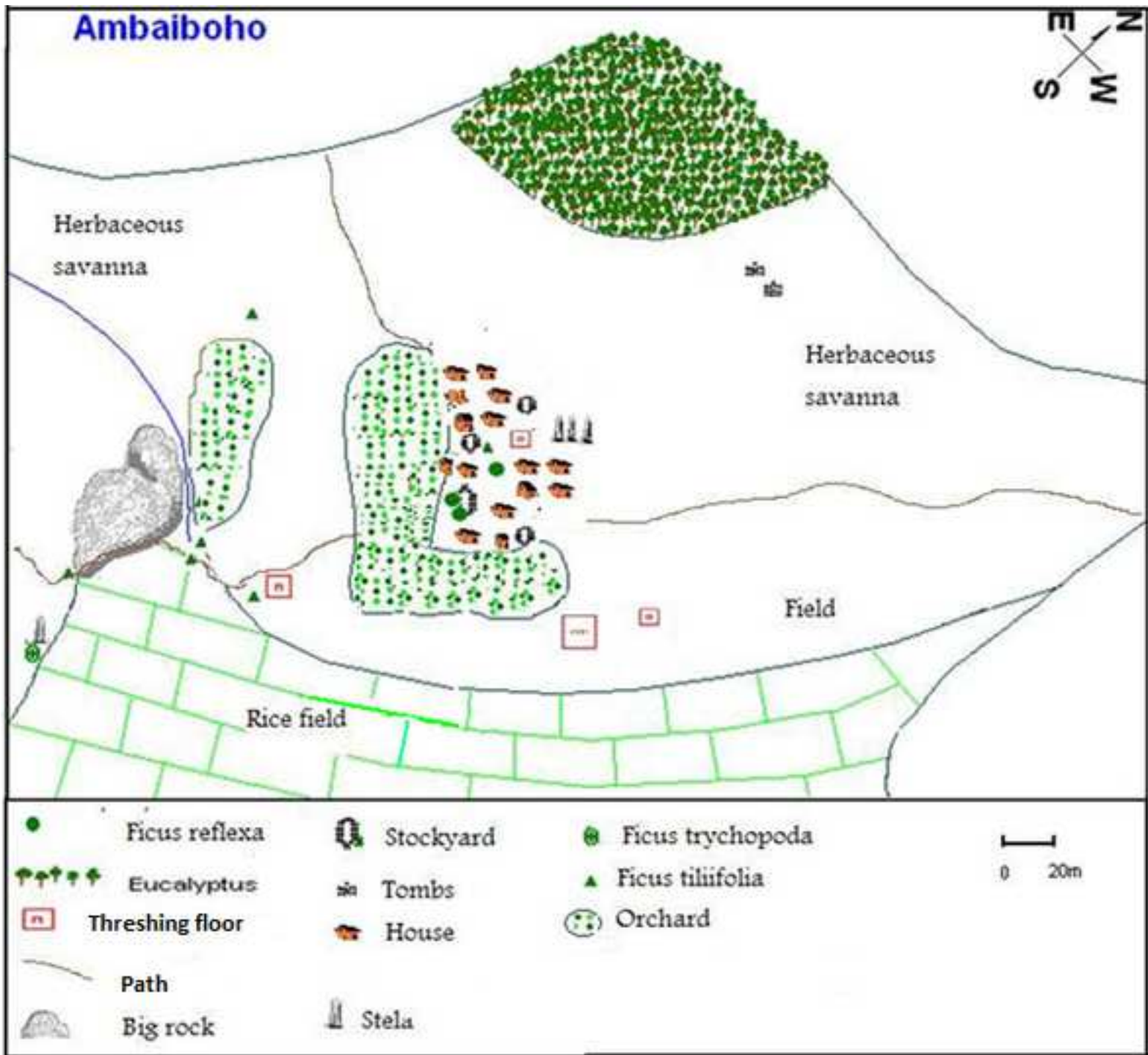
<p><i>F. reflexa</i> Thunberg</p>	<p><i>nonoka,</i> <i>laza</i></p>	<p>sucking milk  famous</p>	<p>past symbol of kings and noble classes (S) increases milk of breast-feeding mothers (M)  When growing on rocks, associated to strength (S)  Protection of houses against thunder and hail (M/S)  Fruit eaten (M)  Living hedge (M)  Tree that commemorates ancestors (S)  Tree that brings happiness (S)</p>	<p>natural reproduction by seeds on stones and planted by cuttings</p>	<p>this tree is protected when growing naturally but can be cut if it affects agricultural production.  it is widely reproduced by cuttings especially to form live hedges around zebu corrals.</p>
<p><i>F. polita</i> Vahl</p>	<p><i>Tsaramady</i></p>	<p>the one that is good</p>	<p>Has medicinal uses and increases milk of breast-feeding women (M, S),  Lucky charm for zebu corrals(S),  Protects zebu against thefts and malevolent deeds (S)  Leaves used for making tea (M)</p>	<p>natural reproduction by seed and planted by cuttings</p>	<p>protected due to its multiple uses</p>

