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INVESTING FOR A SUSTAINABLE NATURAL ENVIRONMENT FOR FUTURE GENERATIONS OF HUMANS, ANIMALS AND PLANTS OF MADAGASCAR

IN THIS ISSUE

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EDITORIAL

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Madagascar rich and intransparent

"If you shut up truth, and bury it underground, it will but grow, and gather to itself such explosive power that the day it bursts through it will blow up everything in its way."

--Émile Zola--

Madagascar is one of the richest countries when it comes to natural and mineral resources. As is the case in many tropical countries, however, this wealth is bluntly coupled with an ever increasing poverty, where more than 92 % of the 21 million inhabitants are living below $US2 a day. Madagascar has received international aid and conservation interests for years, as part of which, millions of dollars have been donated to the country, but with very little to show for it (Horning 2008). When Madagascar appeared to hit rock bottom in 2009, a political coup d'état took place which led to the international donor community curtailing financial support (Randrianja 2012). During the following years, the transitional government did not receive the international support that the previous government had benefitted from. Here we will analyze the pattern of two cases of natural resource governance, both coinciding with a political event.

Case 1 pertains to rosewood: Since 2009, illegal logging and exporting of rosewood has reached unprecedented levels in Madagascar (Schuurman and Lowry 2009, Innes 2010, Randriamalala and Liu 2010) affecting the entire east coast, with highest intensity of pillage in the national parks of Masoala and Marojejy. In 2011, reportedly over 500,000 tons of rosewood were in stocks; discussions among experts at the global table revolved around a solution finding to best deal with these stocks (Randriamalala et al. 2011). However, the issue then went mysteriously silent to a remarkable degree for almost two years. In the meantime, the African Union supported by the international community pushed the current government to organize presidential elections with a first round on 25 October 2013, and the second and final round scheduled for 20 December 2013. Coincidently, in mid 2013 the World Bank requested a "Study to Assess the Options of Disposal of the Illicit Stocks of Rosewood and Ebony"[1] issued 31 July 2013 with a deadline for the expressions of interest fixed at 13 August 2013.

During the last year, a new phenomenon has emerged: inventoried rosewood logs have slowly but regularly been ferreted out of the depots they were stored in. During the early months of 2013, traffickers from Maroantsetra visited the Masoala peninsula and generously offered 1 million MGA per household to turn a blind eye regarding any rosewood. Simultaneously, large vessels positioned just too far to be seen from any shore, were collecting logs transferred to them at night in smaller boats. Encouraged by the incredulous ineptitude on the part of the local legal authorities, this process has been ongoing, even during daylight hours, with the 'mother ships' eventually even clearly visible from the shores. The timber stocks in the known depots have almost been completely cleared out by now. At the end of September 2013 a petition was suddenly circulated by EIA (Environmental Investigation Agency) bearing the message "Urgent Sign-on To Stop Madagascar Illegal Sale of Massive Stockpiles of Rosewood and Ebony" that many people and international and national NGOs have signed[2]. Interestingly, the concerns revolved around the estimated value of stocks, whether they were worth US$5 billion or only US$600 million. The question which goes begging is, why is the World Bank suddenly trying to find a legal solution for the stocks, when they de facto have already been removed from Madagascar and transported to Asia? We propose the following hypotheses as some food for thought: (i) There is insufficient information to assess the quantity and value of the remaining stocks. If any stock does indeed remain, it does represent a threat to the natural resources, and in principle, conservation NGOs cannot support the legalizing of the sale of such stocks. This implies that in the past, the legalizing and therefore selling of timber held in stocks represented a threat to the remaining precious trees, i.e., it has led to further illegal logging (Randriamalala and Liu 2010). (ii) The stockpiled timber has already steadily and consistently been exported to China: the government, the conservation community, and the public are all cognizant of this. There is a complex financial arrangement proposed by the international funding agencies and promoters of democracy, to appease all the parties involved in the case of dealing in illegally-felled rosewood[3].

Hypothesis 1 appears naïve and almost unrealistic, given that the case is well known by all the parties involved. Hypothesis 2 requires a deeper understanding of the financial, legal, and institutional mechanisms involved, since international funding agencies and the World Bank are not allowed to support an illegitimate government (i.e., one which assumed power through a coup d'état). The question which remains alludes to a problem which may be described as "wicked", for lack of a better prescriptive (cf. Rittel and Webber 1973): how can someone make more money from a product which has already been sold?

We will try to shed some light by performing a *reductio ad absurdum*, which entails a step-by-step hypothetical appeasing of every party or individual involved in the rosewood trafficking process. To begin with, we ask the question: where do the interests of the various actors, really lie? This may be answered as follows: (i) Some, such as international funding agencies and NGOs seek a 'green' image. (ii) Others wish to be seen as promoters of democracy (western countries). (iii) Some are in a position of being in dire need of funding: they include certain NGOs and the Malagasy government. (iv) Some are lenders of money: these are the funding agencies and foreign governments. (v) There are some seeking to launder money, i.e., timber sellers and buyers.

To 'green-wash' the illegally-sourced logs, necessitates the issuance of a CITES permit, something which could be lobbied for by NGOs, who would then receive money from the funding agencies, officially to help them protect the wildlife. On the other hand, timber traders and buyers would thereby legalize their business, and push for the supporting of the required democratic process, i.e., the ongoing elections. Therefore, the value of the legalized stocks of wood would lie in its 'greening-up' of the buyers' profiles, and allow some of the laundered money to flow back to Madagascar so that 'business as usual' could continue.

Let's take a step back though: Hypothesis 2 appears to be in the realms of the absurd. The World Bank and other international funding agencies should not take such a risk: despite their interests to support democracy, development and conservation, they should not get involved in the green-washing of illegal timber. Furthermore, international NGOs should never invest effort in lobbying for a CITES permit allowing for sale of illegally logged ebony and rosewood. NGOs are well aware of the risks involved in such a procedure, and legalizing illegally-traded logs could potentially once again open up the forests to further illegal tree felling and trafficking. Which takes us back to square one: the million dollar question that goes begging pertains to the true level of transparency when it comes to the intentions of all parties involved in this process.

The second case is on a smaller scale, and concerns wetlands, which are among the most threatened ecosystems in Madagascar (Thieme et al. 2005, Rabearivony et al. 2010).

Case 2: Alaotra marshlands, vanishing in a puff of smoke? The Lake Alaotra wetland constitutes the biggest wetland system in Madagascar and is of national importance for its fish and rice production. About 23,000 hectares of marshlands fringe the lake, delivering crucial ecosystem services (water, plant material, fish stock) while hosting unique wildlife such as *Hapalemur alaotrensis*, the only primate species living constantly in marshland, or the recently described carnivore *Salanoia durrelli*, also adapted to wetland. International conservation efforts have been ongoing since the 1990s to sustain this wetland biodiversity and ecosystem, leading to the inscription of the entire Alaotra wetland as the third Ramsar site in Madagascar in 2003. The government of Madagascar then acknowledged the system's biodiversity and conservation values by classifying the wetland as a New Protected Area within national law N°381-2007/ MINENVEF/MAEP on 17 January 2007. Though formally protected, there are increasing pressures on this wetland. The region is dominated by rice paddies, with all the terrain already claimed; the marshlands hence represent a future reservoir for rice production. The increasing scarcity in production capacity is further accentuated by changing hydrologic balance and leads to an underproduction of the existing rice fields. This forces resource users further into the remaining marshlands. For example, the number of rice fields within the lakefront (the so called *riz de contre-saison*) has increased significantly in the past years (Ratsimbazafy et al. In press). The same accounts for the number of fires. According to the same authors, the years 2000 and 2004 have been extreme fire years affecting more than 40% of the entire marshland area. In 2012, the number of fires from October to December exceeded 150 cases (ibid). The year 2013 appears set to break any previous records. According to MWC (Madagascar Wildlife Conservation) and DWCT (Durrell Wildlife Conservation Trust), the marshes are being burnt at an unprecedented level with, for example, a few fires affecting several hundred hectares within a few days in October 2013 alone. The local management and monitoring entities such as VOI (*Vondron'Olona Ifototra*) and CFL (*Comité Forestier Local*) are hopelessly overwhelmed by the many fires, while national actors such as DWCT and MWC can only gather evidence to describe the breaches of the legal or regulatory framework that are being perpetrated. It is very interesting to note that marsh (and forest) fires have reached a peak during this electoral period, where some political actors have repeatedly been observed promising land in exchange for votes. Alaotra represents a case specifically where actors outside of the system, instigate local communities to burn marshland for the sake of rice production (Ratsimbazafy et al. In press). However it is difficult to judge clearly when the smoke is so heavy over the lake. As is the case with many other governments, the Malagasy government is faced with the challenge of balancing the interests of its citizens, which are often in stark contrast with those of players or parties within the international community. The value of Madagascar's resource richness is measured differently by the different stakeholders, and thus governance of these natural resources has become increasingly more complex, and promises to do so even more in the near future. What constitutes a serious hindrance in sound governance is the fact that many of the processes are difficult to trace and assess due to an evident lack of transparency as discussed in these two cases. To strengthen governance depends first and foremost on the political will of the hosting country to improve its governance system, and hence to accept monitors to maintain observation over its performance. This however, requires a marked stepping up of transparency and accountability. At present, the bleak and questionable scenario painted by the above two cases presented here, seem to imply that for the people of Madagascar, its rich biodiversity may be more of a curse than a blessing.

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ENDNOTES

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2 http://eia-global.org/news-media/madagascars-transitional-president-threatens-to-sell-illegal-wood-worth-5-b

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3 http://eia-global.org/images/uploads/English_Version_of_Madagascar_Draft_Decree_to_Authorize_Illegal_Sale_of_Massive_Stockpiles_of_Rosewood_and_Ebony_%C2%AC%E2%89%A0_Translated_using_Google_Translate.docx

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ARTICLE

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Farmer preferences and the production strategies of agroforestry nurseries in southeastern Madagascar

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ABSTRACT

Agroforestry projects in Madagascar that promote fruit trees address social and environmental threats to rainforests by reducing farmers' reliance on rice cultivation as long as fruit production is a more economically efficient option. This study aims to understand farmer planting preferences for fruit trees around Ranomafana National Park, specifically related to their ability to transport produce to wider markets. A large social survey assessed current fruit tree cultivation and the fruit planting preferences of farmers, and evaluated differences in farmer preferences based on distance to roads and markets. Survey results from 21 villages and 200 households indicate current fruit cultivation does not correspond well with planting preferences. Households near and far from roads share similar cultivation patterns and planting preferences with one exception: farmers living far from roads prefer to plant coffee significantly more than do those living near roads. This preference for coffee cultivation far from roads is attributed to coffee's relatively high sales price and ease of transport to buyers. This study also assesses current production in two local agroforestry nurseries and suggests new production priorities, notably focusing on coffee and lychee above the currently emphasized citrus fruits.

RÉSUMÉ

À Madagascar, les projets agroforestiers avec des arbres fruitiers peuvent représenter une réponse aux menaces sociales et environnementales qui pèsent sur les forêts naturelles en réduisant la dépendance des agriculteurs vis-à-vis de la riziculture pluviale à condition que la production de fruits constitue une option plus rentable. Les principaux obstacles à la production de fruits sur la périphérie du Parc National de Ranomafana sont le manque de connaissances des agriculteurs quant aux techniques de propagation, la rareté des espèces, variétés et cultivars d'arbres fruitiers qu'il conviendrait de planter ainsi que l'accès limité aux marchés avec des réseaux de transport fiables. Les organisations de développement de la région travaillent à la formation des agriculteurs et leur apportent les moyens initiaux requis pour démarrer des systèmes agroforestiers avec des arbres fruitiers. Cette étude vise à comprendre les préférences des agriculteurs lorsqu'ils plantent des arbres fruitiers à la périphérie du Parc National de Ranomafana et plus particulièrement par rapport à leurs moyens pour transporter leurs produits vers les plus grands marchés. Une importante enquête sociale a évalué l'état actuel de la culture des arbres fruitiers, les préférences des agriculteurs en matière de plantation pour les fruits à produire ainsi que les différences dans les préférences des agriculteurs en fonction de la distance aux routes et aux marchés. Le sondage réalisé auprès de 200 ménages dans 21 villages indique que la culture fruitière actuelle ne correspond guère aux préférences en matière de plantation. Les ménages résidant à proximité ou loin des routes partagent des modes de culture semblables ainsi que leurs préférences en matière de plantation à une exception près : les agriculteurs qui vivent loin des routes montrent une nette préférence pour la plantation de caféiers contrairement à ceux qui vivent à proximité des routes. Cette préférence pour la culture du café loin des routes est attribuée au prix de vente relativement élevé du café ainsi que de la facilité à le transporter vers les acheteurs. Cette étude a également procédé à une évaluation de la production de deux pépinières agroforestières locales et suggère de redéfinir les priorités en matière de production, notamment en mettant l'accent sur les plants de caféiers et de litchi plutôt que ceux des agrumes qui sont actuellement encouragés. Il s'agit de l'enquête de la plus grande envergure qui ait été menée jusque là sur les préférences en matière de plantation d'arbres fruitiers à Madagascar, qui pourrait être reproduite à la fois sur la périphérie de Ranomafana et ailleurs pour aider les organisations de développement à améliorer leur soutien aux agriculteurs pour qu'ils se tournent vers la production de fruits plutôt que la culture du riz pluvial.

INTRODUCTION

Deforestation is a major threat to biodiversity and human populations in Madagascar's eastern rainforests. Of the 'original' 11.2 million hectares of rainforest extant at the island's colonization, 3.8 million hectares (about 34 %) were left by 1985; at the deforestation rates from the 1980's, Madagascar's rainforests will have vanished from all but the steepest slopes by 2025 (Green and Sussman 1990). Deforestation rates in eastern Madagascar slowed during the 1990's, from 1.7 % per year during the period

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from the 1970's to 1990 down to 0.8 % per year from 1990 to 2000 (Harper et al 2007). Current forest cover lost is estimated to be about 0.45 % per year (FAO 2010).

Though the ultimate causes of deforestation throughout the country are debated (Jarosz 1993, Peters 1999, Gezon and Freed 1999, Kull 2000, Nambena 2003, Holloway 2004, Styger et al. 2009), slash-and-burn farming, called *tavy,* is the prominent agricultural technology and leading cause of deforestation in the humid southeastern rainforests (Styger et al. 2007). In the *tavy* system, primary and secondary vegetation is cleared to make way for cultivation of staples such as rice, manioc, or sweet potato. After a series of short fallow periods and yearly cyclones, the deforested land quickly degrades (Nambena 2003, Styger et al 2009). The resulting loss of production requires farmers to cut and cultivate more forest, perpetuating the cycle (Randrianarijaona 1983, Kull 2000, Styger et al. 2007).

AGROFORESTRY. Fruit tree agroforestry systems address immediate causes of deforestation in Madagascar by supplying sustainable income and nutrition to farmers without requiring land conversion (Green and Sussman 1990). In southeastern Madagascar near Ranomafana National Park (NP), these systems are usually mixed stands of native forest trees and exotic woody and non-woody fruit plants. The native trees are opportunistically involved to shade crops like coffee and vanilla, while most of the fruit trees are planted exotics (e.g., citrus, avocado, mango). These orchards' roots stabilize soils and increase infiltration; their canopies shield the soil from sun, wind, and rain; their litterfall replenishes the soil organic material (Young 1989).

Produce from these agroforestry orchards can comprise a substantial portion of farmer income, even enough for farmers to forego rice production, when farmers are able to transport the fruits to wider markets (Freudenberger and Freudenberger 2002, Nambena 2003). Around Ranomafana NP, these markets are most commonly accessible via intermediaries in trucks on the Route Nationale (RN) 45 or the small system of improved roads in the area. These intermediaries sell to vendors or juice manufacturers in the major cities. Thus, walking distances to improved roads and the transportability of different fruits likely impact species and cultivar compositions in agroforestry systems across the landscape.

