Comparison of plant communities on two massifs in Madagascar (Ibity and Itremo) with contrasting conservation histories and current status

En haut (gauche et droite): Vue générale du Massif d'Itremo ; en bas (gauche et droite) : Vue générale du Massif d'Ibity. (Photos par Swanni T. Alvarado)

II. Chapitre 2

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Alvarado, S.T., E. Buisson, H. Rabarison, C. Rajeriarison, C. Birkinshaw and P.P. Lowry II

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Abstract

Deforestation processes and species extinction on islands have made them the focus of substantial efforts to create and strengthen local environmental organizations, establish new protected areas, and improve natural resource management. In Madagascar, despite promising new policies, the flora and fauna are under serious threat. More than 80% of the island shows a significant loss of natural plant cover. Current levels of diversity reflect natural disturbance regimes, with fire representing one of the most important factors. We compare two new protected areas (Ibity and Itremo) with different environmental and management contexts to determine the effects of bush fires on vegetation. Both areas have extensive stands of tapia (*Uapaca bojeri*) woodland. Herbaceous vegetation surveys were carried out enumerating 16 (1m^2) quadrats in each of ten sites on Ibity and seven on Itremo to characterize plant community composition and structure, complemented by tree and shrub surveys within three 40×40m quadrats at each site. Floristic richness is higher at Ibity. Populations of *U. bojeri* are better conserved at Itremo. While the total exclusion of fire is impracticable, careful management should enable the maintenance of natural conditions and at least lead to a reduction in the impacts on the structure of tapia woodland vegetation.

Key words: Protected areas, tapia woodland, *Uapaca bojeri*, management plan, fire regimes

1. Introduction

Conservation at all scales, from landscapes and ecosystems to communities and populations, is achieved through management designed to ensure protection and sustainability based on a set of acceptable objectives. The way in which Protected Areas (PAs) are managed typically depends on the type of protection they have been accorded (e.g. IUCN recognizes six main categories of PAs; Dudley 2008), and differences in management practice can have a profound influence on vegetation and plant communities, even among sites with similar environments (Kirkpatrick 1999). Likewise, differences in land-use practices and/or anthropogenic pressures in the regions around PAs, and variation in the levels of resource use that are permitted within them, can result in differences in the composition and structure of plant communities, even if PAs belong to the same management category (Halpin 1997, Andrew et al. 2011).

Recently, substantial efforts have been undertaken in some regions of the world to establish new PAs and to improve natural resource management (Kull 1996). In the island nation of Madagascar, where 90 parks and reserves covering ca. 2.54% of the land area (IUCN & UNEP-WCMC 2010) are recognized, more than 40 new PAs (NPAs) have been established or are in the process of being created, encompassing an additional 4,326,543ha (Atlas numerique SAPM 2011), of which 2,565,644ha have already formally been granted temporary protection (Ministère de l'Environnement et des Forêts 2010)Ministère de l'Environement et des Forêts, 2010) Ministère de l'Environement et des Forêts, 2010) , an intermediate step toward permanent PA status. The majority of NPAs are being developed and sponsored by non-governmental organizations (NGOs) such as the Wildlife Conservation Society (WCS), Conservation International (CI), the Missouri Botanical Garden (MBG) and the World Wildlife Fund (WWF).

New Protected Areas require management plans, whose development can benefit from useful insights obtained from existing PAs located nearby or situated in different landscapes and/or socio-economical contexts but that share similar ecosystems (Holdgate 1991; Margules & Pressey 2000). However, considering that in 2008, only ~18.6% of global land and sea cover was included in PAs (UNEP-WCMC 2010a), relevant information from NPAs is often not available. It may therefore be necessary to compare an NPA with unprotected areas found in somewhat similar environmental contexts, using them as sources for acquiring useful data and for identifying the disturbances and pressures that threaten the ecosystems, and for identifying appropriate management/disturbance regimes that may be applies to the NPA (Margules & Pressey, 2000).

Disturbances have a marked effect on life form, phenology, density, abundance and distribution patterns of plant populations (Agrawal, 1990), and they influence spatial heterogeneity in plant communities (Collins 1989, 1992; Chaneton & Facelli 1991). In Madagascar, a range of natural disturbance regimes have contributed to the array of vegetation types found on the island (Kull 2000). The analysis of charcoal contained in soil shows that fire was common on Madagascar long before the first humans arrived ca. 1500-2000 years ago (Dewar & Burney 1994). However, human presence is clearly marked by a dramatic increase in fire frequency and a significant spread of grasslands and other open anthropogenic formations (Bartlett 1955, 1956; MacPhee et al. 1985; Burney 1987a, 1987b; Dewar & Burney 1994; Matsumotot & Burneyt 1994; Burney et al. 2004). Some plant communities can be resilient to fire, but changes in their structure and composition nevertheless occur with changes in the timing, frequency and intensity of burning (Guevara et al. 1999). By describing the composition and structure of a community and understanding the disturbance regimes that have influenced them (fire, pasture, floods, etc.), one can seek to explain the various species assemblages that form a contemporary plant community.

We chose to work on two similar massifs, Ibity and Itremo, which are being established as new protected areas within the framework of the "conservation and management of bush fires" program (Bertrand 1998; Kull 2002a) developed respectively by the MBG and Royal Botanic Gardens Kew, in cooperation with CI, the United States Agency for International Development (USAID), the Malagasy government, and local populations. The two NPAs being established at Ibity and Itremo encompass a pair of mountain massifs in central Madagascar situated within the sub-humid zone in the central highlands (Cornet 1974). Currently, the vegetation of these massifs comprises a mosaic of plant communities, which has resulted from the combination of disturbance regime and the types of management, land-use and anthropological pressures that are specific to each massif. The natural disturbance regime, which operated prior to human arrival, was characterized by late-season fires, but today burning occurs earlier and far more frequently due to human intervention (MacPhee *et al.* 1985; Burney 1987a; b; Dewar & Burney 1994; Burney *et al.* 2004). Large areas on both Ibity and Itremo are now covered by grasslands (98.5% and 99.5% respectively), whereas just 132,255ha are occupied by isolated stands of tapia woodland, a distinctive formation dominated by *Uapaca bojeri* (locally known as "tapia") in association with other woody species, many belonging to families endemic to Madagascar, especially Sarcolaenaceae and Asteropeiaceae. The herbaceous stratum of tapia woodland comprises numerous species of Asteraceae, Cyperaceae, Lamiaceae, Poaceae and Rubiaceae.