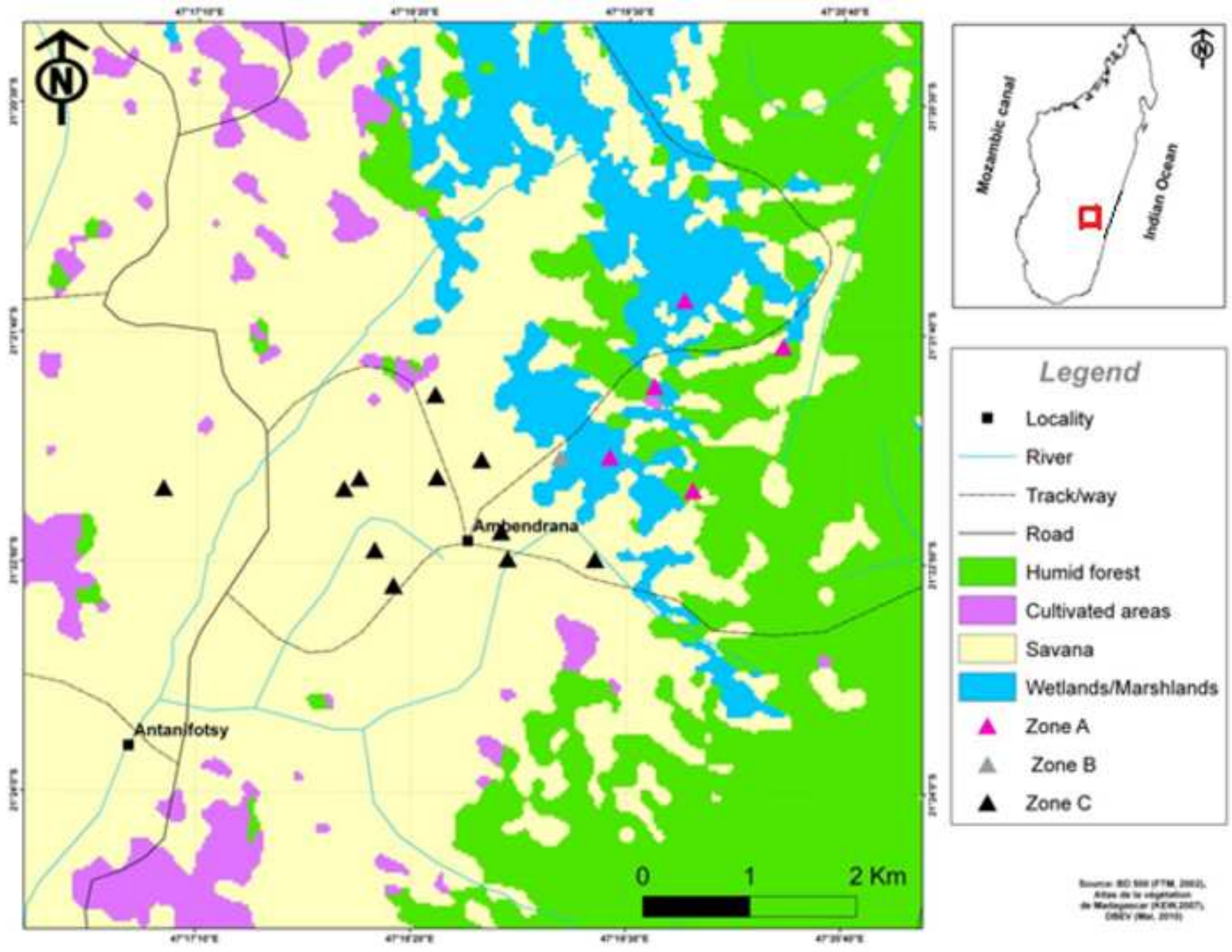
Table 1 *Ficus* species found in the study areas, their major biological and ecological characteristics, habitats and geographical distribution