Most exotic fruits grown in agroforestry systems around Ranomafana NP require specialized propagation techniques (e.g., grafting or air-layering) to efficiently produce marketable quantity and quality. Technical propagation training is rare around Ranomafana NP, and fruit quantity and diversity are limited as a result. Friends of Madagascar (FOM) is a non-profit organization promoting agroforestry projects around Ranomafana NP by providing technical fruit propagation training and boosting fruit supply and diversity in the area via nurseries. In 2010–2011, FOM established its own production nursery as well as one in collaboration with another local NGO, Centre ValBio (CVB). These nurseries grafted, layered, and otherwise prepared seedlings which were given to partnering farmer associations in order to stimulate their agroforestry systems and to provide desirable budstock from which the farmers could propagate their own additional trees. Initially, the nurseries propagated stocks opportunistically, based on what species and cultivars, and what propagation stock of each, were locally available. After one year of nursery operations, FOM sought to increase the diversity of fruit species and cultivars in the nurseries and to determine appropriate stocking ratios according to the preferences of farmers across its sphere of influence. We assessed current nursery production, conducted interviews to identify farmer preferences, and evaluated the role that farmer proximity to transport networks plays in cultivation and preference patterns.

METHODS

STUDY AREA. Ranomafana NP is a montane rainforest preserve in southeastern Madagascar. It covers 41,600 hectares on the highland's eastern escarpment. The park was established in 1991 after an undocumented lemur species, the golden bamboo lemur (*Hapalemur aureus*), was discovered in the area. As part of the Madagascar National Parks (MNP) system, Ranomafana NP restricts resource extraction (ANGAP 2003). These restrictions strain local populations who traditionally collected fuel and timber and practiced *tavy* in the forest. Resource use has since been intensified in the areas around the park. Beyond park boundaries, the landscape is almost entirely deforested, either planted with annual crops or fallowing. The two communes surveyed (Ranomafana and Kelilalina) sit directly east of the park boundary and are home to approximately 26,000 people (Ministère de l'Intérieur 2011). Route Nationale 45, the only paved road and the major commercial artery in the region, bisects the study area.

LOCAL AGROFORESTRY NURSERIES. Two agroforestry nurseries have been evaluated on the eastern side of Ranomafana NP. The first was established in 2010 and is located in the village of Mahatsinjorano in the Kelilalina Commune (S21° 16'43'', E47°31'13''). The second nursery was established in 2011 eight kilometers west in the town of Ranomafana, Ranomafana Commune (S21°15'38'', E47°27'12''). Together these nurseries are capable of housing approximately 4,000 seedlings.

Both nurseries sit next to RN 45, but because the area beyond RN 45 lacks a reliable system of improved roads, seedlings must be transported from the pavement to farmers via footpaths. The growbags in which the seedlings are planted weigh 1–10 kg and must be handled gently during transport. Moreover, distribution anywhere south of RN 45 requires crossing the Namorana River, and no permanent bridges span it in either commune. Due to these factors, any village more than 2.5 km from RN 45 can be considered 'far' by the nurseries; in addition, these distance classes can be used to describe farmers' ease of transporting produce back to RN 45 (Figure 1).

SURVEY METHODS AND QUESTIONNAIRE DESIGN. A social survey was conducted to investigate the current state of fruit cultivation as well as farmer preferences for future cultivation around Ranomafana NP. Local interviewers visited 21 villages within 7.5 km of improved roads on the eastern side of Ranomafana NP; given the difficulty of transporting seedlings beyond improved roads, this study area represents the likely sphere of influence of the two agroforestry nurseries. On average, between nine and ten participants were interviewed in each village, either in their homes or fields; 200 interviews were conducted in total. Participants were chosen by the village elder and split between males and females of three age classes: youth, adult, and elderly. The local interviewers helped in the design of a statement of informed consent to expressly and appropriately communicate to farmers that their participation in the study would not result in them receiving seedlings or

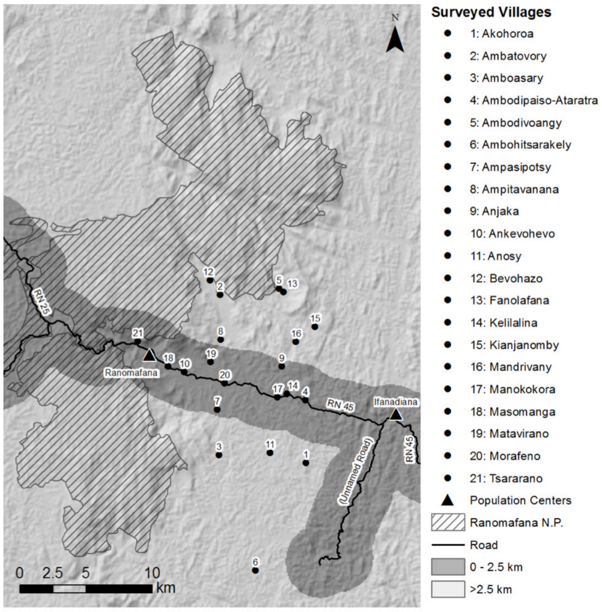

FIGURE 1. Study area and Ranomafana National Park, highlighting the surveyed villages and their Euclidean distances to roads; Projection: Geographic Coordinate System WGS 1984 (Ranomafana NP shapefile provided by Brian Gerber).

other benefits. Participants were read the statement of informed consent to which they responded with verbal agreement. The survey was conducted from February to April 2011.

Surveys were conducted in Malagasy through guided interviews following a questionnaire. The questionnaire had twenty multi-part questions; most questions had both open- and closed-ended elements as well as quantitative and qualitative elements. Interviewers transcribed answers to close-ended questions and recorded notes on answers to open-ended questions. Participants were asked, among other things, to list the fruits they cultivated, the number of stems they grew of each of those, and to quantify what is done with the harvested produce. They were also asked to rank their top five preferences for cultivating fruit trees and to explain those rankings. These preference rankings ranged from 5 to 1, descending from 5 as the "most preferred." For these questions, participants were free to list any plant they considered "fruit"; they were not provided with a multiple-choice set of fruit species and cultivars from which to choose. The number of stems grown was reported for the entire house, but preferences represented the participant's personal opinions. Interviewers then read several statements about satisfaction with local fruit cultivation, and participants indicated their level of agreement with those statements on a Likert scale (Likert 1932). The Likert scale ranged from 1 to 5, with one representing "strongly agree" and five representing "strongly disagree".

SURVEY ANALYSIS. With the interviewers, the questionnaire responses were translated into English and compiled in Excel (Microsoft Office 2010). Average scores for the Likert scale questions were calculated. For current cultivation and planting preference numbers, only the top fifteen fruits grown and the top fifteen preferred to plant were considered; combined, this produced a list of seventeen fruits. The average number of stems grown per household was calculated based on the Borda Count election method (Black 1976) to determine the rank order of all fruits people preferred to plant. In this method, for a given fruit, the number of responses per rank was multiplied by the numerical value of the rank, and all were added up for a total 'Borda value'. Fruits not ranked were assigned an ordinal value of zero, and total Borda values for all fruits were corrected by dividing by the total number of respondents to estimate 'average ranks'. JMP 9.0 Pro (SAS 2012) was used to run Spearman's rank-correlation tests on stems planted versus planting preferences.

Differences in numbers of stems planted and fruit tree preferences between villages near and far from roads were examined. GoogleEarth (Google 2012) was used to digitize the improved roads in the study area, as well as the surveyed villages; these shapefiles were then exported to ArcMap 10. An Euclidean distance raster was created to delineate 'near' versus 'far' at 2.5 km from the road, for the transportation reasons mentioned previously. Ninety-eight participants resided near a road, and 102 were far, with the farthest being 7.5 km from a road. Spearman's rank-correlation tests were used to compare both the number of stems planted and planting preferences reported near and far from roads.

For the top five fruits most frequently grown per household, differences in distances from roads were tested with a one-way ANOVA. Differences between average planting preference ranks for farmers near and far from roads were then identified using the Mann-Whitney U test.

Finally, qualitative responses were grouped into categories such as 'economic', 'consumption', or 'medicinal' motivations for ranking a fruit; many responses fit into more than one category. Frequency tables were built within Excel for these response categories, both in total and delineated by distance from roads.

RESULTS

LIKERT SCALES. Averaged Likert scale scores strongly indicate that respondents i) are dissatisfied with the diversity of fruit they currently cultivate, ii) want to plant more fruit trees on their lands, and iii) want to plant new fruit species and cultivars.

CURRENT CULTIVATION VS. PLANTING PREFERENCES. Spearman's rank-correlation test indicates that correlation between the average number of stems grown per household and the average ranked preference for each fruit is 0.102. Spearman's rank-correlation test describes the degree of correlation between two variables, and it returns a statistic (ρ) between -1 (a perfectly negatively correlated relationship) and +1 (a perfectly positively correlated relationship). The correlation between farmers' current cultivation patterns and their planting preferences is nearly perfectly non-existent (Figure 2, Table 1). Some fruits like banana and pineapple are planted at relatively high numbers yet are not highly preferred for additional planting. Coffee, though, is planted at relatively high numbers but it is also highly preferred for planting. Other fruits such as lychee and mandarin are not cultivated much but are highly desired for planting. Many fruits, like mango, are neither planted much nor highly preferred in the study area.

DISTANCE TO ROADS. The average numbers of stems grown per household are strongly positively correlated (ρ = 0.966, p = <0.0001) between communities near and far from roads (Figure 3). The correlation places each fruit very close to a 1-1 line, indicating that the relationship is not only monotonic but also nearly equivalent. However, most points lie

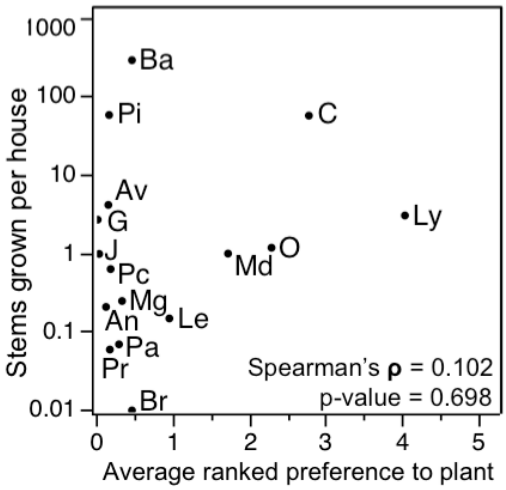

FIGURE 2. Spearman's rank-correlation test between the average number of stems of each fruit grown per household and the average ranked preference to plant each of those fruits, showing no significant correlation. Banana (Ba), Pineapple (Pi), Coffee (C), Avocado (Av), Lychee (Ly), Guava (G), Orange (O), Mandarin (Md), Jackfruit (J), Peach (Pc), Mango (Mg), Annona (An), Lemon (Le), Papaya (Pa), Persimmon (Pr), Breadfruit (Br), Apple (Ap).

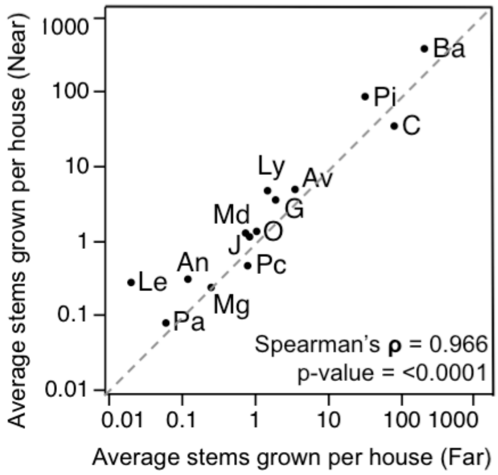

FIGURE 3. Spearman's rank-correlation test between cultivation patterns near and far from roads, showing significant positive correlation between the average number of stems of each fruit grown near and far from roads. Abbreviations as in Figure 2.

above the 1-1 line, suggesting that these fruits are cultivated in higher quantities on farms near roads. Banana is grown significantly more in villages near the road (p = 0.015), and the same is true for lychee (p = 0.0003). In addition to those two, pineapple, coffee, and avocado comprise the top five most cultivated fruits in both distance classes, but there are no significant differences in cultivation numbers for these latter three fruits.

The average preferences to plant each fruit are also strongly positively correlated between farmers near and far from roads (Figure 4). The high ρ(0.914) indicates that farmers near and far from roads have similar planting preferences; indeed, the top five fruits preferred to plant are the same for each distance class. Again, this relationship sits very close to the 1-1 line. The notable exception is for coffee, which farmers far from roads preferred to plant at similar levels to lychee. The Mann-Whitney U test for independence indicates that farmers far from roads report significantly higher preferences for planting coffee than do farmers near roads (p = 0.003).

QUALITATIVE ANALYSIS. Analysis of the qualitative data associated with planting preferences may illuminate the correlations in current cultivation and planting preferences near and far from roads (Table 2). For all of the top five fruits, farmers far from roads mentioned 'consumption' motivations for preferring to grow a fruit more than farmers near roads, and farmers near roads mentioned 'economic' motivations for preferring to grow a fruit more than farmers far from roads. Both distance classes mentioned 'future security' motivations at identical rates for preferring bananas. They also had similar

TABLE 1. Comparison of the average number of stems grown per household (SH), the average ranked preference (RP), and the relative rank order (RRO) for each fruit for all respondents, subdivided for respondents 'near' and 'far' from roads.

	number of stem per household			ranked preference					
				average			relative		
Fruit	total	near	far	total	near	far	total	near	far
Banana	295.4	386.4	208.0	0.5	0.6	0.3	6.5	6.0	10.0
Pineapple	59.4	87.9	32.1	0.2	0.1	0.2	13.0	15.0	11.0
Coffee	58.3	35.3	80.5	2.8	2.0	3.6	2.0	3.0	2.0
Avocado	4.2	5.0	3.5	0.1	0.1	0.1	14.0	13.0	12.0
Lychee	3.1	4.8	1.5	4.0	4.1	4.0	1.0	1.0	1.0
Guava	2.7	3.6	1.9	0.0	0.0	0.0	17.0	17.0	17.0
Orange	1.2	1.4	1.1	2.3	2.5	2.1	3.0	2.0	3.0
Mandarin	1.0	1.3	0.7	1.7	1.9	1.5	4.0	4.0	4.0
Jackfruit	1.0	1.2	0.8	0.0	0.0	0.0	16.0	16.0	16.0
Peach	0.6	0.5	0.8	0.2	0.2	0.1	11.0	10.0	14.0
Mango	0.3	0.2	0.3	0.3	0.2	0.4	8.0	11.0	7.0
Annona	0.2	0.3	0.1	0.1	0.1	0.1	15.0	14.0	15.0
Lemon	0.2	0.3	0.0	0.9	1.3	0.6	5.0	5.0	5.0
Papaya	0.1	0.1	0.1	0.3	0.2	0.3	10.0	9.0	9.0
Persimmon	0.1	0.1	0.0	0.2	0.2	0.1	12.0	12.0	13.0
Breadfruit	0.0	0.0	0.0	0.5	0.4	0.5	6.5	7.0	6.0
Apple	0.0	0.0	0.0	0.3	0.3	0.4	9.0	8.0	8.0

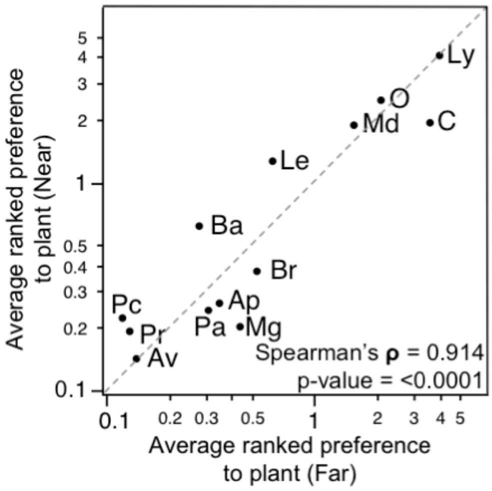

FIGURE 4. Spearman's rank-correlation test between planting preferences near and far from roads, showing significant positive correlation between the average ranked preferences to plant each fruit near and far from roads. Abbreviations as in Figure 2.

rates of citing 'medicinal' motivations for preferring to grow lemons. When asked which fruits they would prefer to sell, only farmers far from roads mentioned 'transportation' motivations, and the fruit most frequently preferred for 'transportation' motivations was coffee.

DISCUSSION

Freudenberger and Freudenberger (2002) have documented that farmers in the study area are willing to forego rice cultivation – and the implicit *tavy* associated with upland rice cultivation – and instead purchase rice with revenues from fruit as long as they have access to wider markets. However, lacking access to such markets, these farmers may redouble their efforts at subsistence crop production, risking further environmental degradation. Respondents in our study demonstrated that access to wider markets broadened their economic opportunities: farmers near roads were more likely to mention 'economic' motivations for ranking their fruit planting preferences, and farmers far from roads were more likely to mention 'consumption' motivations.