Within the context of the development of vegetation management plans for Ibity and Itremo, we compared the vegetation of these two massifs in order to identify the roles and impacts of the different environmental situations on vegetation. Specifically, we have aimed to: 1) describe the composition and structure of tapia woodland on these two massifs, and 2) determine the factors influencing tapia woodland vegetation for both NPAs. Our ultimate goal is to provide information that can be used to help formulate recommendations for developing sustainable management plans for the tapia woodlands at Ibity and Itremo.

2. Methods

2.1. Study area

Ibity and Itremo, the only quartzitic mountain massifs in Madagascar, are located in the central highlands southwest of the capital city, Antananarivo. Ibity Massif is situated 25km south of the town of Antsirabe (47°01'E 20°07'S) and is oriented approximately north-south, covering an area of 193km^2 and an elevational range of 1400m to 2254m. Itremo Massif, located 200km southwest of Ibity and 35km west of Ambatofinandrahana (46°38'E 20°35'S), covers 971km^2 and ranges from 1400m to 1923m elevation. The climates of the Ibity and Itremo regions are characteristic of tropical highlands, classified as Cwb by the Köppen classification system (Köppen 1900; Peel *et al.* 2007), with warm weather, dry winters and rainy summers. Two main periods can be distinguished: in summer (November-May) the maximum average temperature is around 25°C and the minimum is at least 12°C. In winter (June-Octobre), the minimum average temperature often oscillates around 0°C. Average annual rainfall is 1583mm at Ibity and 1416mm at Itremo (based on data from 1961 to 1990; Meteorology Service of Ampandrianomby). The soils of the Ibity massif are ferrallitic and classified as lithosols on quartzitic substrate, mainly formed of metamorphic rocks of the schisto-quartzo-calcareous series. A small area of granite, covering less than 5% of the total mountain, is found on the northeast slope (Birkinshaw *et al.* 2006). Ibity reaches 2254m in elevation, the highest quartzitic mountain in Madagascar. The soil of Itremo massif, classified as lithosols on quartzitic substrate, is mainly formed of schist-quartzitic rocks and has the largest area of exposed quartzitic substrate in Madagascar (Birkinshaw et al. 2004). The highest point of Itremo is 1923m above sea level.

2.2. *Vegetation sampling*

Seventeen fragments of tapia woodland (hereafter referred to as sites) were selected for study, ten at Ibity (seven on quartzitic and three on granitic soil, reflecting the relative area covered by these two soil types) and eight at Itremo (five on quartzitic and three on granitic soil). The sites were classified as being quartzitic or granitic according to the simplified geology map of Du Puy and Moat (1996, 1998). Most of the existing tapia fragments in each massif were studied, with the exception of just a few that were difficult or/and dangerous to access. On Ibity three of the four fragments located on the granitic soil and seven of the ten on the quartzitic soil were studied. On Itremo three of the five fragments on the granitic soil and five of the eight fragments on quartzitic soil were studied.

In order to sample vegetation composition and structure in tapia woodland we used a method adapted from Fukushima et al. (2008) and Kull et al. (2005). At each site, we randomly established three 40×40m plots. In tapia fragments of limited size, only one or two plots were marked. In each 40×40m plot, all individuals with a diameter at breast height (DBH) of more than 10cm, i.e., those that comprise the canopy, were recorded and measured; within each of the large plots, a 20×20m subplot was established (Figure II-1) within which all individuals with a DBH of 5-10cm (lower canopy) were measured. Similarly, a 10×10m plot was also established within which all the individuals with a DBH between 1-5cm (midstory) were measured, along with a 5×5m plot in which individuals with a height lower than 1.30m or a DBH between 0-1cm (understory) were measured. For herbaceous species, 16 1×1m plot were randomly established at each site. In total, for both massifs, 43 plots measuring 40×40m were delimited in tapia woodland along with 255 plots of 1m×1m in the herbaceous stratum. For each individual, canopy cover (m^2) and total height were estimated, and DBH was measured. For herbaceous species the percent cover of each taxon in each of the $1m^2$ quadrats was assessed. Sampling was carried out between June and August 2009. Species identifications were confirmed in Antananarivo at the reference herbarium of the Tsimbazaza Botanical and Zoological Park and at MBG's offices.

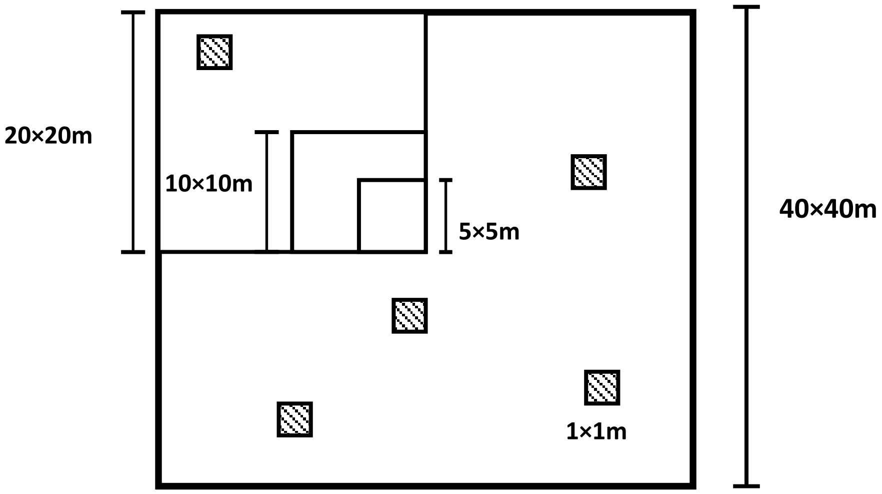

Figure II-1: Arrangement of sampled plots in tapia woodland: 40×40m plot (for trees of DBH ≥ 10cm), 20×20m plot (for trees of DBH 5-10cm), 10×10m plot (for trees of DBH ≥ 1-5cm), 5×5m plot (for trees of DBH < 1cm) and five of the 16 1×1m random plot (for herbaceous species).

2.3. *Statistical analyses*

To assess differences in species richness (response variable) between the two massifs and the two main soil types (quartzitic and granitic) along with possible interactions between these factors, species richness data were analyzed with linear mixed effect models using the *lme* function (Pinheiro & Bates 2000), R-package nlme). The sites and the plots at each site were treated as random factors to account for both differences in soil type and statistical dependence between measurements for different species in the same plot. They were checked for a normal distribution using the Lilliefors test and square root transformations were made as necessary. The homogeneity of variance was confirmed with the Bartlett test. We expected species richness to be higher on the quartzitic soil because some species are restricted to this substrate; we also expected richness to be higher at Itremo because the vegetation on the massif seemed less heavily impacted. To evaluate differences in the composition of tapia woodland areas, a Correspondence Analysis (CA) was carried out on on percent covers of each species. We expected to find some patterning in species composition depending on the soil and the massif.