Table 2 Sex and age distribution of people interviewed in Ambendrana and Sahabe

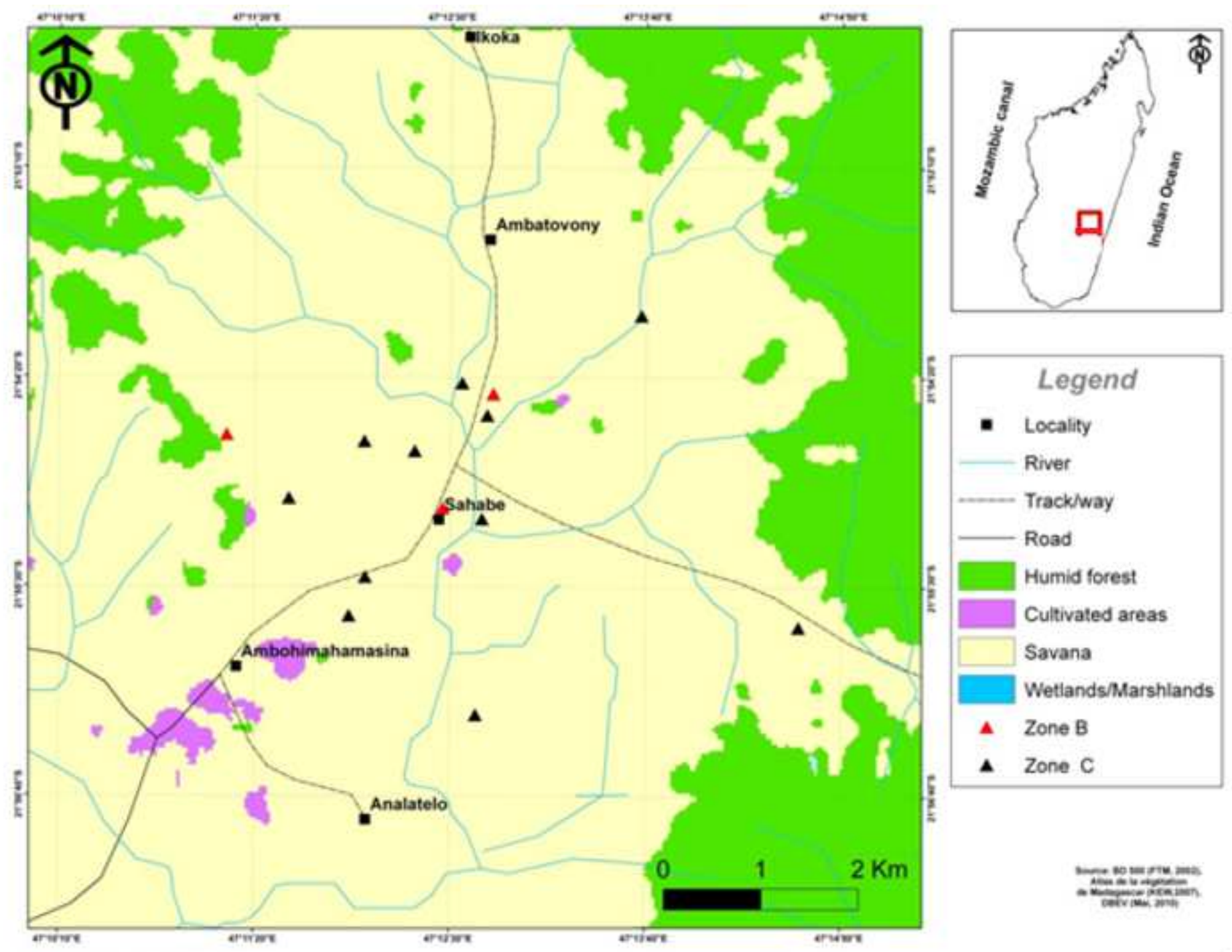
Table 3 The social-ecological facets recorded in Ambendrana and Sahabe