It is not only farmers' physical access to markets but also their supply of valuable, transportable fruits that allows them to forgo upland rice cultivation. Styger et al. (1999) reported that farmers in villages near Ranomafana NP but far from roads might be able to profit from indigenous fruits if they had easier access to markets, if the fruits kept better, and if they could get better prices for the fruits. As a result, indigenous fruits are not currently commercialized, or else done so at a minute scale for low prices. Indeed, respondents in our study, when considering which fruits they would prefer to cultivate and sell, did not mention indigenous fruits; the top ten most preferred fruits on our list of production priorities are exotic species. Both studies, then, suggest that indigenous fruits are currently unlikely to provide enough income for farmers to forgo rice cultivation. Therefore, focusing on indigenous fruits could waste time and resources in agroforestry projects intending to supplant *tavy*. Moreover, if farmers in the region are able to consistently produce desirable, exotic fruit crops, local governments might be incentivized to create and maintain more effective systems of roads into the deforested countryside. Such a transport network could support a permanent focus on fruit production, and even facilitate indigenous fruit commercialization as well.

Development organizations focusing on agroforestry projects around Ranomafana NP must find ways to ensure that fruit production is as attractive as possible, especially in the face of difficult transportation. Aside from building roads, then, this involves aligning seedling production in the agroforestry nurseries with farmer planting preferences. Those preferences theoretically reflect the farmers' appreciation of the economic and nutritional values of fruits. Therefore, producing and planting fruit trees according to farmer preferences will help ensure that the trees have the greatest chance of receiving care from the farmers and thus surviving to sustain farmers' livelihoods.

At the time of this survey, nursery stocks were not aligned well with farmer planting preferences. Respondents across the study strongly indicated that they are dissatisfied with both the quantities and diversity of fruit they currently cultivate, and that they are interested in planting more fruit. In addition, in the qualitative responses associated with the Likert questions about satisfaction, respondents commonly assured interviewers that they had open, unused land on which to plant fruit trees. These responses highlight local demand for nursery products and support the expansion of species and cultivars currently stocked in the nurseries. However, since there is no correlation between the fruits farmers currently cultivate and those they would prefer to cultivate, the roles of agroforestry nurseries are more complicated than merely filling gaps between cultivation and preferences.

Cultivation patterns and planting preferences are similar throughout the study area, which means that a single, appropriately stocked nursery can supply any project in the area regardless of distance to roads. But, the dissimilarities related to geography are just as important to consider for properly equipping farmers to choose fruit production over upland rice cultivation.

Farmers near roads are less interested in the difficulty of transporting their fruits, possibly because they have easy access to the intermediary collection trucks on the roads. Significantly more bananas ($p = 0.015$) and lychees ($p = 0.0003$) are grown near roads than far from roads. Both bananas and lychees are sold at high weight to price ratios, which means that they may not be as profitable for countryside farmers to transport over the hills to the road.

Conversely, coffee is preferred to plant significantly more by farmers far from roads than by those near roads, a difference we attribute to coffee's transport efficiency. In response to the survey question "List the top five fruits you would prefer to sell, in order of preference…", only farmers far from roads mentioned "transportation" as a consideration when selling fruit, primarily coffee. Coffee beans are small fruits with disproportionally high market prices. In comparison, a stalk of bananas, which weighs about 20 kg, would fetch the same price as 2.5 kg of coffee at the time of this study. Over difficult mountain footpaths, transporting coffee makes more economic sense than heavy, relatively cheap fruits like bananas. Fruits like coffee allow farmers far from roads to most efficiently engage wider markets.

There are other considerations beyond transport efficiency that influence local fruit cultivation. Lemons and bananas, for example, filled specific niches throughout the study area. Lemons were preferred for their natural medicinal qualities.

TABLE 2. Response rates (%) for different categorical motivations for preferring to plant the top five favorite fruits. Categorical motivations: consumption (Co), economic (Ec), current low quantity (CLQ), flavor (Fl), transportation (Tr), productivity (Pr), land improvement (LI), medicine (Me), future security (FS), other (Ot); distance classes (DC): n=near, f=far, t=total.

		Fruits				
Categorical Motivation (%)	Distance	Lychee	Coffee	Orange	Mandarin	Lemon
Consumption	near	33.3	56.5	33.3	38.3	29.3
	far	48.5	66.7	56.2	52.5	30.8
	total	41.2	63.1	44.6	45.4	29.9
Economic	near	94.6	78.3	85.3	93.3	97.6
	far	90.9	72.6	78.1	86.4	73.1
	total	92.7	74.6	81.8	89.9	88.1
Current low quantity	near	9.7	10.9	16.0	18.3	4.9
	far	10.1	6.0	11.0	8.5	0.0
	total	9.9	7.7	13.5	13.5	3.0
Flavor	near	10.8	--	9.3	6.7	2.4
	far	16.2	--	8.2	3.4	0.0
	total	13.5	--	8.8	5.0	1.5
Transportation	near	1.1	0.0	0.0	0.0	--
	far	2.0	10.7	2.7	1.7	--
	total	1.6	6.9	1.4	0.8	--
Productivity	near	5.4	6.5	5.3	10.0	4.9
	far	2.0	0.0	1.4	6.8	3.9
	total	3.7	2.3	3.4	8.4	4.5
Land improvement	near	1.1	4.4	--	--	--
	far	0.0	2.4	--	--	--
	total	0.5	3.1	--	--	--
Medicine	near	--	--	1.3	0.0	29.3
	far	--	--	0.0	3.4	26.9
	total	--	--	0.7	1.7	28.4
Future security	near	--	--	--	--	--
	far	--	--	--	--	--
	total	--	--	--	--	--
Other	near	1.1	8.7	--	--	--
	far	4.0	4.8	--	--	--
	total	2.6	6.2	--	--	--
Sample Size N	near	93	46	75	60	41
	far	99	84	73	59	26
	total	192	130	148	119	67

Bananas have no definite growing season and can be harvested and sold year-round, unlike most other fruits. Thus, bananas were commonly mentioned across the study area as sources of money in emergency situations, adding to a family's financial stability. Moreover, the top five fruits most preferred to plant were preferred primarily for 'economic' motivations but 'consumption' motivations were also strongly present, indicating that these fruits can play a role in supplanting farmers' reliance on the cultivation of subsistence crops.

We have presented a unified list of suggested priorities for agroforestry nurseries around Ranomafana NP (without banana, which does not need to be propagated in nurseries). While the same fruit species and cultivars can be planted in any agroforestry project in the study area, our recommendations do not necessarily translate to fixed production ratios. It will remain for nurseries to decide how many seedlings of each fruit to propagate, based on the expected yields and values of the different fruits, as well as the given project's distance to a road. For example, coffee ought to be prioritized in agroforestry projects far from roads, based on its high preference by remote farmers as well as its conservation and economic value: coffee production requires an overstory for shade, which encourages the protection of native stands; coffee stumps re-sprout after being cut, which discourages yearly burning; and in the study area, coffee's high transport efficiency makes it an economically valuable fruit for remote farmers to produce. As the nurseries decide production ratios of the prioritized fruits, however, diversification must be stressed; what is currently preferred and economically beneficial may change by the time a project's seedlings are producing crops.

Because farmers' preferences are subject to change, it is vital that agroforestry project managers continue to track those preferences. At the time of this publication, Styger et al.'s (1999) study is the only other social survey focused primarily on farmers' fruit preferences in Madagascar. They interviewed twenty-four participants in two villages far from roads in the

Ranomafana Commune and nearer Ranomafana NP's primary forest. The researchers were focused on villager preferences for indigenous fruits and the potential for those fruits to be consumed or commercialized as part of agroforestry systems in the area. Our study built on Styger et al.'s (1999) work in Ranomafana by replicating their demographic cross-section; collecting a larger sample size (200 respondents); allowing farmers to state preferences for any fruit, indigenous or exotic; and interviewing farmers both near and far from roads in order to make prescriptions for the development organizations based near roads but working across the landscape. The scale of our study provides a current and reliable cross-section of fruit growers around Ranomafana NP from which agroforestry project managers can begin to base their production and outreach strategies. The major weakness of this investigation, which ought to be addressed in follow-up studies, is that our survey was conducted in one three-month window. This may have allowed a temporal bias into the preferences we recorded, specifically related to the economic trends in fruit prices at the time of the survey, instead of capturing the possible fluctuations in fruit popularity over the course of a year. We attempted to buffer the effects of such a bias with a large sample size. However, since the top two most preferred fruits were out of season at the time of the survey, it appears that such a bias did not considerably affect our findings.

Future work will involve increasing the diversity of cultivars of each fruit grown in the nurseries and continuing to train farmers to propagate their own seedlings. The cultivars currently grown in the study area (including the nurseries) are not necessarily those best suited to the environment or human needs. Since different cultivars often do not bear fruit at the same times, increasing cultivar diversity allows farmers to experience longer growing and harvesting seasons, thereby avoiding low prices in saturated markets.

Moreover, while satisfying farmer preferences increases buy-in for agroforestry systems, it is important to note that those preferences are based on their imperfect knowledge of available fruit species and cultivars, and there is room to influence future preferences. For example, neither avocado nor mango is highly desired in the study area, but this might be a reflection on the local cultivars of each, not the species themselves. Mangos around Ranomafana NP are usually susceptible to anthracnose, causing them to mature slowly and produce poorly, but a hardier and more palatable cultivar may interest local farmers. The avocados in the study area are small, bland, and rot quickly on trees, but cultivars exist elsewhere in the world that could produce more desirable fruits.

Development organizations, Malagasy university researchers, and local and national governments all share the responsibility of building farmers' awareness of alternative fruit species and cultivars as well as of new economic and consumption opportunities for fruits. University research to identify viable cultivars could expedite the otherwise trial-and-error approach currently in place, and even open the doors to legally sourcing desirable budstock or seedlings from outside the country if necessary. Researchers could also continue to monitor fruit production preferences, begin describing the actual economics of fruit production supplanting upland rice cultivation, and disseminate that information to those providing agroforestry resources to farmers. Ideally, the burden of training farmers and providing starter budstock and seedlings would fall primarily to government agencies; however, it seems even more crucial that these agencies focus on the establishment and maintenance of reliable transport networks so that farmers can sell what they are able to produce. Without such access to markets, fruit tree agroforestry efforts in the area may well be in vain (Freudenberger and Freudenberger 2002). Around Ranomafana NP, development organizations are currently the main advocates of agroforestry projects. As such, these organizations must continue to focus on aligning their strategies with farmer preferences in order to best support fruit production over upland rice cultivation.

CONCLUSIONS

Conservation managers may hesitate at the suggestion of promoting agroforestry systems focused on exotic fruits rather than on endemic species. Given the rate and extent of deforestation in southeastern Madagascar, though, supporting fruit tree agroforestry systems – even exotic ones – is an important beginning step in protecting and reestablishing a healthy, sustainable environment. This is especially true considering the alternative can be hillside cultivation of staples like rice using *tavy*. Encouraging farmers to adopt sustainable practices, then, involves managers' consideration of farmer needs and preferences in order to maintain buy-in and ensure the long-term success of those practices. In this case, managers are able to tailor their support of agroforestry systems based on a system's location by understanding that farmers have different planting patterns and preferences related to their distances from market networks on the road.

It is recommend that agroforestry nurseries in the study area propagate stocks based on the list provided above which is applicable to the entire study area, but prioritize efficiently transported fruits like coffee in projects far from roads. The nurseries must now decide how to address farmer preferences by producing appropriate numbers of seedlings and acquiring advantageous cultivars of each fruit.

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

TABLE S1. Demographic breakdown of survey participants, which included a secondary school (CEG) class as one unit.

TABLE S2. Likert scale questions and results, showing the average response score for each statement.

TABLE S3. Frequency of mentioning "transportation" motivations for preferring to sell the top six fruits preferred to plant. All mentions of transportation come from farmers far from roads.

TABLE S4. Current fruit production in the two agroforestry nurseries established by FOM, in ranked order by number of seedlings produced.

TABLE S5. Final ranked recommendations for agroforestry production priorities.

TABLE S6. Survey questionnaire, in English and Malagasy, used to conduct guided interviews.

ARTICLE

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The Eco-Geo-Clim model: explaining Madagascar's endemism

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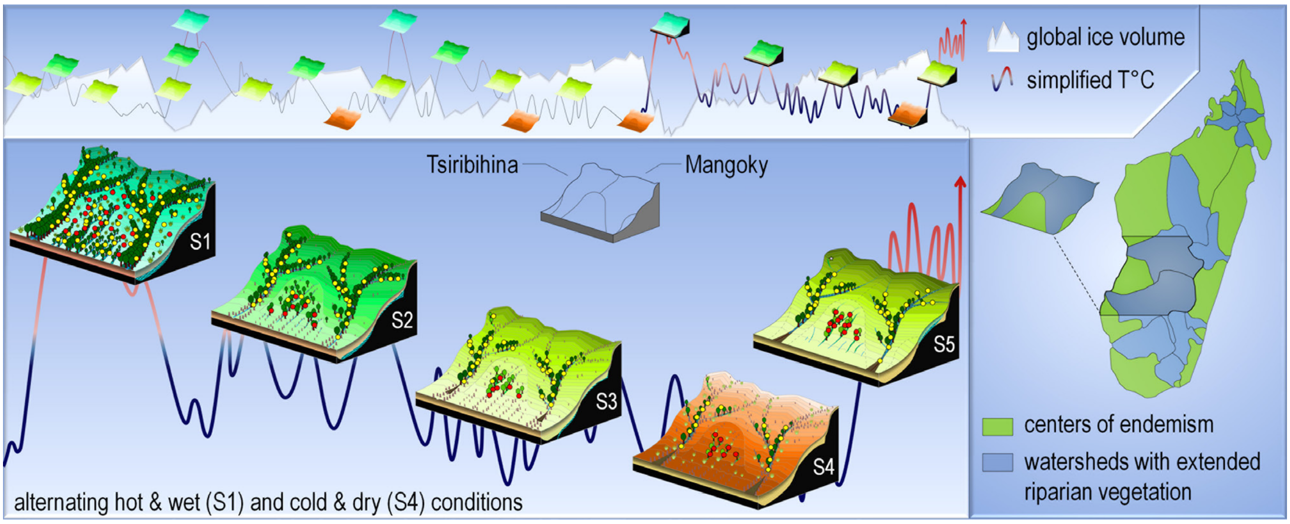
ABSTRACT



Paleoclimatic oscillations (top left) driving tropical island endemism by producing alternating wet (S1) and dry (S4) conditions (bottom left), with Madagascar's centers of endemism (right panel, green) located between watersheds with headwaters at high altitude and extended riparian forest (right, blue).

RÉSUMÉ

Les oscillations paléoclimatiques au cours du Pléistocène ont influencé tous les termes du bilan d'énergie stationnel (rayonnements, flux de chaleur latente, flux de chaleur dans le sol et flux de chaleur sensible). Associées aux précipitations, ces fluctuations ont contrôlé les bilans hydriques stationnels. Les bilans hydrologiques des bassins versants sont l'intégration spatiale et temporelle de ces bilans hydriques. La végétation et plus généralement la biomasse végétale sont dépendantes de ces deux types de bilans. L'interface entre l'atmosphère et la végétation est occupée par les sols et les formations superficielles, celles-ci sont le résultat de la dégradation des roches et de l'érosion des versants. Lorsqu'ils existent, ces sols ou géosols sont hérités de périodes humides antérieures.

La disponibilité en eau est l'élément majeur de la vie végétale et animale, or celle-ci a fluctué au cours du Pléistocène ; lors de périodes sèches, les bilans sont déficitaires, la biomasse diminue, l'érosion hydrique domine l'altération, le paysage entier évolue d'amont en aval. Lors des bilans hydriques humides le retour vers un état voisin de l'actuel n'a pas été immédiat car chaque composante du milieu naturel possède une résilience temporelle propre. La proximité d'un bilan hydrique stationnel positif est indispensable à la survie de la faune et de la flore sylvicoles. Dans le cas de l'endémisme à Madagascar, cette difficulté a été résolue de deux manières opposées et a produit deux types d'endémisme. D'une part par l'existence de cours d'eau prenant leurs sources à haute altitude, d'autre part par certains reliefs résiduels dans lesquels l'eau libre existe exceptionnellement. 1) Au cours du Pléistocène, les hauts reliefs ont eu une alimentation permanente en précipitations, les sources et les cours d'eaux ont été alimentés, les ripisylves sont restées humides. À l'opposé, lors des périodes sèches, l'aval des bassins versants a été sec, les écoulements discontinus, les forêts ont reculé, les animaux associés ont disparu. Ce n'est pas

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le cas de sous bassins versants dans lesquels un écoulement a été pérenne et où la forêt et sa faune associée ont pu subsister. 2) Dans certaines parties basses, profitant de spécificité géologiques et géomorphologiques, des milieux exceptionnels ont facilité la conservation, la transformation et l'évolution de certaines espèces endémiques. Ce processus est dénommé modèle Eco-Geo-Clim.