To estimate differences in tapia woodland structure between massifs and between soil types, as well as possible interactions between these factors, linear mixed effect models with the *lme* function were used as above on three response variables: height, percent cover, and DBH of *Uapaca bojeri* and all other woody species. We expected these variables to be higher at Itremo because the surrounding area is less densely populated and also higher on granitic soils because they are generally richer in nutrients. Then, two variables, the height of individuals > 1m and the DBH (response variable) of *Uapaca bojeri* and all other woody species, were divided into classes to characterize the distribution of woody species within tapia woodland. Kruskal-Wallis tests followed by Wilcoxon tests adjusted by a Bonferroni correction were run to assess differences between classes for each massif separately. To determine differences between the two massifs for each DBH and height class, additional Wilcoxon-tests were run. Again, we expected values to be higher at Itremo and on granitic soil. To determine differences between the two massifs for each DBH of common woody species, t-test or Wilcoxon-tests were run. All analyses were carried out using the software R (The R Foundation for Statistical Computing, version R2.13.0).

3. Results

3.1. Species richness in Ibity and Itremo

We found a total of 120 and 84 species at Ibity and Itremo, respectively, belonging to 41 and 26 families and 83 and 60 genera. Woody species richness was significantly lower on granitic soil at Itremo (2.5±0.62 species); it was intermediate on quartizitic soil at Itremo (5.7±0.65 species), and highest for both soil types at Ibity (7.9±0.38 species) ($F_{soil\times massif}=8.4$, $p<0.01$; Figure II-2a). The species most closely associated with *Uapaca bojeri* (the dominant tree element) at both Ibity and Itremo include members of Sarcolaenaceae (*Leptolaena pauciflora, Pentachlaena latifolia, Sarcolaena oblongifolia, Schizolaena microphylla, Xerochlamys bojeriana,* and *X. diospyroidea*), *Aphloia theiformis* (Aphloiaceae), two species of *Asteropeia* (*A. densiflora* and *A. labatii* - Asteropeiaceae) and *Schefflera bojeri* (Araliaceae). Species richness of the herbaceous stratum was lower on Itremo quartzitic soil (5.6±0.23 species) than on other combinations of site and soil type (6.5±0.16 species; $F_{soils\times massifs}=14.5$, $p<0.001$; Figure II-2b).

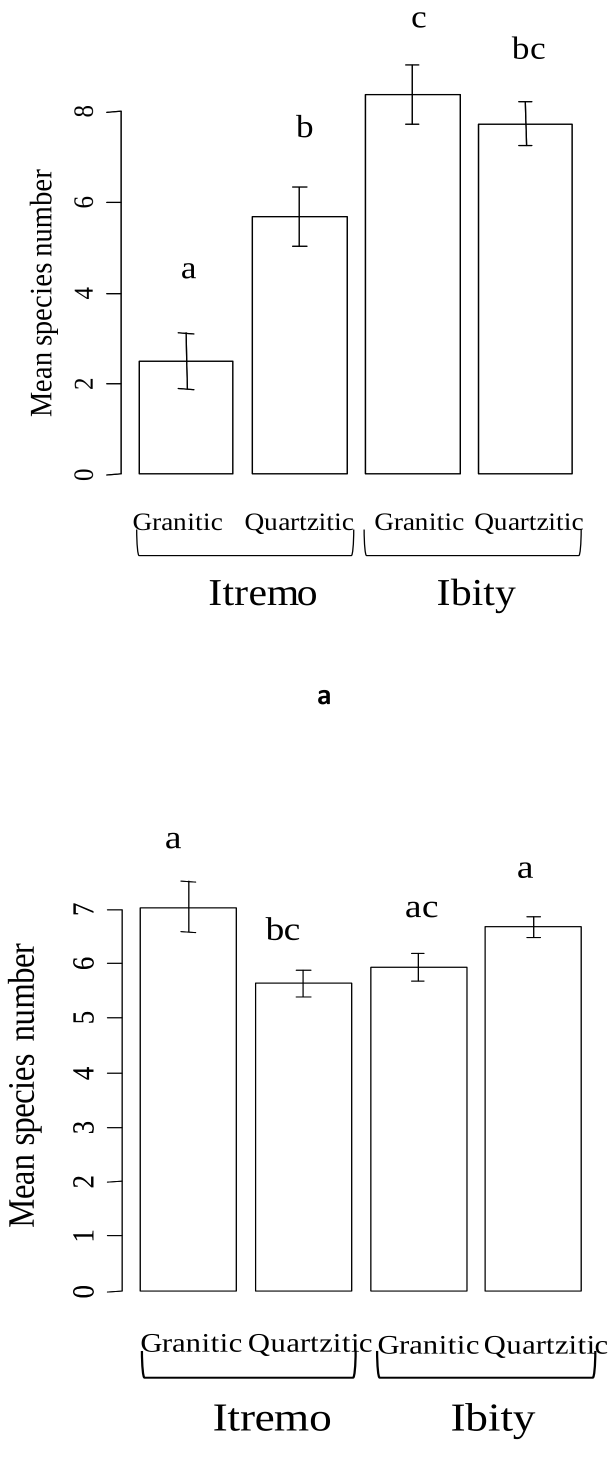

Figure II-2: Mean species richness by soil type (granitic vs. quartzitic) and massif (Ibity and Itremo). Species richness (a) is represented by the mean number of woody species per 1600m² ($F_{soil \times massif}$=8.4, p<0.01); (b) by the mean number of herbaceous species per 1m² ($F_{soil \times massif}$=14.5, p<0.001); lower case letters indicate the results of post-hoc Tukey tests (p<0.05). Total numbers of woody and herbaceous species for Ibity were 33 and 87 respectively; and total numbers of woody and herbaceous species for Itremo were 18 and 66 respectively.

3.2. Woody species and understory composition

In total, we found 18 woody species on Itremo, of which 11 are trees and 7 shrubs, as compared with 33 on Ibity, with 12 trees and 21 shrubs. Some species are common to the two massifs (viz. *Aphloia theiformis, Asteropeia densiflora, Sarcolaena oblongifolia,* and *Schefflera bojeri,* among others). The Correspondence Analysis of the woody species composition showed a difference in composition between Ibity and Itremo on the first axis (42.5%) (Figure II-3).