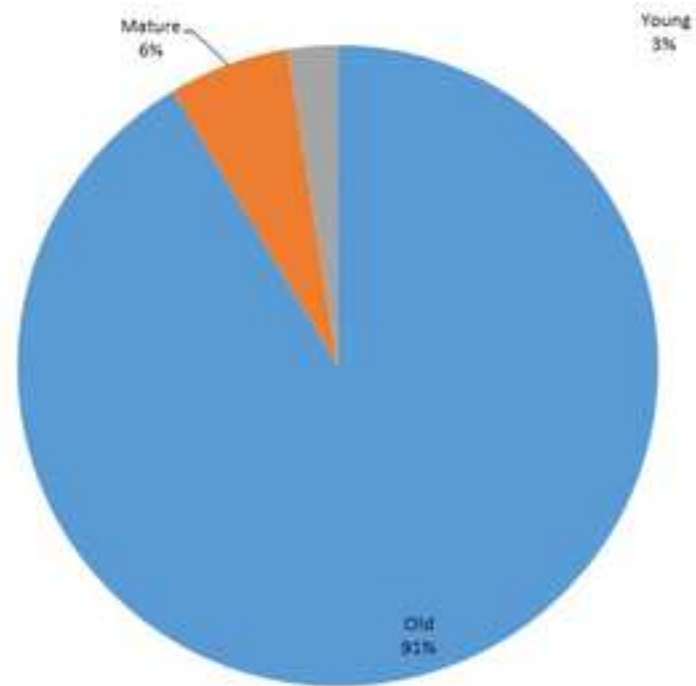




Source: BD 500 (FTM, 2002), Atlas de la végétation de Madagascar (KEN, 2007), OBEV (MIA, 2011)







**Fig.1** Location of the two study sites Ambendrana and SahabeRanomafana and Andringitra National Parks and the forest corridor, Madagascar

**Fig.2** Schematic representation of one hill with the elements of the landscape observed in Ambaibofo (Ambendrana)

**Fig.3** Localization of hills investigated in Ambendrana

**Fig.4** Localization of hills investigated in Sahabe

**Fig.5** Photo showing *F. tiliifolia*, saved from the forest on the edge of a paddy field

**Fig.6** Population structure of *Ficus tiliifolia* in Ambendrana and Sahabe


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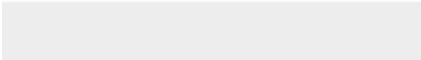
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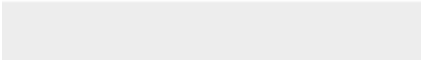
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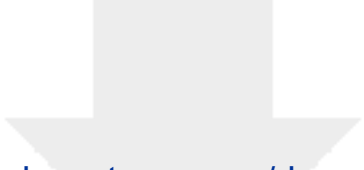
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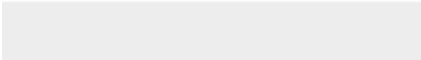

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