INTRODUCTION

The main features used to explain the current distribution of many endemic taxa in the flora and fauna of Madagascar include its topographic asymmetry, with a narrow eastern slope (27 % of the total area) and a broad western slope (73 %), and its climate, with the eastern windward slope uplifting the humid trade winds from the south-east and the leeward western slope in the rain shadow of the highlands receiving rain only during the austral summer (Cornet 1974, Donque 1975, Lourenço 1996, Dewar and Richard 2007). These features have often been used in various phytogeographical classifications of the island (Baron 1890, Perrier de la Bâthie 1921, Humbert and Cours Darne 1965, Moat and Smith 2007), in which most of the area was classified as forest of various kinds, where the majority of endemic taxa occur (Goodman and Benstead 2005). These endemic taxa are not distributed randomly on the island, but the climatic zones recognized today are not sufficient, by themselves, to explain, for example, the current distribution pattern of Malagasy lemur taxa. The phyto- and zoogeographical classification systems proposed during the 20^{th} century are consistent with the contemporary distribution of taxa or forest types, without considering the conditions under which these ecosystems evolved; they do not, however, take into account changes in these ecosystems during recent geological time.

The Earth's surface is a complex interface between (i) the atmosphere, i.e., the climate with its radiative and advective components, (ii) the biosphere, and more specifically its floral and faunal elements, and (iii) the topography, with its soils, surface formations, and rocks, including their historical dimension, which determines their physical characteristics, i.e., the functional characteristics described by the hydrodynamic and thermal equations. These biological and physical elements interact and adapt in a nonlinear manner through time and space. Earth's climate varies with its orbital parameters (Hays et al. 1976), and the resulting Milankovitch periodicities have characterized the last three million years of comparatively rapid climate shifts (Rahmstorf 2009), i.e., mainly during the Pleistocene (2.6 Ma), as recently circumscribed (Leigh Mascarelli 2009). During colder phases, more of the Earth's water is stored as ice (especially at higher latitudes) and sea level is lower. For example, sea level was as much as 120m lower than today during the Last Glacial Maximum (LGM) ca. 20,000 years ago (Church and Gregory 2001, Milne et al. 2009). In cooler times of low sea level and extended drought, less water is in circulation and river courses are longer, while the total quantity of circulating water is reduced on the continents, and there is a greater number of rivers and streams with discontinuous flow. Climate change has influenced the geomorphology of entire landforms as well as biological evolution and extinction (Jansson and Dynesius 2002, Rabosky et al. 2012, Blois et al. 2013). During colder phases, when icecaps extended to lower latitudes, at times reaching ca. N and S 40°, the climate at tropical latitudes is drier and colder, and forests recede. When the climate is again warmer, lower latitudes experience hotter and more humid conditions, and forests expand (e.g., Assi-Kaudjhis et al. 2010).

One recent hypothesis to explain the current distribution of endemic taxa in Madagascar, the centers of endemism hypothesis, sensu Wilmé et al. (2006, 2012), considers (i) Quaternary climate oscillations, (ii) the extent of forest, and (iii) rivers and their ability to maintain riparian vegetation and their associated fauna during the driest climatic events, and in particular those with headwaters at high altitude. According to this hypothesis, these riparian forests functioned as dispersal corridors during periods when the climate became wet (Wilmé et al. 2006). The underlying mechanistic model proposed by Wilmé et al. (2006, 2012) specifically compares rivers with headwaters at high altitude, which drain most orographic rainfall, with those whose headwaters are situated at mid- or low altitude. In the present article, we summarize the biotic factors and the main abiotic factors of this model, which we refer to as the 'Eco-Geo-Clim' model. More specifically, the climatologic, geomorphologic, and hydrologic features involved are detailed, highlighting their influence on ecological processes. The way in which recent paleoclimatic oscillations have driven local endemism in forest taxa is also illustrated.

FRAMEWORK

The conceptual framework of the Eco-Geo-Clim model is biogeographically defined, i.e., it considers geographical phenomena occurring in a given area as causal factors leading to the spatial and temporal distribution of species. Specifically, it addresses two questions: How are the distributions of faunal and floral species influenced by the dynamics of abiotic factors? How have these factors been shaped by paleoclimatic oscillations through time? The model also considers vegetation and the fact that it relies intimately on water, whether by intercepting rainfall, which is sufficient for certain vegetation types, or by uptake of water directly from unsaturated soil layers or the saturated phreatic zone below the water table. Riparian vegetation found along streams and rivers uses groundwater to grow. At the scale of a catchment or watershed, the vegetation cover is usually denser in places where the water table is shallow, e.g., typically close to rivers and streams. When trees don't suffer from water stress, they have higher aboveground productivity and can support higher animal biomass. Not only is the vegetation denser in areas with more available water, but species diversity can also be higher (e.g., Dorman et al. 2013a, b and references therein). Riparian forests are known to have higher levels of diversity than the surrounding vegetation, especially in the drier regions of Madagascar, but also in areas of humid rainforest (Langrand and Wilmé 1997).

GEOGRAPHICAL CONTEXT. The model illustrated here considers two major watersheds (drainage basins) on Madagascar's western slope that have tributaries at high altitude: the Mangoky to the south, with its headwaters on Andringitra mountain, culminating at the island's second highest summit (2658m); and the Tsiribihina watershed, whose headwaters lie below Madagascar's third highest summit (2642m). Both the Mangoky and the Tsiribihina flow throughout the year. The area situated between the lower portions of these large watersheds, the Central Menabe, is composed itself of the smaller watersheds and interfluves of rivers with headwaters at mid- or low altitude. The basins of these intermittent rivers receive little orographic rainfall, have only seasonal flow, and dry out for several months during the year (dry season), especially in situations where the headwaters are at lower altitudes.

MODEL TIME SCALE. Recent climatic oscillations that occurred in Madagascar during the Pleistocene are considered, i.e., over a total period of several hundred thousand years. The most reliable information on temperature variation during this period is based on data obtained from the northern hemisphere and the Antarctic, and there is a considerable paucity of comparable data from Madagascar; pollen analyses from the island are sparse and only available for the last 40,000 years (e.g., Gasse and Van Campo 2001, Virah-Sawmy et al. 2009). Here the last global climatic oscillation is illustrated, i.e., over a period of a little more than 100 millennia, from the graphics presented in Elderfield et al. (2012), to include the LGM and the preceding warm maximum, during which maximum deglaciation took place.

GEO-ECOLOGIC FACTORS. The model presented by Wilmé et al. (2006, 2012) emphasized the importance of rivers and the altitude of their headwaters in explaining the current distributions of some narrow-ranged endemic species. Here further detail is introduced, using a number of geomorphological and hydrologic features, including additional aspects of rivers and the water in the unsaturated upper soil layers, the water-saturated phreatic zone, and their evolution during periods of climatic change. Groundwater recharge from rainfall involves two main mechanisms: (i) slow infiltration through the unsaturated soil horizons, old geo-soils and superficial formations, to the water table below, and (ii) rapid recharge through sinkholes, which are typically found in sedimentary formations such as karstic residual landforms (e.g., *tsingy* limestone formations in western Madagascar). The geomorphologic and hydrologic evolution on limestone areas is understood as karstic landforms where water is absent on the surface but is maintained in caves, avens and subterranean hydrologic systems (e.g., Veress et al. 2008, Kaufmann 2009).

Geologically, the Menabe is a monoclinal sedimentary formation dipping towards the Mozambique Channel. Most landforms found in the region date from wetter periods than the present, as shown by its surface lithology, with dissected sand cover, resulting mainly from the evolution of the hydrologic system in western Madagascar. The Menabe is situated within a dry region; perennial moisture exists only where groundwater is available. Examples of landforms that can capture and maintain soil moisture in an otherwise dry environment include various areas as the Makay sandstones in the lower portion of the Mangoky watershed and upper valleys of the Menabe, as well as other Menabe sandstones. The landforms of Makay quartz sandstones resemble karstic limestone formations found in some tropical areas; the lithology and both the tectonic and geomorphologic evolution have sculpted a relief with convex summits, steep lower slopes and faulted valleys. In the resulting deep gorges, evapotranspiration is reduced and underground water is maintained in their alluvial sand filled lower portions. This exemplifies the Eco-Geo-Clim model, which applies equally well in all of Madagascar's sedimentary basins.

BIOTIC FACTORS. The extent and persistence of riparian forests are linked to perennial water availability, and for some species, to the presence of adaptations to floods and/or the capacity to produce roots that can reach the water table (Naiman et al. 1993). Riparian forests are found in both dry and humid areas in Madagascar, but are most prominent in the driest environments, such as along the Mandrare and Onilahy rivers in southern Madagascar, where *Lemur catta* and *Propithecus verreauxi* occur in high densities. The mid- and lower portions of these large rivers are located in dry environments; in this region precipitation is low and unpredictable, while evapotranspiration is high (cf. Dewar and Richard 2007). Riparian forests are denser than the surrounding drier, more open formations because trees have access to water from a shallow phreatic zone, allowing higher levels of transpiration, and the production of greater biomass, including leaves, flowers and fruits. A forest cover can be maintained along the river course even when it is extremely narrow or in some places runs underground during certain season.

ASSUMPTIONS. Water availability is the only abiotic factor acting at the same spatial scale as the biotic factors invoked in the Eco-Geo-Clim model. As biotic factors respond to water availability, they act at the same spatial scale, although their spatial and temporal resilience is different (cf. Moritz and Agudo 2013). In Figure 1, the spatial and temporal availability of water is considered for forest ecosystems, along with the responses to these changes of two hypothetical forest taxa that differ in their tolerance to a drying environment; species Y (yellow) has low tolerance to dry conditions and is assumed to disappear with increasing drought; species R (red) can cope with aridification and can thus survive longer under increasingly dry environmental conditions. In a situation where the two species are in competition with one another, e.g., over food resources, species Y has a competitive advantage over species R. Figure 1 also refers to 'niche conservatism', defined as the retention by a species over time of ecological traits related to its niche (i.e., the set of biotic and abiotic conditions in which the species can persist (Wiens et al. 2010)). Such taxa could be illustrated by the Gray mouse lemur (*Microcebus murinus*), corresponding to the yellow species in Figure 1, and Madame Berthe's mouse lemur (*M. berthae*) as the red taxon, which is endemic to the Central Menabe. The underlying assumption in the model is that forest taxa that cannot persist under dry conditions would be confined to riparian forests during drier periods, while those that exhibit more plasticity with regard to aridification would be able to persist in drier forests.

ECO-GEO-CLIM: A MODEL THAT CONSIDERS ECOLOGICAL, GEOMORPHOLOGICAL AND CLIMATOLOGICAL FEATURES

Three scenarios of Quaternary paleoclimatic oscillation are presented to illustrate the mechanisms of the Eco-Geo-Clim model (Figure 1):

(I) A humid period during which precipitation is abundant (Figure 1, relief S1). The soils are humid, groundwater is abundant, rivers are flowing all the time, and forest cover is expanding.

(II) A humid to dry period during which precipitation decreases (Figure 1, reliefs S2, S3, S4). Rivers with headwaters at high altitude are able to capture moisture in the form of orographic precipitation. Soils on slopes and around springs are initially moist but as the climate dries and precipitation decreases, they become more dry and water flow in rivers decreases. Rivers and streams with headwaters at lower altitudes experience intermittent flow and can totally dry out, seasonally or even permanently. Some rivers with headwaters at higher altitudes will maintain flow in the middle portion of their courses, where the surface layers are humid and groundwater is still abundant, but forest will recede where water disappears.

(III) A dry to humid period during which precipitation increases (Figure 1, relief S5). The flow of rivers with headwaters at higher altitude increases, whereas those with lower altitude headwaters where groundwater is fed by precipitation will remain isolated from adjacent watersheds for extended periods of time.

CENTERS OF ENDEMISM

Using the mechanism summarized in Figure 1, the group of small watersheds and interfluves present between the lower portions of the Tsiribihina and Mangoky watersheds comprise a center of endemism (Wilmé et al. 2006) in which some species have become isolated and evolved in pockets of remaining vegetation found on residual landforms. Several geological formations found in the Central Menabe could have retained such pockets of vegetation, in particular limestone formations with subterranean water circulation, as found along the lower portion of the Kirindy River, or sandstone formations where deep canyons maintain a comparatively high amount of moisture in their lower portions (Waeber et al. In press).

The alternating wet and dry periods of the Pleistocene were variable in time and space, but regardless of their dura-

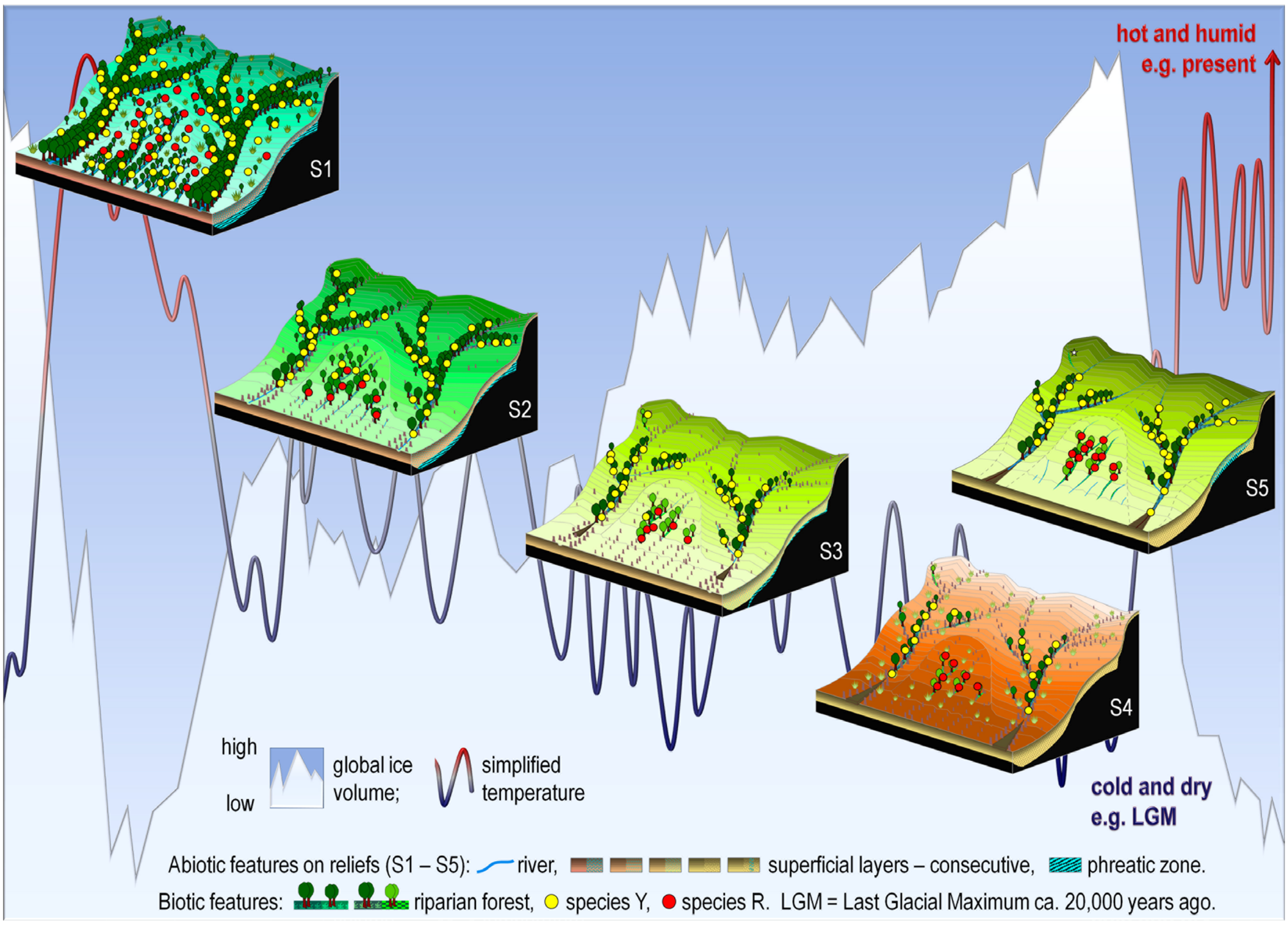

FIGURE 1. Evolution, during paleoclimatic oscillations, of abiotic factors, including surface layers, slope, phreatic zone, and rivers, and of biotic features, including riparian forest and two hypothetical forest species. (altitude not to scale).