Uapaca bojeri represents 82% of the trees counted on Ibity (112 individuals out of a total of 137 trees on average per 1600m^2) versus 72% on Itremo (58 individuals of *U. bojeri* out of 80 total trees on average per 1600m^2). We found Itremo to be characterized by a greater number of individuals of species of Sarcolaenaceae [*Leptolaena pauciflora* (1%), *Sarcolaena oblongifolia* (14%), *Schizolaena microphylla* (2%) and *Xerochlamys diospyroidea* (6%)] and the genus *Asteropeia* [*A. labatii* (1%) and *A. densiflora* (0.1%)]. Ibity, by contrast, is characterized by *Xerochlamys bojeriana* (3%), *Sarcolaena oblongifolia* (1%), *Pentachlaena latifolia* (1%), *Asteropeia densiflora* (1%) and exotic species such as *Pinus kesiya* (3%; for family names of species see Appendix 4 (Annexe 4) of the thesis). We also observed differences in composition depending on soil type (granitic vs. quartzitic) on the second axis of the Correspondence Analysis: *Eucalyptus robusta* and *Maesa lanceolata* occur only on granitic soil (Figure II-3). Among herbaceous species, *Loudetia simplex* and *Ctenium concinnum* (both Poaceae) were dominant on both soil types, based on their percent cover. Some other herbaceous taxa were only present on quartzitic soil (e.g., *Digitaria debilis, D. biformis, Imperata cylindrica, Microchloa kunthii, Panicum cupressifolium* and *Secamone buxifolia*), whereas we found only a few on granitic soil (e.g., *Costularia laxa, Cyperus amabilis, Elionurus tristis* and *Biophytum sensitivum*). Overall the composition of herbaceous species was relatively similar on both massifs, although species richness was higher on Ibity (87 species vs. 66 on Itremo). *Cynodon dactylon*, *Eragrostis tenuifolia* and *Stachys filifolia* were thus present only on Ibity. A large number of seedlings of woody species, such as *Erythroxylum buxifolium* and *Xerochlamys diospyroidea*, were observed at Itremo.

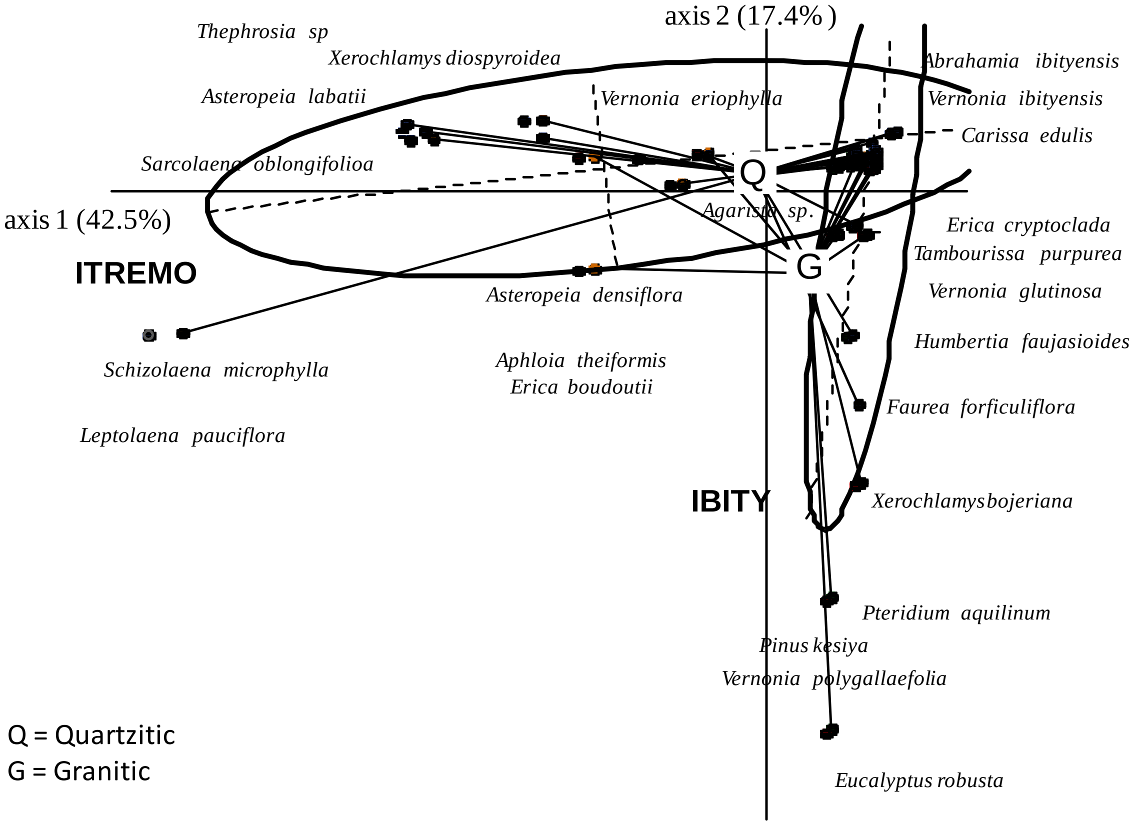

Figure II-3: Correspondence Analysis of woody species composition in tapia woodland of the Ibity and Itremo massifs; G= granitic and Q= quartzitic. Only those species that contributed substantially to the analysis are indicated.

3.3. Structure of tapia woodland

The canopy cover of *Uapaca bojeri* at Itremo (13.1±1.27 m^2) was significantly denser than at Ibity (6.6±0.58m^2), regardless of soil type (e.g., on granitic soil, the value for Itremo was 16.0±2.70m^2 whereas on Ibity it was 5.6±1.45m^2; $F_{soil\times massif}$ =6.1, p<0.05; Figure II-4). Moreover, individuals of *U. bojeri* were significantly smaller at Ibity (average size 3.3 ± 0.10m) than at Itremo (average size 5.1 ± 0.28m, with some individuals exceeding 10m) (F_{massif}=38.1, p<0.001). We found no difference in height according to soil type. The distribution of *U. bojeri* by height class for the individuals > 1m showed more intermediate size trees at Ibity (1-4m stratum: 24.9% on Itremo *vs.* 80.1% on Ibity; W=316642.5, p<0.001) and more large individuals at Itremo (4-8m stratum: 67.9% on Itremo *vs.* 17.2% on Ibity, W=239306.5, p<0.001). On Ibity, no individuals of *U. bojeri* were taller than 8m while 2.3% exceeded this height on Itremo. The same tendency was observed when all other woody species were considered together.