S1: Situation during a humid phase: rainfall is abundant and river flow is high and continuous; the surface layers are moist and the phreatic zone is well fed; forest cover is expanding. Species Y (yellow) is abundant in riparian and other forest formations; species R (red) is more common in other (non-riparian) forests as a consequence of competition with Y in riparian forests. S2: Situation as the climate becomes drier: rainfall decreases, evaporation is higher, rivers with headwaters at lower altitudes dry up, and rivers with headwaters at higher altitudes are fed intermittently, at least along their mid-portions. The site-specific hydrologic balance decreases, surface layers dry up, and the water table drops. Slope instability increases as erosion becomes more widespread. Forests recede, disappearing from drier areas but persisting along rivers where the water table remains close to the surface. Species Y disappears from the driest areas but is able to survive in riparian forest where conditions remain suitable; species R survives in drier forests, but suffers from increased competition with species Y in riparian forest. S3: Situation as the climate dries further: river flow decreases and becomes sporadic; river courses become longer as sea level drops; slopes are more unstable with increased erosion and river sedimentation; an alluvial fan appears at the knick point. The site-specific hydrologic balance decreases further, surface layers become drier, and water table drops further. Forests recede even more. Species Y disappears from dry forests, reduced populations survive in riparian forest only along larger rivers with higher altitude headwaters; species R survives in the remaining pockets of dry forest. S4: Situation during the most arid phases: soil horizons are dry, the phreatic zone is discontinuous except below the mid-portion of rivers with high altitude watersheds and in isolated pockets within residual reliefs (e.g., karsts). Forests recede further, becoming limited to the riparian zone, which is drier along the small rivers. Species Y is restricted to riparian forest along rivers with high altitude headwaters, while species R is limited to watersheds with headwaters at low altitude, within the last remaining pockets with adequate moisture to maintain a forest cover. S5: Situation after a dry phase, when the climate becomes wet again: rainfall and river flow increase, surface layers become wet, the phreatic zone is once again fed. Some tributaries reconnect to the main rivers. Forests expand along these tributaries. Species Y disperses along the expanding riparian forest as tributaries aggregate to the re-establishing river system; species R is a narrow-ranged taxum endemic to the Central Menabe.

tion and extent, similar causes (i.e., a climatic oscillation) are likely to have had similar effects on the abiotic and biotic features considered in our model, allowing some forest taxa, as the climate became more humid, to expand and disperse along tributaries in systems with high altitude watersheds, while populations in isolated forest fragments may have diverged, leading to speciation, in watersheds whose headwaters are at low altitude. Although a single climatic oscillation may only bring about speciation in a limited number of groups, it could lead to the loss of one or more local populations, as in lemurs and birds, or even to extinction of species, as documented in the recent subfossil record (e.g., Burney et al. 2004), whereas other species may have experienced contraction of their range, as in *Hypogeomys antimena* (Crowley 2010).

CONCLUSION

During the Pleistocene, riparian forests in Madagascar acted during dry periods as refugia for forest-dwelling fauna and flora, and functioned as dispersion corridors during wetter periods, allowing species to extend their ranges along tributaries when orographic rainfall was sufficient for runoff to reach low-lying areas. The Eco-Geo-Clim model holds that the main factors involved in the maintenance of forests species include the availability and accessibility of water. During drier periods, forest species occurring in centers of endemism survived in refugia, typically found among residual reliefs where water storage capacity was higher. Given the hydrologic balance of the rivers flowing through these centers of endemism, riparian forests, and their capacity to act as dispersal corridors, were limited compared to those encountered in watershed with headwaters at high altitude.

The Eco-Geo-Clim model suggests that any geosystem able to store water and make it available to trees can be regarded as a potentially key element for the survival of forest taxa in Madagascar, and any place where this process operated during the driest phases of past climatic oscillations may have served as a refuge for forest taxa. The local topography, the superficial formations and the biota – each with its own velocity and resilience – are the end products of the impacts that Quaternary climate and its changes have had on the evolution of landscapes. The endemism generated in this manner can thus be regarded as resulting from the transformation of a landscape in time in conjunction with climatic change.

The model proposed here may be helpful to understand and explain how local endemism in Madagascar has been shaped and driven by paleoclimatic oscillation, although it provides little insight regarding the possible future of the island's endemic biodiversity in the face of current anthropogenic climatic change. The Eco-Geo-Clim model does, however, reveal one certainty: any site with a positive hydrologic balance, including those where riparian forests occur, must be taken into consideration for ensuring that Madagascar's unique biodiversity will be protected in the changing climate of the coming centuries.

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

FIGURES S1 to S6. Evolution, during paleoclimatic oscillations, of abiotic factors, including surface layers, slope, water table, and rivers, and of biotic features, including riparian forest and two hypothetical forest species.

TABLE S1. Glossary.

ARTICLE

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Les Sapotaceae de Madagascar, deux nouvelles espèces du genre *Mimusops* L.

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ABSTRACT

Members of the family Sapotaceae, occurring in Madagascar's various forest types, are mostly known as *nanto* in local dialects; some of their cultural and social values are described here. While the circumscription of *Mimusops* is well-defined, the delimitation of species within the genus remains unclear and their identification is often difficult. A study of herbarium specimens assigned to this genus deposited in key herbaria, two in Madagascar (TAN and TEF) and three outside the country (G, MO and P), revealed two new species: *Mimusops boeniensis* Randrianaivo sp. nov. and *Mimusops masoalensis* Randrianaivo sp. nov. This brings the number of *Mimusops* species recognized in Madagascar to 16. Both of these newly recognized species are illustrated, and detailed information is provided concerning their morphology and the differences between them and other members in the genus, as well as on their ecology and distribution.

RÉSUMÉ

Les Sapotaceae de Madagascar sont rencontrés dans tous les types de forêt de l'île et sont connus sous un même nom vernaculaire sur l'ensemble du territoire, *nanto*. Les *nanto* sont importants dans la Société malgache et leur valeur culturelle est décrite ici. La circonscription taxinomique de *Mimusops* est bien définie. En revanche, la délimitation entre les différentes espèces au sein du genre reste confuse et l'identification des récoltes est souvent difficile. L'étude des spécimens d'herbier connus dans les herbiers nationaux (TAN et TEF) et internationaux (G, MO et P) nous a néanmoins permis de reconnaitre et de décrire deux nouvelles espèces : *Mimusops boeniensis* Randrianaivo sp. nov. et *Mimusops masoalensis* Randrianaivo sp. nov., le nombre d'espèces malgaches de *Mimusops* passant ainsi de 14 à 16. Cet article s'attache ensuite à fournir une description morphologique détaillée et illustrée de ces deux espèces ainsi que des renseignements sur leur distribution et leur écologie. Les différences qu'elles présentent avec les espèces les plus proches sur le plan morphologique sont par la suite discutées.

INTRODUCTION

NANTO DANS LA CULTURE, L'HISTOIRE ET L'ÉCONOMIE.

À l'exception de *Chrysophyllum boivinianum* (Pierre) Baehni qui est appelé *Famelona*, toutes les espèces malgaches de Sapotaceae sont communément appelées *nanto* ou *nato*. Le *nanto* a un rôle économique, culturel et biologique important à Madagascar. Son bois est souvent cité parmi les essences utilisées dans la construction traditionnelle. Le bon bois de *nanto* est recherché pour l'ébénisterie, la charpente, la parqueterie, la confection des traverses de chemin de fer, de pirogues monoxyles, des pilotis, des longrines, des chapeaux de pont ainsi que de toutes parties de bâtiment (Gueneau 1971a, b). Caractérisé par une forte résistance aux activités dégradantes des microorganismes du sol, le bois de *nanto* est traditionnellement utilisé pour la construction de piliers de maisons. Par exemple, les piliers du Palais de la Reine de Manjakamiadana à Antananarivo ont été spécialement construits avec du bois de *nanto* en provenance de la forêt d'Ambinanindrano, à l'Est d'Ambositra.

Dans le domaine culturel ancestral malgache, les *nanto* jouent un rôle culturel particulier. Selon Boiteau (1985), ce mot vernaculaire viendrait du mot 'to' qui signifie vérité et qui ferait allusion à une propriété magique de l'arbre. Cette croyance s'illustre par exemple lors d'une cérémonie de sacrifice ou *joro* lors de laquelle le sang, qui occupe toujours une place importante, est parfois remplacé par l'écorce des *nanto* qui est généralement de couleur rouge sang. Certaines espèces de *nanto* font partie des plantes tinctoriales dont l'écorce a été utilisée pour la teinture dans certaines régions de Madagascar (Dubard 1914). D'où un dicton malgache « *Lambamena asoka hodi-nanto, izay mamerina indroa manana ny antitra* » qui signifie littéralement 'le linceul teinté deux fois de suite avec l'écorce de *nanto*, a une couleur rouge plus foncée'. En outre, les Sapotaceae jouent également un rôle biologique important dans les écosystèmes forestiers. La famille est surtout entomogame, la dissémination des baies sucrées est assurée par les oiseaux et certains mammifères comme les lémuriens (Judd et al. 2002). Les fruits de certaines espèces du genre *Mimusops* sont également vendus au marché surtout sur la côte Est de l'île.

LES SAPOTACEAE À MADAGASCAR. La famille des Sapotaceae est représentée à Madagascar par dix genres dont quatre endémiques, et 82 espèces actuellement reconnues dont 79 sont endémiques (Madagascar Catalogue 2013). Cette famille de plantes nécessite une révision en ce qui concerne les taxons de Madagascar (Morat et Lowry 1993). Linné (1758) a décrit le genre *Mimusops* et les études systématiques du genre ont été multiples depuis plus de 250 ans. Les travaux menés par Aubréville (1974) sur les collections de Madagascar déposées dans l'herbier de Paris (P) pour la publication de la famille des Sapotaceae dans la Flore de Madagascar et des Comores ont révélé une grande diversité de *Mimusops* à Madagascar. Friedmann (1980) est le dernier à avoir décrit une nouvelle espèce malgache dans le genre, *M. antsiranensis* F. Friedmann, à partir d'un spécimen récolté en 1962 par René Capuron au sommet d'Anosiarivo, dans le massif calcaire de la Montagne des Français à Antsiranana, au Nord de Madagascar (Figure 1). Au total, 14 espèces de *Mimusops* sont actuellement connues de Madagascar. Le genre *Mimusops* appartient à la tribu des Sapoteae (Gautier 2013). Ce sont des plantes ligneuses variant de la taille de buissons à de très grands arbres. Les feuilles sont simples, alternes, insérées en spirales aux extrémités des rameaux, sans stipules. La fleur est 4-mère, le calice est formé de 8 sépales valvaires, disposés sur 2 verticilles de 4 ; la corolle est soudée à la base en un tube très court avec 8 lobes, chaque lobe est muni d'une paire d'appendices parfois laciniés à la base ; l'androcée est formé de 8 étamines épipétales, insérées au sommet du tube de la corolle, les filets sont bien distincts ; les staminodes sont également au nombre de 8, alternant avec les étamines et de même longueur, toujours pubescents sur la face externe et le rebord ; l'ovaire est 8-loculaire, pubescent ou glabre, le style est grêle et long. Le fruit est une baie charnue, indéhiscente qui conserve à sa base les deux cycles de sépales, il renferme une ou plusieurs graine(s) pourvue(s) d'une petite cicatrice hilaire circulaire, basiventrale.

La présente étude décrit deux nouvelles espèces en utilisant les caractères morphologiques des différents organes, tout en mettant en relief les caractères distinctifs des espèces reconnues dans les travaux précédents, et propose une carte de distribution de ces deux espèces à partir des données de spécimens actuellement disponibles.

MÉTHODES

Les spécimens d'herbiers constituent le principal matériel d'étude (Aubréville 1972). Accompagnés de notes de terrain adéquates, ils constituent une source d'informations fondamentales (Jeffrey 1982). Malgré l'existence de méthodes modernes comme la biologie moléculaire, les études basées sur la morphologie ont été jugées suffisantes pour décrire de nouvelles espèces de Sapotaceae. Les échantillons des herbiers de MO, P, TAN et TEF ont été consultés et tous les détails végétatifs et floraux ont été minutieusement examinés. Les taxons décrits ont été comparés aux espèces connues du genre. D'autres informations ont été relevées dans la base de données Tropicos (http://www.tropicos.org) et Madagascar Catalogue (2013) du Missouri Botanical Garden pour compléter les informations issues des récoltes. Les caractères ou combinaisons de caractères spécifiques uniques ont été retenus pour distinguer les espèces les unes des autres, plus particulièrement le port de la plante, le diamètre à hauteur de poitrine (dhp en cm), le type d'écorce, la forme et les dimensions du limbe foliaire, le type de nervation, le type de pétiole, la pilosité de l'ovaire, le type de pédicelle, la forme et les dimensions des fruits, le nombre et la forme de graines dans les fruits, la forme de la cicatrice hilaire et la distribution géographique.

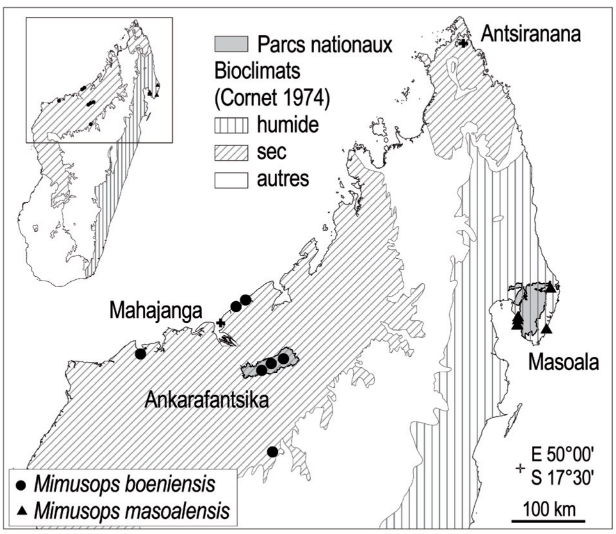

FIGURE 1. Station de récoltes des deux nouvelles espèces de *Mimusops*.

RÉSULTATS ET DISCUSSION

MIMUSOPS BOENIENSIS RANDRIANAIVO SP. NOV.

Type : Madagascar. Région Boeny, District Ambatoboeny, Commune Andranofasika, Parc National Ankarafantsika, E046°33'36", S16°07'48", février 1997, fleur ; Rabevohitra 3107 (SF 34831) (holo- : TEF! TEF000877).

Paratypes : Rabevohitra 2470 (SF 33699) (TEF), Ampijoroa Station Forestière, janvier 1992, E046°29'24'', S16°10'48'', fleur ; Rabevohitra 2693 (TEF), Ampijoroa Station Forestière, février 1994, E046°29'24", S16°10'48", fruit ; Rabevohitra 2709 (TEF) ; Ampijoroa Station Forestière, février 1994, E046°29'24'', S16°10'48'', bouton floral, fleur ; Rabevohitra 2791 (TEF), Ampijoroa Station Forestière, février 1994, E046°29'24'', S16°10'48", bouton ; Réserves Naturelles (Ramamonjisoa) 2914 (K, MO, P, TEF), Parc National Ankarafantsika, janvier 1951, E047°04'30", S16°09'50", fleur ; Rakotozafy 1848A (TAN), Soalala, juillet 1997, E045°19'30'', S16°06'00'', fruit ; Rakotozafy 1848E (TAN), Soalala, juillet 1997, E045°19'30", S16°06'00'', fruit ; Randrianaivo 646 (CNARP, MO, P, TAN), Antsahanitia-Mahajanga, mai 2001, E046°26'01'', S15°35'18", 20 m, fruit ; Randrianaivo 972 (CNARP, MO, P, TAN), Katsepy-Mahajanga, décembre 2003, E046°10'45'', S15°49'14'', 46 m, bouton, fruit ; Randrianasolo 521 (G, MO, P, TAN), Ampijoroa Station Forestière, novembre 1996, E046°49', S16°18', 200 m, fruit ; Service Forestier (SF)122 (P), janvier 1949, E046°57'00'', S17°19'00'', 480 m, fruit ; SF 10581 (Raboanary Rajaona 43) (P), Marosakoa, août 1954, E046°29'24'', S16°10'48'', fruit ; SF (Capuron) 11992 (G, P, TEF), Ankarafantsika, mai 1957, E046°33'36''–E047°08'24'', S15°35'24''–S16°12'00'', fruit ; SF 24315 (Capuron) (TEF), Ampasimaniry-Mahajanga, novembre 1965, E046°30'00'', S15°31'00'', 0 m, fruit.