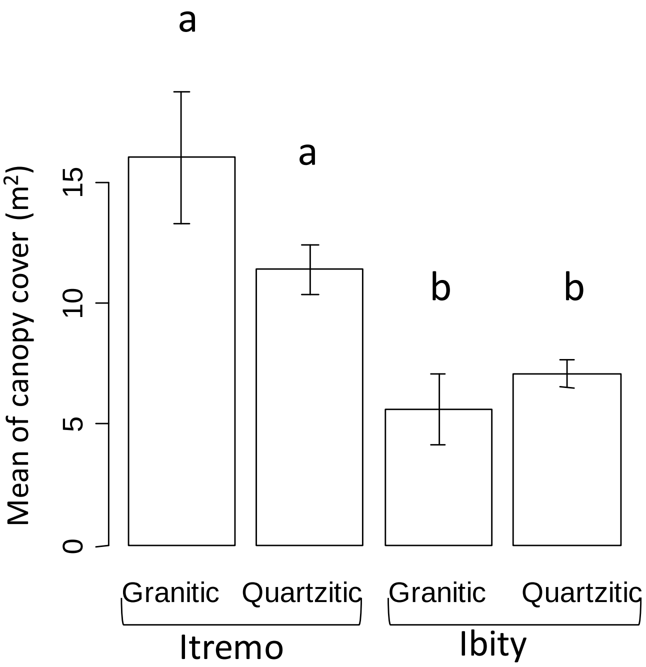

Figure II-4: Mean canopy cover of *Uapaca bojeri* (m^2) at Ibity and Itremo massifs ($F_{soil \times massif} = 6.1$, $p<0.05$). Lower case letters indicate the results of post-hoc Tukey tests ($p<0.05$).

The average DBH of *Uapaca bojeri* was significantly greater on Itremo (16.1±0.84cm) than on Ibity (9.5±0.52cm) ($F_{massif}=57.4$, $p < 0.001$), and no difference was found according to soil type. Individuals of *U. bojeri* were not equally distributed among the DBH classes on the two massifs (Kruskal-Wallis $Chi^2=105.4$, $p<0.001$ for Ibity and 38.7, $p<0.001$ for Itremo) (Figure II-5). The percent of individuals of *U. bojeri* with a DBH 5-10cm was significant higher on Ibity (6.1% on Itremo *vs.* 36% on Ibity; W=66, $p<0.001$). However, there were more individuals of *U. bojeri* with the DBH classes >20cm on Itremo (DBH class 20-30cm: 6.27% on Itremo *vs.* 1.29% on Ibity; W=378, $p<0.001$; DBH class 30-40cm: 1.21% on Itremo vs. 0.21% on Ibity; W=341 $p<0.001$; and DBH class 40-50cm: 0.32% on Itremo vs. 0% on Ibity; W=259, $p<0.05$). Similarly, there were more individuals with a DBH <1cm were on Itremo (66.1% on Itremo *vs.* 18.6% on Ibity; W=282, p=0.07) and more individuals with a DBH between 1-5cm (8.7% on Itremo *vs.* 28.1% on Ibity; W=146, $p<0.08$). Individuals with a DBH between 10-20cm were equally represented on both massifs (11.8% on Itremo *vs.* 15.8% on Ibity; W=227, p=0.794).

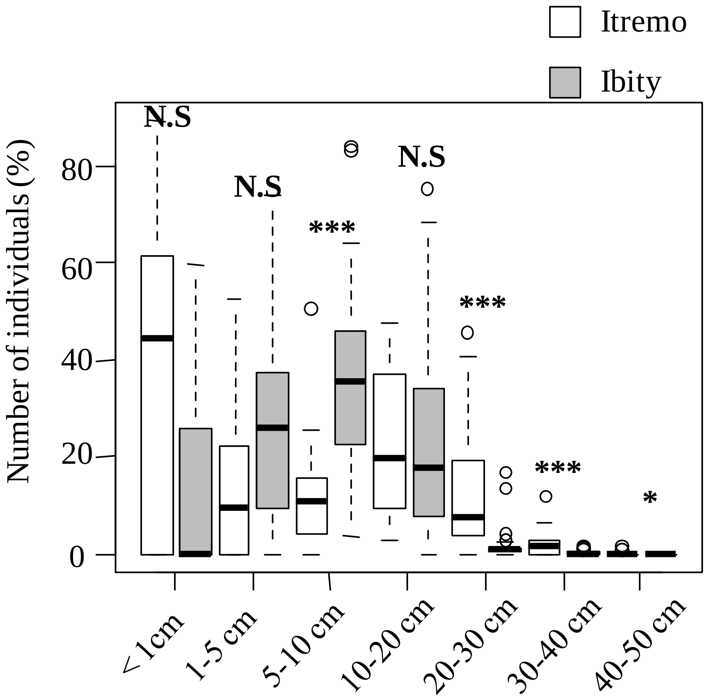

Figure II-5: Percent of individuals of *Uapaca bojeri* in each DBH class (cm) at Ibity and Itremo massifs. Wilcoxon tests were run for all DBH classes; they were significant for DBH class 5-10cm (W=66; $p<0.001$), 20-30cm (W=378; $p<0.001$), 30-40cm (W=341; $p<0.001$) and 40-50cm (W=227; $p<0.05$).

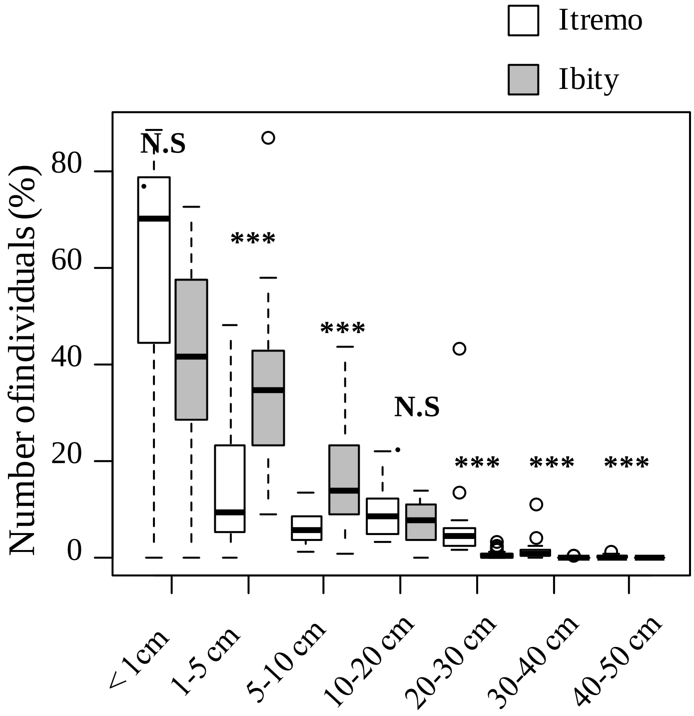

Figure II-6: Percent of individuals of all woody species (except *Uapaca bojeri*) per DBH class (cm) at Ibity and Itremo massifs. These tests were significant for DBH class 1-5cm (W=37; $p<0.001$), 5-10cm (W=45.5; $p<0.001$), 20-30cm (W=428.5; $p<0.001$), 30-40cm (W=381; $p<0.001$) and 40-50cm (W=297; $p<0.001$).