Diagnose*: Tree with small obovate leaves less than 6.5 cm long, glabrous ovary, small ellipsoid fruit (18–20 mm x 36–40 mm) monospermous, and persistent reflexed calyx* (Figure 2).

Description : Arbre de 2,5 m à 12 m de hauteur ; diamètre à hauteur de poitrine (dhp) de 5 à 15 cm ; écorce gris-noir crevassée longitudinalement. Présence de latex blanc dans toutes les parties. Feuilles elliptiques à obovées, glabres, obtuses à arrondies au sommet, cunéiformes à la base; limbe de 3,5–6 x 1,5–3 cm ; nervation réticulée, généralement finement marquée sur les deux faces ou parfois légèrement effacée sur la face supérieure; pétiole grêle, 5–15 mm de long x 1–1,2 mm de section, pubescent. Fleurs fasciculées à l'aisselle des feuilles ; pédicelle de 1 cm de long environ; lobes des sépales extérieurs long de 5–6 mm, pubescent extérieurement; pétales, étamines, et staminodes tôt caduques. ; ovaire glabre. Fruit ellipsoïde, 18–20 mm x 36–40 mm, apiculé, contenant une seule graine (22–24 x 15–16 x 13–14 mm) pourvue d'une cicatrice basiventrale (6 x 5 mm) ; pédicelle 12–15 x 1,2 mm, calice révoluté sur les fruit.

Floraison : janvier–février.

Fructification : mars–novembre.

Noms vernaculaires : *nato*, *nanto*

Étymologie : le nom fait référence à la toponymie de la localité du spécimen type, la région Boeny.

Particularités : *Mimusops boeniensis* (Figure 2) est caractérisé par la glabrescence de l'ovaire qui la différencie de la plupart des espèces du genre. *M. boeniensis* et *M. occidentalis* sont deux espèces connues pour le caractère glabrescent de leurs ovaires et rencontrées dans le bioclimat sec (sensu Cornet 1974). Néanmoins *M. boeniensis* se distingue par la taille et la forme de ses feuilles et de ses fruits. Chez *M. boeniensis*, les feuilles sont relativement petites et obovées avec un limbe de moins de 6,5 cm de longueur, courtement pétiolées, les fruits sont petits, pyriformes inversés et monospermes, alors que chez *M. occidentalis*, les feuilles sont assez grandes, étroitement oblongues avec un limbe de plus de 7,5 cm de longueur et un pétiole long et grêle ; les fruits sont plus grands, sphériques à ovoïdes et souvent polyspermes. Il est possible qu'il existe des hybrides avec *M. capuronii* var. *retusa* Aubrév. dans l'Ankarana (L. Gautier In litt.).

Statut de conservation : *Mimusops boeniensis* a une aire de distribution restreinte, à cheval sur les régions Boeny et Betsiboka. Quatre des cinq sous-populations connues sont distribuées en dehors du réseau des Aires Protégées et une seule a été recensée dans le Parc National Ankarafantsika (Figure 1). Le passage presque régulier de feux de brousse dans ce parc n'assure pas une protection suffisante à cette sous-population. Avec une aire d'occurrence (EOO) de l'ordre de 19 300 km², une aire d'occupation (AOO) de 63 km² et n'étant présente que dans quatre stations (locations), *M. boeniensis* est évalué comme En Danger EN B2ab (ii, iii, iv, v). par application des catégories et critères de la Liste Rouge de l'IUCN (2012).

MIMUSOPS MASOALENSIS RANDRIANAIVO SP. NOV.

Type : Madagascar, Région Analanjorofo, District Maroantsetra, forêt littorale de Tampolo, Parc National Masoala, 18 octobre 2001, E049°57'38", S15°43'45", 10 m d'altitude, fruit, Randrianaivo 703, (holo- : TAN! TAN001987 ; iso- : MO).

Paratypes : Aridy 512 ; Labat 3421 (MO, P, TEF), Andranobe-Masoala, octobre 2001, E049°57'54", S15°40'20", 270 m ; Rabevohitra 3309 (SF 35066) (TEF), Tanambao-Masoala, mai 1998, E050°11'24", S15°42'00", fruit ; Rahajasoa 1120 (TAN), Andranobe-Masoala, mars 1995, E049°5', S15°38'S, fruit ; Randrianaivo 104 (G, MO, P, TAN), Sahafary-Masoala, juillet 1997, E050°13'12", S15°10'12", fruit ; Randrianaivo 109 (G, MO, P, TAN), Sahafary-Masoala, juillet 1997, E050°13'12", S15°10'12", fruit ; Randrianaivo 115 (G, MO, P, TAN), Sahafary-Masoala, juillet 1997, E050°13'12", S15°10'12", fruit ; Randrianaivo 667 (G, MO, P, TAN), Tampolo-Masoala, octobre 2001, E049°57'24", S15°44'12", 200–400 m, fruit ; Schatz 3022 (G, MO, P, TAN), Ambanizana, Masoala, décembre 1990, E049°34'48", S15°22'48", 0–10 m, fruit ; Vasey, N. 240 (G, MO, P, TAN), Andranobe-Masoala, décembre 1994, E049°57'51", S15°40'24", 110–260 m, fruit ; Vasey, N. 321 (G, MO, P, TAN), Andranobe-Masoala, janvier 1995, E049°57'51", S15°40'24", 110–260 m, fruit. Diagnose : Tree with large leathery leaves, limb simple, long petioles (5–6 cm), rare fruit on flowering branches, sepals having an outer hull (Figure 3).

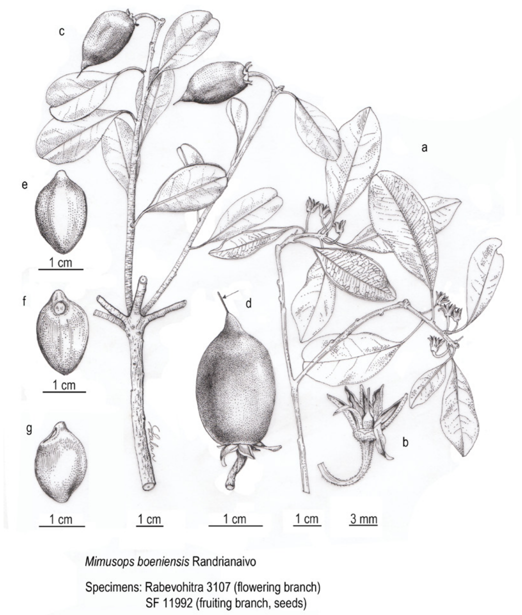

FIGURE 2. *Mimusops boeniensis* Randrianaivo. (a : rameau florifère, b : fleur, c : rameau fructifère, d : fruit, e : graine vue dorsale, f : graine vue ventrale, g : graine vue latérale, dessins Roger Lala Andriamiarisoa)

Description : Arbre de 12–35 m de hauteur ; diamètre à hauteur de poitrine (dhp) 50–65 cm ; présence de latex blanc dans toutes les parties, écoulement de latex relativement faible par rapport aux autres espèces du genre ; écorce gris-noir crevassée longitudinalement et rouge à l'intérieur ; parties jeunes recouvertes de poils roux. Feuilles 14–36 x 7–16 cm ; limbes obovés ou oblongues, arrondis, légèrement émarginés au sommet, cunéiformes à la base, épais et coriaces, initialement velus brun-argenté sur les faces inférieures, puis glabrescents ; nervation secondaire réticulée, généralement distincte sur la face inférieure, parfois légèrement effacée sur la face supérieure ; pétioles robustes, longs jusqu'à 5–6 cm, environ trois fois plus longs que les pédicelles fructifères. Fleur inconnue. Fruit ovoïde ou ellipsoïde (4,5–7 cm x 2,5–3,5 cm), brun clair, arrondi et parfois apiculé au sommet, inséré à l'aisselle des feuilles ou de leurs cicatrices, renfermant une graine à testa vernissé et pourvu d'une petite cicatrice hilaire circulaire basiventrale, rugueuse et mate contrastant avec le brillant du reste de la graine ; calice persistant sur les fruits, brun, sépales extérieurs nettement carénés mesurant 10 mm; pédicelle robuste, 2 cm de long environ.

Floraison : inconnue.

Fructification : septembre–juillet.

Noms vernaculaires : *nanto voarantoala, voaranto*

Étymologie : le nom fait référence à la toponymie de la localité du type, la presqu'île Masoala (Figure 1).

Distribution : *Mimusops masoalensis* (Figure 3) est rencontré sur la presqu'île Masoala, dans le Nord-Est de Madagascar (Figure 1), dans une forêt dense humide de basse altitude depuis le niveau de la mer jusqu'à 400 m d'altitude.

Particularités : *Mimusops masoalensis* (Figure 3) se distingue des autres espèces de *Mimusops* de Madagascar par la combinaison de caractères suivants : grandes feuilles coriaces, à pétiole long (5 à 6 cm) et à marge simple, et un nombre réduit de fruits sur les rameaux florifères, les fruits aux sépales présentant une carène extérieure. Sur le terrain, *M. masoalensis* peut être confondu avec *M. voalela*, *M. longepedicellata* ou *M. coriacea* par la taille des feuilles, mais s'en distingue par son pédicelle plus court et son pétiole relativement court. *M. antongilensis* est aussi une espèce de la presqu'île Masoala proche de *M. masoalensis* par ses feuilles relativement grandes et coriaces. *M. masoalensis* s'en distingue par ses feuilles plus larges et le bord du limbe simple.

Statut de conservation : *Mimusops masoalensis* n'est connu que de la presqu'ile Masoala. Son aire d'occurrence (EOO) est de 292 km² et son aire d'occupation (AOO) de 45 km². Quatre sous-populations sont connues dont deux seulement sont distribuées dans l'aire protégée de Masoala. Dans la mesure où cette région est sous la menace des cyclones, *M. masoalensis* est classé En Danger EN B1ab (i, ii, iii, iv) + 2ab (i, ii, iii, iv) selon les catégories et les critères de la Liste Rouge de l'IUCN (2012).

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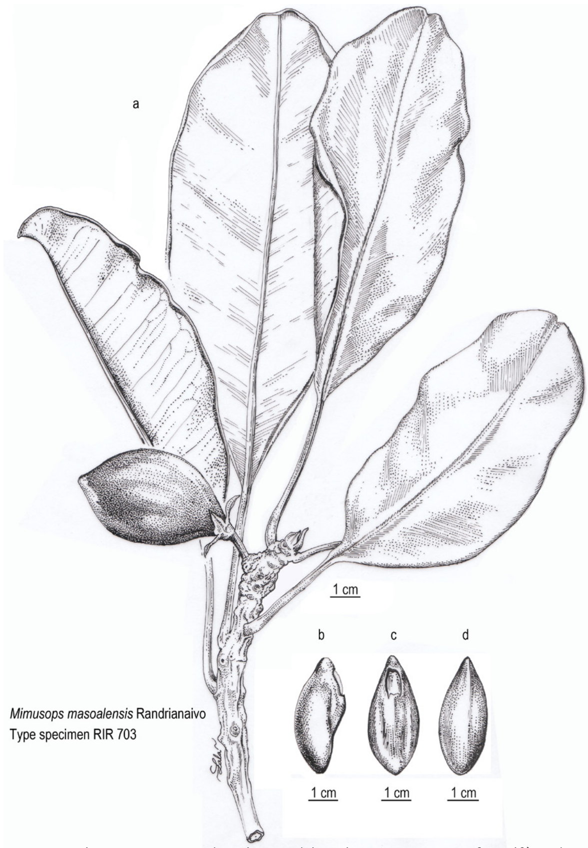

FIGURE 3. *Mimusops masoalensis* Randrianaivo. (a : rameau fructifère, b : graine vue latérale, c : graine vue ventrale, d : graine vue dorsale, dessins Roger Lala Andriamiarisoa)

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

FIGURE S1. Holotype of *Mimusops boeniensis* Randrianaivo.

FIGURE S2. Holotype of *Mimusops masoalensis* Randrianaivo.

TABLE S1. Acronyms of the main herbaria holding specimens collected in Madagascar.

ARTICLE

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Limestone cliff-face and cave use by wild ring-tailed lemurs (*Lemur catta*) in southwestern Madagascar

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ABSTRACT
Ring-tailed lemurs live in a range of habitats in southwestern Madagascar. To date, much of the knowledge of ring-tailed lemur ecology, biology and behavior come from riverine gallery forests sites. Recent years have seen an expansion of comprehensive research on this resilient species, including areas of limestone spiny forest along Madagascar's southwestern coast. This work is documenting newly discovered behaviors by this species. The regular use of cliff-faces and embedded crevices and caves by ring-tailed lemurs in southwestern Madagascar are reported here. Cave use by several anthropoid primates has been explained as a thermoregulatory behavior. It is suggested that cliff-face and cave use by these ring-tailed lemurs serves several purposes, including resource acquisition, thermoregulation, and as an anti-predator avoidance strategy in the absence of suitable large sleeping trees. Observations indicate that the limestone boundaries of the Mahafaly Plateau and their associated xerophytic scrub forests warrant further conservation attention, given the presence of behavioral variation and increasing threats to this endangered primate species.

RÉSUMÉ
Lemur catta occupe divers habitats dans le Sud-ouest de Madagascar. L'écologie, la biologie et le comportement de *Lemur catta* sont actuellement mieux connus des populations vivant dans les forêts riveraines et les zones environnantes. Pour mieux comprendre cette espèce de lémurien, les recherches ont été étendues à d'autres habitats dont les forêts épineuses du plateau calcaire qui est situé le long du littoral Sud-ouest de Madagascar. Dans cette étude nous rapportons les comportements récemment découverts de *Lemur catta* qui utilise les falaises et les grottes dans le Sud-ouest de Madagascar. L'utilisation des grottes par la plupart des primates hominoïdes est liée à un avantage thermorégulateur offert par ce milieu. Dans notre cas, l'exploitation de falaises et de grottes par *Lemur catta* semble être associée à un mécanisme permettant d'échapper aux prédateurs et à l'absence de grands arbres qui devaient servir de dortoirs. De sorte que les falaises et les forêts épineuses du plateau calcaire Mahafaly ont besoin d'une conservation particulière car nos résultats de suivis montrent que les changements de comportement du lémurien emblématique de cette région trouve vraisemblablement son origine dans la dégradation de l'environnement de cette espèce.

INTRODUCTION
Ring-tailed lemurs (*Lemur catta*) are a resilient primate species, inhabiting a wide range of habitats across southern and southwestern Madagascar that includes areas of heavy human disturbance (e.g., Sauther et al. 1999, Gould 2006, Jolly et al. 2006). Spanning a range from the southernmost point in Madagascar (Cap Sainte Marie), across the spiny forests and dry deciduous riverine forests of the Atsimo-Andrefana Region, through the high-altitude Andringitra Massif and surrounding highlands, ring-tailed lemurs live within a range of challenging environments in terms of temperature variation, droughts, cyclones and differing levels of anthropogenic change (Goodman et al. 2006, LaFleur 2012). *Lemur catta* is also the most terrestrial of all living lemurs, and exploits a wide range of resources, depending on the habitat (e.g., Sauther et al. 1999, Goodman et al. 2006, Gould 2007). To date, most of what is known about this species' biology, ecology, and behavior comes from long-term studies (> 25 years) at two riverine gallery sites, the Bezà Mahafaly Special Reserve and Berenty Private Reserve (Gould 2007). Only recently has information on this species been available from more xeric spiny forest areas, including along the limestone plateau of Madagascar's southwestern region (Sauther and Cuozzo 2008, Kelley 2011, Cuozzo and Sauther 2012, LaFleur 2012). In this paper, the use of caves and cliff fissures by ring-tailed lemurs at two sites, Tsimanampesotse National Park and the Tsinjoriake New Protected Area, both located in southwestern Madagascar, is described in detail for the first time, and possible ecological functions of this behavior discussed.