As was found for *Uapaca bojeri*, the individuals of the other woody species were not equally distributed among the DBH classes on the two massifs (Kruskal-Wallis = 108.6, p<0.001 for Ibity and 77.7, p<0.001 for Itremo) (Figure II-6). The distribution of woody species by DBH class showed that individuals with a DBH <1cm were well represented on both Itremo and Ibity (69.5% and 42.0% respectively; W=234.5, p=0.649). The percent of individuals with a DBH between 1-5cm and 5-10cm were significantly higher on Ibity (DBH class 1-5cm: 12.8% on Itremo *vs.* 35% on Ibity; W=37, p<0.001; and DBH class 5-10cm: 5% on Itremo *vs.* 16% on Ibity; W=45.5, p<0.001). However, the percent of individuals of the DBH classes >20cm was higher on Itremo (DBH class 20-30cm: 3.71% on Itremo *vs.* 0.54% on Ibity; W=428.5, p<0.001; DBH class 30-40cm: 0.68% on Itremo *vs.* 0.07% on Ibity; W=381, p<0.001; and DBH class 40-50cm: 0.09% on Itremo *vs.* 0% on Ibity; W=297, p<0.001). Individuals with a DBH between 10-20cm were equally represented on both massifs (7.1% on Itremo *vs.* 6.2 on Ibity; W=177.5, p=0.339. On Itremo, eight species had a mean DBH larger than 5cm and six had a DBH that exceeded 10cm, whereas on Ibity, five species had a mean DBH larger than 5cm, only one which exceeded 10cm (Table II-1). The DBH values of four species of the seven shared between the two massifs were significantly higher on Itremo (viz. *Sarcolaena oblongifolia, Pinus kesyia, Uapaca bojeri* and *Erica boutonii*, in decreasing order of mean DBH, Table II-1).

Table II-1: Mean DBH (in cm) of the main woody species in tapia woodland on the Ibity and Itremo massifs. W indicates the results of Wilcoxon tests and t of t-tests.

Species	Itremo	Ibity	W/t	p-value
Sarcolaena oblongifolia	17.6 ±0.7	3.7±0.3	W = 6480	<0.001
Pinus kesiya	17.4±2.1	7.6±0.6	W = 567	<0.001
Uapaca bojeri	16.3±0.3	9.0±0.1	W = 2228916	<0.001
Schizolaena microphylla	16.0±1.6			
Asteropeia labatii	15.5±1.7			
Agarista sp.	15.5±3.2			
Syzygium parkeri		11.8±0.1		
Asteropeia densiflora	6.8±4.5	1.9±0.2	W = 20	0.087
Xerochlamys diospyroidea	5.0±0.5			
Schefflera bojeri	1.7±1.0	6.0±0.6	t = -2.9	0.073
Eucalyptus robusta		5.6±0.4		
Faurea forficuliflora		4.7±0.2		
Vaccinium emirnense		4.3±1.9		
Weinmannia stenostachya		4.1±2.7		
Rhus taratana		3.6±0.4		
Senecio leandrii		3.4±3.1		
Erica boutonii	2.8±0.48	1.0±0.1	t = 5.4	<0.001
Radamaea montana		2.3±0.5		
Pentachlaena latifolia		2.0±0.2		
Aphloia theiformis	1.1±0.2	1.1±0.2	t = -0.02	0.985

Uapaca bojeri clearly dominated the other woody species in terms of number of individuals (Table II-2). In particular, in both the canopy and lower canopy, *U. bojeri* represented more than 50% of the trees counted. On Itremo, 94% of individuals forming the canopy were limited to two species, *U. bojeri* and *Sarcolaena oblongifolia*, and 95% of individuals in the lower canopy are represented by these two species plus *Schizolaena microphylla* and *Xerochlamys diospyroidea*. The midstory was characterized by *U. bojeri*, *S. oblongifolia*, *S. microphylla*, *X. diospyroidea* and *Erica boutonii* (in decreasing order of number of trees). On Ibity, by contrast, the canopy was dominated by *U. bojeri* only, and the midstory was represented by young individuals or sprouts of *U. bojeri*, by young individuals of *Xerochlamys bojeriana* and *Pentachlaena latifolia*, and by shrubby species of *Erica (E. boutonii and E. cryptoclada)*.

Table II-2: Mean number of individuals (%) of the principal woody species at the Itremo and Ibity massifs according to their DBH (cm). (A) Canopy (DBH>10cm); (B) Lower canopy (DBH to 5-10cm); (C) Midstory (DBH to 1-5cm); and (D) Understory (DBH<1cm).

Species	**Itremo**				**Ibity**			
	Canopy	**Lower canopy**	**Midstory**	**Understory**	**Canopy**	**Lower canopy**	**Midstory**	**Understory**
Uapaca bojeri	78.7±2.2	58.4±0.7	38.2±0.5	45.5±1.5	92.8±1.9	84.1±0.5	30.5±1.1	16.8±0.6
Sarcolaena oblongifolia	15.4±2.1	13.9±0.5	9.1±0.3	6.8±0.3	0.5±0.2	2.1±0.1	2.4±0.1	
Xerochlamys bojeriana						3.3±0.09	17.8±0.2	18.6±1.0
Pinus kesiya	0.6±0.2				2.8±0.3	2.3±0.08	3.7±0.3	3.5±0.3
Xerochlamys diospyroidea	1.6±0.4	17.8±0.5	34.5±1.3	25±0.8				
Rhus taratana					1.2±0.09	2.9±1.1	2.9±0.1	
Pentachlaena latifolia					0.5±0.05	0.7±0.03	6.4±0.2	6.2±0.3
Schefflera bojeri			3.6±0.5	1.1±0.4	0.8±0.07	1.3±0.04	1.6±0.06	
Erica boutonii		4±0.7	12.7±1.8	1.1±0.3			6.1±1.0	8±1.3
Schizolaena microphylla	2.2±0.9	5±0.5	1.8±0.3	1.1±0.2				
Erica cryptoclada						0.3±0.03	2.9±0.5	12.4±1.0

4. Discussion

Comparisons of floristic richness and of structure (canopy cover, height and DBH), as seen by the number of species, genera and families, show that Ibity is significantly richer than Itremo, but the latter massif shows a better preserved structure in which trees are bigger and canopy cover is denser than at Ibity, a situation that can be explained by differences in management regime and human impact (Kirkpatrick 1999; McIntyre & Hobbs 1999).

4.1. The human contexts at Ibity and Itremo

While the two massifs studied have similar climates, plant assemblages, geological conditions and geomorphology, they differ with respect to the type of management applied by their respective local communities. The human population is denser around Ibity (Birkinshaw *et al.* 2006), where three rural districts have a total estimated population of about 34,000 people living in an area of ca. 5km2. By contrast, while the area around Itremo also has three rural districts, only one of them, located on the eastern side of the massif, has a significant population of about 6,250 people in 10km^2, whereas the western side of Itremo is almost completely unpopulated (Birkinshaw et al., 2004), giving the total area (ca. 970km^2) an average population density of ca. 5 inhabitants per km^2. The denser human population around Ibity results in more intense anthropological pressures, mainly a higher frequency of bush fires.

Another factor influencing the structure of tapia woodland is traditional management practices, which appear to have spared remnants stands because this vegetation plays an important role in the local economy as a source of fuel wood, edible fruits, mushrooms and medicinal plants, and as habitat for wild silk worms (Borocera madagascariensis), whose cocoons are collected by local residents to produce cloth (Gade 1985; Kull 2002a; Alvarado *et al.* 2012). Historically, the communities may have protected tapia woodland and may have actively used fire as a management tool for tapia and the production of silk moth cocoons (Du Puy & Moat 1996; Kull 2002a; Kull *et al.* 2005; Birkinshaw *et al.* 2006). Today, silk production and cattle raising are the driving forces for fire management at both sites.

4.2. Tapia woodland and fire

Fire has been regarded by many ecologists as the major ecological factor affecting the structure of vegetation in tropical Africa (Trapnell 1959; Lawton 1978; Chidumayo 1987). Its impact depends mainly on the development of the herbaceous layer, which is in turn dependent on the nature of the canopy. A study carried out by Lawton (1978) in miombo woodland vegetation in Zambia, dominated by species of *Brachystegia* and *Julbernardia* and also containing species of *Uapaca*, showed that fire was one of main factors determining structure and composition, but also played a major role in the degradation of these woodlands. Regular burning at the end of dry season produces a vegetation type dominated by herbaceous species, whereas sites burned every four years towards the start of the dry season support a predominantly woody vegetation (Trapnell 1959; Campbell 1996). Thus, in these parts of Africa, intense fires in the late dry season influence the development of the herbaceous layer, to the detriment of an understory characteristic of woodlands (Trapnell 1959). Although there are no direct information on fire frequency on Ibity and Itremo, we hypothesize that it is higher at Ibity because of the larger human population in its surroundings and a resulting higher demand for pasture land and silk production. This is consistent with the results found on the composition and structure of tapia woodlands: at Itremo, the understory comprises numerous seedlings of woody species and the tapia woodland canopy is denser, whereas at Ibity, the canopy is more open, with an herbaceous stratum dominated by various Poaceae.

While the impact of fire on savannas and woodlands has been well studied in the miombo of Africa (Trapnell 1959; Lawton 1978; Chidumayo 1987, 1989; Campbell 1996), the dynamics of Madagascar's endemic tapia woodland remain poorly known (Koechlin et al. 1974; Kull 1998, 2002). Many species of *Uapaca* are quite fire tolerant, including *U. densifolia* from Ambohitantely forest in Madagascar (Rakotoarisetra 1997), and *U. kirkiana, U. pilosa* and *U. nitida* found in African miombo woodland (Campbell 1996). *Uapaca bojeri* likewise presents the typical characteristics of pyrophytic trees, such as the capacity to regenerate by sprouting, thick bark and weakly flammable leaves (Campbell 1996). These biological characteristics suggest that frequent fires and the current fire regime found at Ibity and Itremo favour the dominance of this species and produce open, nearly monospecific stands of tapia woodland (Koechlin *et al.* 1974; Gade 1996; Kull *et al.* 2005). Indeed, earlier studies have shown that more than 90% of the trees in this vegetation type are *U. bojeri* (Rakotoarivelo 1993; Kull 2002; Kull et al. 2005), exceeding the dominance of *U. kirkiana* in miombo vegetation, which ranges from 54% to 74% (Lawton 1978) as well as the levels founded on Ibity and Itremo (82% and 72% respectively).

The dominant species in tapia woodland are mainly fire resistant, a situation similar to that found in miombo vegetation in Africa (Trapnell 1959). While ecological succession following fire exclusion has not yet been studied for tapia woodlands, the work of Trapnell (1959) showed that *Uapaca kirkiana* occupies an intermediate state of succession between fire tolerant woodlands and fire sensitive dry evergreen forests. The exclusion of fire from frequently burned sites allows fire sensitive species to establish, which can grow to become co-dominant in the canopy, eliminate the herbaceous understory, and consequently reduce subsequent fire intensity after their establishment. Since *U. bojeri* appears to be an ecological analogue to *U. kirkiana*, it is possible that fire control in areas with tapia woodland will promote the regeneration of this species and will permit the establishment of a more diversified and complex woody vegetation.

The vertical structure of miombo woodland has been described as simple (Lawton 1978; Chidumayo 1987), with a strong canopy layer, a few understory species, and a minimal herbaceous layer (Chidumayo & Frost 1996; Frost 1996). This structure is influenced by edaphic and climatic conditions, fire regime, herbivory, and past and present land use (Desanker *et al.* 1997), and is the result of the combined effects of shading induced by the open canopy and caused by mild, early season fires (Campbell 1996; Frost 1996). In the tapia woodlands of Ibity and Itremo, the canopy is most likely not dense enough to suppress the growth of saplings. The small proportion of woody individuals observed in the understory in Ibity is possibly a result of the frequent passage of bush fires, which kill young plants (Chidumayo, 1989). Fire can alter the number and type of species growing in a region by killing individuals that have not attained sufficient height or bark thickness to withstand the heat, and by damaging or destroying unprotected living tissues (Hoffmann *et al.* 2009). Although *Uapaca bojeri* is fire tolerant, frequent burning can also destroy adult trees and prevent their natural regeneration (Perrier de la Bâthie 1921; Chidumayo 1989; Gade 1996). Koechlin et al. (1974) showed that frequently burned tapia woodland has more numerous sprouts than closed woodland and sites subjected to fewer fires. If burning occurs early in the dry season when the woody species are dormant, its impact is minimal and limited to evergreen species, which will regenerate under such an early-fire regime (Trapnell 1959; Lawton 1978; Chidumayo 1988). However, burning later in the dry season, after new leaves have appeared, may cause damage to adult trees. Kull et al. (2005) showed that woody species in tapia woodland largely regenerate by sprouts. The same study showed 3% seedling mortality in unburned plots as compared to 35% mortality in burned plots, although two thirds of the apparently dead individuals in the burned plots re-sprouted during the following rainy season. (Rakotoarivelo 1993) showed that 61% of the young stems arise from sprouts, 24% from suckers, and only 15% from germination.