Cave use is rare among primates, but has been previously reported among continental African and Asian anthropoid primates, including chimpanzees, baboons, and langurs. A variety of hypotheses have been put forth regarding this behavior,

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many positing thermoregulation as a key reason (Pruetz 2001, 2007, Huang et al. 2003, McGrew et al. 2003, Barrett et al. 2004, Workman 2010). For example, cave use among chimpanzees in southeastern Senegal looks to be an "opportunistic" behavior in response to high temperatures (Pruetz 2007: 318). Explanations for cave use by primates also include access to water, obtaining nutrients through geophagy and predator avoidance (McGrew et al. 2003).

Among Madagascar's strepsirhine primates, only anecdotal observations of cave use have been previously reported. Ring-tailed lemurs at Andrahomana cave, in southern Madagascar have been seen resting and feeding during the daytime in this cave (Vasey et al. 2013). At Isalo National Park, on the southern edge of Madagascar's central highlands, ring-tailed lemurs were observed entering caves to lick the soil as well as using caves during the day and at night (Dinets, pers. com). Finally, a single report from northern Madagascar describes crowned lemurs (*Eulemur coronatus*), using a cave to drink water (Wilson et al. 1989).

Early reports by Perrier de la Bâthie (1927) described ring-tailed lemurs using the vertical cliff-faces of the Andringitra Massif, central Madagascar. A more recent study of these high-altitude (ranging above 2,000 meters) *L. catta* on the Andringitra Massif, near the northern boundary of this species' range in south-central Madagascar, has documented the use of fissures and overhangs in the granitic outcrops as sleeping sites (Goodman et al. 2006). Goodman et al. (2006) hypothesize that i) caves serve as shelter in response to cold temperatures at this altitude, and/or ii) caves and rock overhangs may be a way of avoiding predation by the endemic fossa (*Cryptoprocta ferox*). Gould (pers. comm.) has recently observed a small *L. catta* troop (n = 4) that uses a small cave in the Ambalavao region of the highlands, in the same region as the Andringitra Massif. This population lives in habitat with no forest cover due to slash-and-burn agriculture, and survives on anthropogenic resources such as crops and fruit trees. This example of ring-tailed lemur cave use is likely a result of human action rather than ecological adaptations such as thermoregulation or predator avoidance, and is similar to langur cave use described by Li and Rogers (2005), where these monkeys use caves and limestone karst as a refuge in response to deforestation and expanding cultivation. In fact, all of the scattered, fragmented *L. catta* populations in this highland region may be using the granitic slopes, massifs and caves as a refuge, as the surrounding areas are void of continuous forest, subject to frequent intentional burning (e.g., Goodman and Langrand 1996), and are marked by vast expanses of cultivated land (Cameron and Gould 2013). Data on ring-tailed lemur cliff-face and cave use in areas of continuous forest, but without the large sleeping trees present in riverine gallery forest areas such as Bezà Mahafaly Special Reserve and Berenty Private Reserve, would add to current anecdotal reports from this and other species and provide valuable data to interpret and explain this behavior beyond it being a response to anthropogenic effects.

METHODS

As part of the authors' long-term collaborative research on the ecology, biology and behavior of ring-tailed lemurs in southwestern Madagascar, research has been carried out along the western edge of the Mahafaly Plateau, Atsimo-Andrefana Region. Data presented here are based on a cumulative 11 months of direct observations, supplemented with data from camera traps. The authors have spent varying amounts of time at Tsimanampesotse National Park (E43°46'–43°50', S24°03'–24°12') ranging from several weeks to seven months: May/June 2006 (MLS, FPC, IAJY); May/June 2007 (MLS, FPC, IAJY); June 2008 (MLS, FPC, IAJY, MML); September 2010 through April 2011 (MML); August 2013 (ML). During the seven-month behavioral study, camera traps monitored daily lemur activity as well as predator behavior. Tsimanampesotse is a 42,000 ha National Park representing the western most escarpment of the limestone Mahafaly Plateau and is constructed of Cenozoic limestone (DuPuy and Moat 1998). A highly seasonal habitat, most rainfall occurs between December and February with annual rainfall rarely exceeding 500mm (Donque 1975, APAAT Protected Areas Report: http://bioval.jrc.ec.europa.eu/APAAT/pa/2307/), although during this same time period during this research rainfall was only 400mm (LaFleur 2012). Temperature also varies dramatically with daytime highs of well over 40°C, although mean daily temperatures range between 22.5°C and 35.8°C (LaFleur 2012). The area is also affected by high winds, frequent droughts and cyclones (Andriatsimietry et al. 2009, LaFleur 2012). At Tsimanampesotse census data on five groups are available from 2006, 2007 and 2010–11: Vintany (n = 12–20 adults), ILove (n = 9–13 adults), Akao (n = 9–15 adults), Capture Be (n = 14 adults) and Miandry (n = 12 adults). For this report the focus is on three lemur troops that have been regularly observed, Vintany, ILove and Akao, including during the above-mentioned continuous seven-month study. Standard focal sampling methods were used during this study (LaFleur 2012). The Vintany and ILove troops inhabit an area above saline Lac Tsimanampesotse, in the limestone spiny forest on the western edge of the Mahafaly Plateau. Akao spends parts of its time along the eastern edge of Lac Tsimanampesotse, as well as ascending the western edge of the escarpment. Tsimanampesotse contains dry spiny forest with open-canopied dwarf flora of the Euphorbiaceae, Didiereaceae, Bombaceae, and Fabaceae families as well as areas of semi-deciduous trees (LaFleur 2012, Jacky Youssouf, unpub. data). To characterize the habitat at Tsimanampesotse in 2007 three areas encompassing the lemur groups have been evaluated using seven transects covering a total of 300x10 meters for each of the three areas.

Most recently (2012), the authors expanded their work to include an area north of Tsimanampesotse and the Onilahy River mouth/Saint Augustin Bay, in the Tsinjoriake New Protected Area, between 15km and 25km south of Toliara (E43°45'36", S23°26'53"). This newly protected area encompasses approximately 25,000 ha of limestone cliffs and southwestern dry spiny forest thicket as well as coastal mangroves. A total of 12 20x50 m vegetation transects were carried out to characterize the lemur's habitats. During a brief previous survey in 2007 by the University of Brighton, *Lemur catta* were reported to sleep in trees near a cave area and within nearby crevices (Scott et al. no date). In April 2012 members of the research team carried out an intensive month long study of ring-tailed lemurs at Tsinjoriake that included daily census, habitat analyses and behavioral ecology (Ravelohasindrazana 2013, Ravoavy 2013). LALR and JFR also conducted interviews and administered questionnaires to 30 community members regarding their use of resources in the area. Eight ring-tailed lemur groups were observed using focal sampling within two locations during April 2012. These were: Ambanilia troops; Mailaka (n = 5), Ekipa (n = 11), Fetry (n = 3), Tsy misaraky (n = 2), and Antsifotse troops; Troop 1 (n = 2), Troop 2 (n = 3), Troop 3 (n = 4) and Troop 4 (n =5). In July/August 2013, a second preliminary ecological survey was conducted, including the use of camera traps, of *Lemur catta* and their habitats at two locations in the Tsinjoriake Protected Area, one in the Binabe area including the Grotte (or cave) of Binabe and the Grotte Ambanilia area where the Sarodrano Peninsula meets the mainland, north of the mouth of Onilahy River.

RESULTS

During each of the seven time periods spent observing *Lemur catta* at Tsimanampesotse and/or Tsinjoriake, at least some troops within these larger populations regularly, and for the ILove troop at Tsimanampesotse exclusively, used cliff-face crevices and/or small caves as sleeping sites at night (Figure 1). This was true during the continuous seven-month study of this troop from September 2010 through April 2011. Of interest, not all troops at these localities exhibit this behavior. At Tsimanampesotse the Vintany troop regularly sleeps in a large cluster of *Ficus* sp. trees at the top of a vertical limestone depression, where these lemurs sometimes descend to drink water. The Akao troop at Tsimanampesotse was never seen using cliff-face areas as sleeping sites; rather, they regularly slept in a stand of introduced Australian pines (*Casuarina equisetifolia*) along the eastern lake margin. Vegetation transects revealed that there were very few large (> 10 cm DBH) *Ficus* sp. or *Tamarindus indica* trees available for sleeping (20 of 225 trees measured), and the majority of these are found near limestone sinks that may also contain steep cliff-faces and/or caves.

At Tsinjoriake, of the eight troops observed, four commonly used one of three caves for sleeping at night (Grotte Binabe: Troops 2 and 4; Grotte Binakely: Troop 3; Grotte Ambanilia: Ekipa Troop). During the 2013 visit to the area no direct observations of the lemurs using Grotte Ambanilia were made, but fresh *L. catta* fecal material near the entrance was found, indicating they were still using this cave as resting or sleeping sites.

In addition to their use as nightly sleeping sites, larger caves within limestone sinks/depressions commonly contained pools of water that were used by lemurs as drinking sites at both Tsimanampesotse (Figure 2, cf. Video 1) and Tsinjoriake (at Grotte Sarodrano and Grotte Binabe). The larger caves were also used as 'day caves' during the hot season apparently to cool off at Tsimanampesotse. At Tsimanampesotse members of ILove group also lick the limestone walls around the caves and fissures (cf. Video 2). Large trees in the area, those greater than 10 cm in DBH (*Ficus marmorata*, *Poupartia sylvatica*, *Tamarindus indica* and *Noronhia* sp.), are limited to coastal mangrove forest and a small gallery forest as well as within the immediate vicinity of large limestone caves that contain pools of water. The majority of the vegetation is dwarfed, with heights less than 2.5m (cf. Zafisamimanana 2012, Ravelohasindrazana 2013, Ravoavy 2013). Thus, four of the eleven troops observed at both locations used cliff-face crevices and/or caves as sleeping sites and most troops were also observed using large caves as drinking sources and/or potentially as refugia from excessive heat along the western edges of the limestone Mahafaly Plateau. These data greatly expand the knowledge of ring-tailed lemur cave use in Madagascar, which to date has been primarily anecdotal.

DISCUSSION

Cave use by non-human primates has been linked to thermoregulation, predator avoidance, and/or resource access, as well as refugia in response to human actions such as deforestation (e.g., Pruetz 2001, 2007, Huang et al. 2003, McGrew et al. 2003, Goodman 2006, Workman 2010). Similar to the langurs of Southeast Asia discussed earlier (Huang et al. 2003, Workman 2010), ring-tailed lemur cave use in the Andringitra and Tsaranoro region much further north of Tsimanampesotse and Tsinjoriake is likely linked to deforestation, given only remnant forests exist in these areas (Goodman and Langrand 1996, Cameron and Gould 2013). As the areas in which observations of cliff-face and cave use display intact forests, at least until recently, it is unlikely that cave use in this region is a direct response to deforestation.

FIGURE 1. The ILove troop lemurs on cliff-face, about to enter small sleeping caves at Tsimanampesotse National Park. Arrow denotes one of the sleeping caves.

FIGURE 2. The ILove troop drinking water from the Grotte Mitoho at Tsimanampesotse. Photo by Violaine Pellicheroo, with permission from the author.

Large caves with pools of fresh water do provide important sources of drinking water during the day at both study sites, especially since these are available year round (LaFleur 2012). In addition, at Tsinjoriake there are also limestone seeps along the edges of the coastal Mangrove forests which make fresh water available during low tide, and which are used by some lemur troops (e.g., Ekipa troop). Goodman et al. (2006) put forth the interesting question of whether ring-tailed lemurs can exist in areas without fresh water and suggest that, especially in spiny forests, they may meet their water needs from their diet and/or from dew that collects on plants overnight. At a highly anthropogencially altered habitat in the Cap Sainte-Marie region of southern Madagascar, Kelley (2011) reports only one instance of ring-tailed lemurs drinking water and suggests the lemurs there also receive their water requirements from their foods, particularly the introduced *Opuntia* sp. Nevertheless, the fact that lemurs living within the spiny forest habitats of Tsimanampesotse and Tsinjoriake do seek out and use fresh water resources support the hypothesis that access to water may be significant, and that pools of fresh water within such caves or fresh water emanating from limestone seeps are an important aspect of their ecology in these intact spiny forests. It is also possible that, like at Isalo National Park, the lemurs may practice geophagia by ingesting soil within cave environs. To date this has not been observed within the actual caves but has been seen in other areas (LaFleur 2012). However, as noted above, in August 2013, MML observed ring-tailed lemurs licking the walls of limestone cliffs where they sleep at Tsimanampesotse. As water precipitates out of the limestone and dries it may provide access to minerals for these lemurs. This licking behavior, along with geophagia, has been widely noted among ring-tailed lemurs living in gallery forest sites (e.g., Jolly 1966, Loudon et al. 2006).

Cave use in this region may also be a way to stay cool during the hot wet season as well as to stay warm during the cool dry season (at Tsimanampesotse temperatures range from 10.4° C to 41.9° C but can be even hotter or cooler in more open areas (LaFleur 2012)). While some ring-tailed lemurs likely use day caves to escape the extreme heat, as observed for Fongoli chimpanzees (Pruetz 2001, 2007), it is important to distinguish between day and night use of caves, as different pressures (e.g., predation, ambient temperatures) likely vary throughout the day. At Tsimanampesotse, the ILove troop used the small cliff-face crevices and caves for sleeping without exception during all the observations, and at all times of the year, from the scorching Austral summer, where temperatures regularly range above 40°C to the cool late Austral fall and early winter when temperatures can fall as low as the single digits °C (LaFleur 2012). In addition, for the troops studied at Tsimanampesotse only the ILove troop used caves and fissures for night sleeping, while neither the Vintany nor the Akao troops did. As the ILove and Vintany troops live only several hundred meters from each other on top of the western escarpment of the Mahafaly Plateau, they experience similar temperature conditions, and thus would be expected to respond to these stressors in a similar way, given the availability of numerous limestone depressions and cliff-faces in Vintany's range. Similarly, the Akao troop used a large stand of *Casuarina equisetifolia* at the eastern edge of the Lac Tsimanampesotse, along a marshy area each night throughout the observations in May/June 2006. During that period, temperatures at night dropped near the single digits °C, with high humidity. Thus, these lemurs sleep under quite cold conditions, yet have never been observed using caves along the escarpment as night sleeping sites, despite their daily use of this escarpment area for foraging. There are also a variety of behavioral responses to temperature challenges. At Tsimanampesotse during periods of excessively high temperatures (at or greater than 40°C) the lemurs spent considerable time resting in the shade and licking their hands and feet to cool off (LaFleur 2012). During especially cold mornings the ILove troop left its caves at daylight and formed 'lemur balls' on the limestone surface above their sleeping caves until the sun was high enough to allow individual sunning. Similarly, at Tsinjoriake the lemurs visited the mangroves during the hottest period of the day, where they could rest and feed in the shade of these larger trees, but did not use these trees to sleep overnight. Thus, thermoregulation alone is unlikely to be the primary reason for sleeping at night in caves and fissures.

As noted by Anderson (1998), primates spend about half of their lives within sleeping sites, and where primates choose to sleep is thus an important aspect of their behavioral ecology. Numerous studies have indicated that sleeping sites appear to be selected to provide some safety from predation (cf. reviews in Anderson 1998, Bitetti et al. 2000, Cui et al. 2006, Cheyne et al. 2012). Especially critical is a sleeping site that allows early predator detection or provides difficult access for an approaching predator. For example, both talapoin and tufted capuchin monkeys choose sleeping areas where approaching predators create noise and vibrations (Gautier-Hion 1970, Zhang 1995). Sympatric Kloss's gibbons (*Hylobates klossi*) and Mentawi langurs (*Presbytis potenziana*) on Siberut Island, Indonesia, both use tall emergent sleeping trees, but the gibbons preferentially select trees with few large lianas. Human hunters, who use the large lianas to climb into the trees, are thus able to kill far more langurs than gibbons (Tenaza and Tilson 1985, Cheyne et al. 2012). Habitat structure is especially essential for understanding variation in anti-predation behavior (Enstam 2007). For example, patas monkeys on continental Africa live in open savannas with few large sleeping trees and thus individuals have a dispersed sleeping pattern with one individual sleeping in a tree. Within the same habitat, African vervets will sleep in tall trees within riverine forest habitats and thus all individuals may sleep in one tree (Enstam 2007). Hamadryas baboons (*Papio hamadryas*) living in the highlands of Ethiopia, are especially relevant here: their habitat has few sleeping trees, but they solve this dilemma by sleeping on sheer cliff-faces (Kummer 1968).