4.3. Other factors influencing tapia woodland

We found clear differences in the composition of the canopy and lower canopy between the Ibity and Itremo. Species of Sarcolaenaceae and other woody taxa are better represented on Itremo. In Ibity, exotic species such as *Eucalyptus robusta* and *Pinus kesiya* planted for reforestation represent one of the main threats to tapia woodland (Kull *et al.* 2005) given that they are heliophilous and fast-growing, and thus colonize outside planted areas. Moreover, these introduced tree species are known for their capacity to exhaust soil nutrients, to use water rapidly and in large quantities, and to acidify the soil (Malik & Sharma 1990; Lisanework & Michelsen 1993; Michelsen *et al.* 1996), and they also negatively impact the establishment of the herbaceous stratum (Lisanework & Michelsen 1993), thereby increasing soil erosion and degradation of the understory. Furthermore, at Ibity we also recorded the highly inflammable fern *Pteridium aquilinum*, considered a typical pioneer species, in degraded, burned or deforested zones (Silva & Matos 2006), where it impedes the establishment of native species by producing allelopathic substances (Pakeman & Marrs 1992; Pakeman et al. 1994).

As in African miombo, the current state (structure and floristic composition) of tapia woodland in Madagascar is determined by biotic and abiotic factors (Desanker *et al.* 1997). The sclerophyllous woodlands dominated by *Uapaca* and *Sarcolaena* are a very restricted vegetation type. The main remnants, found in Isalo National Park (south of Itremo) as well as the Ibity and Itremo massifs, occur on sandstone and quartzite/granitic substrates, respectively, and have different species compositions (Du Puy & Moat 1996). This vegetation type is frequently present on poor soils, and edaphic conditions thus seem to be an important factor in determining their presence. We found a difference in species richness and cover canopy between the two main soil types (granitic and quartzitic) on Itremo and on Ibity. Woody species richness was highest on granitic soil at Ibity and lowest on this soil type at Itremo. Canopy cover responded in an inverse manner; it was lowest on granitic soil at Ibity and the highest on granitic soil at Itremo.

There is a clear anthropogenic nature to tapia woodland in the region studied, as it was long managed using traditional methods, which allowed sustainable extraction of forest resources for local consumption, selective cutting and the use of fire as a management tool (Kull 2002a; Alvarado *et al.* 2012). Today tapia woodland is still partly managed using traditional methods, but newer practices have caused degradation through increased cultivation and grazing on the low slopes, illegal exploitation and marketing of natural resources, reforestation with exotic tree species such as *Eucalyptus* spp., *Pinus* spp. and silver wattle or silver mimosa (*Acacia dealbata* Cunningham), and changes in the fire regime (Alvarado *et al.* 2012). On Ibity, reforestation activities recently developed by HOLCIM, S.A. (a large Swiss-based company whose local headquarters is located in the town Antsirabe) in the northern part of the massif have introduced exotic species there as well, which are now dispersing and beginning to invade the natural vegetation.

5. Conclusion

Tapia woodland is an anthropologic vegetation type, resulting from the interaction of localized edaphic conditions, human activities and fire. Today, observed differences in the vegetation between the Ibity and Itremo massifs can only be interpreted based on the available qualitative information regarding these factors. Differences in the way humans have managed the landscapes at Ibity and Itremo have had a strong influence on the pressures that have impacted woodland vegetation, as seen by differences in structure and floristic composition. The main recommendations for the NPA managers are:

1. The exotic species found during our study mainly occurred on on Ibity, where they have been planted and have spread to nearby disturbed areas. The vegetation management plan should aim to remove exotic trees, particularly those close to or within the NPAs. While planting fast growing exotic species is a way to provide adequate quantities of fire and construction wood to local communities and thereby lower demand on native species, this practice should be limited to lower-lying areas that have already been totally converted to agricultural use.

2. The greater frequency and extent of intentionally setting bush fires on Ibity as compared to Itremo has led to greater diversity among woody and herbaceous native species. The understory on Itremo is less rich in species but the canopy appears to be better preserved. Our study provides potentially valuable information to those responsible for managing of these NPAs with regard to the current state of the remaining tapia woodland and priorities for its conservation. While fire is unquestionably one of the main factors that influence the natural regeneration of tapia woodland, total exclusion of burning is neither practical nor realistic because it forms an integral part of the traditional agro-pastoral practices of those living around the two massifs. Moreover, total exclusion of human-set fires would lead to the accumulation of ground litter, which could serve as fuel for naturally set fires (e.g., by lightning) that would almost surely be much more intense and destructive to natural vegetation. The adoption of a management strategy based on a fire regime intermediate between that of Ibity and Itremo would in all likelihood make it possible: i) to decrease the dominance of Poaceae on both massifs that may compete with young individuals of woody species and with other herbaceous taxa while also reducing the risk of destructive fires by limiting the accumulation of flammable litter; and ii) to increase the rate of survival of woody species recruits after burning and improve woody species regeneration. In absence of precise information on fire frequency on both massifs, controlled burnt in early fire season (March-May), when the ground litter is not completely dry, may be useful to reduce fuel and thus, to reduce fire severity and the risk of fire spread to areas where it is not desired.

3. Selective exploitation plays an important role in the conservation of tapia woodland. The economic importance of *Uapaca bojeri* fruits and of the habitat provided by this and other woody species for wild silk worms should be factored into management planning.

Future efforts to understand the impact of fire on the current state of tapia vegetation will require more detailed, quantitative information on several important factors. The fire regime should be characterized based on GIS analyses of satellite images as it is not known precisely yet for these NPAs (Jacquin *et al.* 2011a). A study of germination and plant phenology of the main woody species is needed, and an evaluation of seedling survival and establishment should be conducted in order to assess limitations to the reproductive and regenerative capacities of these species. The managers of the Ibity and Itremo NPAs will need to include a restoration protocol in their management plans to strengthen woody plant populations and expand the area currently occupied by tapia woodland.