Goodman et al. (2006) were the first to suggest that the use of limestone crevices and/or overhangs on vertical cliff-faces as night sleeping sites by ring-tailed lemurs could be an anti-predator strategy, specifically in response to endemic fossa (*Cryptoprocta ferox*). Thus, another possible explanation for cave use among the studied lemurs is that using crevices and caves as night sleeping sites at Tsimanampesotse and Tsinjoriake may provide some safety from night-active predators within a habitat with a relative paucity of large trees for suitable sleeping sites. Studies of ring-tailed lemurs in gallery forests document that this species either chooses sleeping trees that are tall and have broad dense canopies that are large enough to accommodate the entire troop, or stands of tall trees that allow all individuals to sleep near one another (Sauther et al. 1999). In over 25 years of study at the Bezà Mahafaly Special Reserve, ring-tailed lemurs have never been observed to use any night sleeping sites other than large trees, even when troop size exceeds 20 individuals (MLS, pers. observ.). Given the variety of known lemur predators at Bezà Mahafaly Special Reserve, including *Cryptoprocta ferox*, wild cats, feral dogs and a diversity of avian raptors (Sauther 1989, Gould and Sauther 2007) use of such sleeping trees may be an anti-predator strategy, especially as ring-tailed lemurs also exhibit predation sensitive foraging strategies (Gould and Sauther 2007). That ring-tailed lemurs seek out safe night sleeping sites is also supported at other sites. For example, two troops of ring-tailed lemurs studied in the Cap Sainte-Marie region of southern Madagascar used stands of introduced *Opuntia* sp. as night sleeping areas, despite there being remnant stands of larger trees in traditionally protected sacred forests (Kelley 2011). Here, remnant stands of sacred forests are very small in area and widely dispersed, and ring-tailed lemurs were never observed to use these as night sleeping areas except in one instance, where the lemurs slept in a hedge of *Opuntia* sp. near one of these sacred forests.

At Tsimanampesotse *Ficus* sp., *Tamarindus indica* and *Casuarina equisetifolia* are the only trees large enough to provide potential sleeping trees for a lemur troop. *Ficus* sp. and *T. indica* are rare. Only 20 of the 255 trees on our transects with a DBH > 10 cm were these species, and these were typically found near the caves that form in limestone depressions. *C. equisetifolia* is only found along the marshy banks of Lac Tsimanampesotse. Unlike the degraded areas of Cap Sainte Marie (Kelley 2011), there are no hedges of *Opuntia* sp. at Tsimanampesotse. One habitat difference between the Vintany, Akao and ILove troops at Tsimanampesotse is that both Vintany and Akao troops have access to trees tall and large enough to accommodate an entire ring-tailed lemur troop and are thus suitable as sleeping sites. It is also important to note that the stand of *C. equisetifolia* trees used by the Akao lemurs is surrounded by thick marsh ferns of *Acrostichum aureum* at the base of the trees, which are difficult and noisy to move through, thus likely inhibiting terrestrial predator access to these trees. Also, these lemurs have been observed to use the plants to avoid avian predators, by quickly descending from the *Casuarina equisetifolia* into the ferns. The ILove troop sleeps in the cliff-face crevices/caves that border a deep limestone depression despite there being a few large *T. indica* and *Ficus* sp. trees in their range. In August 2013, a new troop was observed in a different area at Tsimanampesotse using a large cave as their nightly sleeping site. Around this cave are a number of large *Ficus sp.* trees, yet this group does not use them as night sleeping sites. While a long-term study of ring-tailed lemur cave use is needed, these observations indicate caves are viewed as acceptable and, in some areas with larger trees, even as preferred night sleeping sites. Recent observations also indicate that ring-tailed lemurs may perceive sleeping caves as important refugia from nocturnal predators but not necessarily diurnal ones. In one case, as the ILove troop was entering their caves and crevices in the evening, one individual started alarm calling at a raptor flying over the caves. All lemurs quickly came out of the cave and scanned the area for the hawk. This is similar to anti-predator behaviors exhibited by Bezà Mahafaly gallery forest ring-tailed lemurs, which will orient towards avian prey and often mob them (Sauther 1989).

Both, the fossa (*Cryptoprocta ferox*) as well as wild cats (*Felis silvestris*) have been documented to occur at Tsimanampesotse and fecal analyses indicate fossa prey on ring-tailed lemurs here (LaFleur 2012). While fossa are adept climbers, they are not able to climb high canopy trees very well, due to their large size (Hawkins 2003). At Tsimanampesotse the camera trap data indicate that fossa can scale narrow tall trees, thus rendering these types of trees useless as safe sleeping sites. Also, the only known successful predation of a lemur during the 2010–2011 study period was on an infant in the Vintany group, whose body was found beneath this troop's sleeping tree, a large broad *Ficus* sp. The infant clearly showed two large canine puncture wounds on the neck (LaFleur 2012). Thus at Tsimanampesotse, given that access to sleeping caves and crevices requires scaling a vertical cliff-face, it likely does provide safety from night-active fossa and nocturnal wild cat predation and this may explain why some lemur troops use caves even though larger trees may be nearby.

Further evidence of cave use for predator avoidance is seen at Tsinjoriake. Important predators include packs of village dogs as well as fossa. At this site there are only a few areas that contain large trees. This includes the mangrove forest and a small gallery forest as well as areas directly next to Grotte Binabe and Grotte Binakely. Within both the mangrove forest and the small gallery forest the majority of trees have a DBH of < 10 cm (mangrove: 92 %; gallery forest: 64 %, Ravelohasindrazana 2013). There are large trees (> 10 cm DBH) around Grotte Binabe, but these are few in number and are found only directly next to the cave. At the Grotte of Binabe and Binakely the lemurs regularly uses cliff-face crevices and caves for sleeping that would be difficult for fossa and wild cats to scale. Similarly, the Ekipa troop uses a group of caves that are located on the side of a limestone cliff that vertically drops precipitously into the ocean. The situation for the Ekipa troop is, however, slightly more complex. Earlier observations (Scott et al. no date) noted that, in addition to this cave, this group also used a stand of *Tamarindus indica* trees by a hotel for sleeping. Work by the research team in April 2012 also noted this. However, in June 2012, one month of camera trapping in this area showed no images of lemurs there. Most recently, in July/August 2013, the local research guide informed the research team that the Ekipa troop is no longer using these tamarind trees due to a large and growing pack of domestic dogs in the area, which apparently blocks the terrestrial access route to this fragmentary stand of trees. Thus, the Ekipa troop appears to now exclusively use the cave located on the limestone cliffs for sleeping, presumably to avoid these introduced predators. Given the long coexistence of *L. catta* and endemic predators in southwestern Madagascar, it is suggested that cliff-face and cave use is a natural part of the *L. catta* behavioral repertoire and is then available when needed, such as in the highland region in response to human actions (i.e., deforestation).

This novel behavior by ring-tailed lemurs expands the knowledge of primate cave use, previously reported in detail only for anthropoid primates, and when viewed through the lens of human evolution provides a broader context to interpret cave use by human ancestors (e.g., McGrew et al. 2003, Pruetz 2007). These data also aid the interpretation of cave use in primate paleobiology. For example, a recent study found fecal pellets in Anjohikely Cave in northern Madagascar, attributed to extinct

Archaeolemur (Vasey et al. 2013), suggesting that this large, semi-terrestrial lemur may have used the cave for shelter and nutrients. A clearer understanding of cave use in extant lemurs could thus expand the understanding of the paleoecology of this extinct species. The ongoing collaborative work on these ring-tailed lemur populations will allow the testing of various hypotheses regarding primate cave use.

Tsimanampesotse is one of the only protected areas of Cenozoic limestone habitats on the Mahafaly Plateau (DuPuy and Moat 1998). These authors also noted the importance of other areas of the Mahafaly Plateau, specifically along the escarpment edge towards Saint Augustin, which today encompasses the new Tsinjoriake Protected Area. However, we are just beginning to understand the ecology of ring-tailed lemurs in spiny forest habitats (e.g., Kelley 2011, LaFleur 2012) as most studies of ring-tailed lemurs have been in gallery forest habitats (Sauther 1999, Gould 2007). Given the importance of limestone caves for safe shelter, nutrition and drinking sites among ring-tailed lemurs it is essential that these habitats remain intact. However, the limestone cliffs and southwestern dry spiny forest thicket as well as coastal mangroves of southwestern Madagascar are currently under intense human pressure, including the development of limestone mining operations such as Gulf Industrial Limited's Soalara Limestone Project near the mouth of the Onilahy River. Ring-tailed lemurs, recently classified as an endangered species by the International Union for the Conservation of Nature (IUCN) Species Survival Commission (SSC), are threatened by deforestation and habitat degradation throughout southwestern Madagascar. Tsimanampesotse can now be added as a habitat undergoing extensive anthropogenic change. As recently as August, 2013 trees were being actively harvested as cattle forage, construction materials, and for carving pirogues. Based on the discovery of forest traps and communications with local people, ring-tailed lemurs are also now actively hunted in the area. Until now, poaching of ring-tailed lemurs (and other mammals) in southwestern Madagascar has remained relatively rare, due to widespread traditional taboos. However, rapid social change, along with the well-established existing black-market trade in radiated tortoises (*Astrochelys radiata*) and the demand for alternative or luxury bushmeat in Madagascar's cities have resulted in a niche for harvesting ring-tailed lemurs. Similarly, Tsinjoriake is especially affected by its close location to the large city of Toliara. For example, questionnaires indicate that 14 of the 39 tree species used by ring-tailed lemurs are also used to produce charcoal in the area including *Tamarindus indica* and *Ficus* sp. (Ravelohasindrazana, 2013, Ravoavy, 2013). The questionnaires also indicate that adult ring-tailed lemurs are hunted by humans (using dogs) as a food resource. Infant ring-tailed lemurs become pets and are sold in Toliara for between 3,000 and 4,000 Malagasy Ariary (about $US1.36–1.81) while smoked ring-tailed lemurs sell for 4,000–5,000 Malagasy Ariary ($US1.77–2.21). One of the biggest threats to this protected area is the collection of firewood to fuel the production of bricks at Ankoronga. It is estimated that the production of bricks in the village consumes 1,200–1,500 cart-loads of dead wood per month (Andriamahafaly 2010). The Tsinjoriake New Protected Area has recently been established as a community-based ecological reserve (initially developed under the auspices and guidance of the *Programme Germano-Malgache pour l'Environnement Coopération Allemande* / GIZ, a European NGO that provided funds for local development of this reserve. GIZ/GTZ also laid the groundwork for local community development). The continued support of the Tsinjoriake reserve and community development project now rests on local Malagasy researchers, scientists and community developers, who are responsible for obtaining funds to fully implement the project. Towards this end, JY and the University of Toliara are working with GIZ/GTZ and the local community TAMIA to facilitate community development and training to enable sustainable development and energy use at Tsinjoriake.

These areas have rarely been included in long-term lemur (and other faunal) research and conservation. Although not as speciose (in terms of lemurs) as rainforest habitats, with only *Lemur catta* and *Microcebus griseorufus* observed by the authors, these coastal areas are rich in endemic plant, bird and reptile species and do hold important information for understanding lemur evolution and the presence of unique lemur traits (e.g., LaFleur 2012). As such, they deserve immediate conservation attention.

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Video 1: <http://www.youtube.com/watch?v=8qnBWSMqF_I&feature=youtu.be>

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

Video clip showing Ilove troop lemurs at Tsimanampesotse scaling vertical limestone cliff and entering sleeping caves. Video by Michelle Sauther.

FIGURE S1. Lemur from the Akao troop in *Casuarina equisetifolia* tree on lake margin (A) and within the marshy ferns of *Acrostichum aureum* at the base of these trees (B) at Tsimanampesotse National Park, 2006.

FIGURE S2. Lemurs from the Grotte de Binabe troop on the cliff-face at Tsinjoriake Protected Area.

FIGURE S3. Cave above Sarodrano peninsula, where the "Ekipa" troop sometimes sleeps.

FIGURE S4. Spiny forest habitat at Tsinjoriake. The arrow is pointing at a tree that is 2 m. tall.

FIGURE S5. ILove troop ring-tailed lemurs huddling in a "lemur ball" on limestone rocks after leaving sleeping caves at Tsimanampesotse National Park.

SHORT NOTE

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The *fitoaty*: an unidentified carnivoran species from the Masoala peninsula of Madagascar

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ABSTRACT

Little is known about carnivoran ecology and population dynamics in northeastern Madagascar, especially on the little studied Masoala peninsula. This leaves the status of threatened carnivores on the Masoala peninsula poorly understood. Even less is known about the relative taxonomic position and role of domestic, feral, and possible wild cats in Madagascar. Adequate conservation of the Masoala peninsula will remain limited until the status, threats, and roles of felines and native carnivorans in regional system dynamics are documented. Six of the ten carnivoran species belonging to the endemic family Eupleridae, as well as introduced civets, domestic dogs, and cats are known to exist on the peninsula. This paper reports an animal of unknown identity in the Masoala carnivoran assemblage, the *fitoaty*. Specifically it, (i) reports preliminary observations on the *fitoaty* collected on the Masoala peninsula, and (ii) describes *fitoaty* distribution and habits based on local knowledge. *Fitoaty* appear to have a broad geographic range on the peninsula and to prefer contiguous forests near and within the Masoala National Park. The author tentatively identifies the *fitoaty* as *Felis* sp. but extensive carnivoran trapping and genetic testing of the *fitoaty* are needed to adequately assess the range and identity of this carnivoran and its potential impact on local ecosystems.

RÉSUMÉ

L'écologie et la dynamique des populations de carnivores du Nord-est de Madagascar sont mal connues, plus particulièrement sur la presqu'île Masoala qui a été peu étudiée. Ce manque de connaissances empêche de statuer sur le degré de menace auquel font face les carnivores de la presqu'île. Il en est de même de la position taxinomique et du rôle écologique des chats domestiques et sauvages à Madagascar. La conservation de la presqu'île Masoala finira par pêcher tant que le statut, les menaces et les rôles des félins et des carnivores autochtones ne seront pas documentés dans la dynamique régionale. Parmi les dix espèces de carnivores appartenant à la famille endémique des Eupleridae, six sont connues de la presqu'île Masoala. La civette allochtone, les chiens domestiques et des chats ont également été recensés sur la presqu'île. Cet article décrit un animal d'une identité inconnue de la communauté des carnivores de la presqu'île Masoala, le *fitoaty*. Plus spécifiquement, il présente l'observation d'un carnivore non identifié par l'auteur d'une part et les résultats d'une évaluation indirecte à travers des enquêtes villageoises portant sur la présence de cet animal sur la presqu'île Masoala, d'autre part. À l'exception de sa grande taille (avec un poids estimé à 3–4 kg), d'une musculature développée, d'un pelage noir uniforme, court et brillant, et de ses yeux rouge-orangé, la morphologie du *fitoaty* rappelle celle d'un chat domestique. Il semblerait que le *fitoaty* serait distribué sur une vaste étendue géographique de la presqu'île Masoala. Contrairement aux chats sauvages rencontrés ailleurs à Madagascar, le *fitoaty* semble préférer les forêts du Parc National de Masoala et de ses environs. Même dans les villages où le *fitoaty* a été vu à de nombreuses reprises, il est considéré comme rare. Le *fitoaty* est provisoirement identifié comme une espèce de félins, à savoir *Felis* sp. mais une appartenance spécifique dépendra des résultats d'un programme de capture des carnivores et du dépistage génétique du *fitoaty* qui permettra également d'évaluer sa distribution et son impact éventuel sur les systèmes locaux. Dans la mesure où la presqu'île Masoala abrite l'un des derniers grands blocs de forêt humide de basse altitude à Madagascar et que les carnivores allochtones sont connus pour leurs impacts négatifs sur les espèces autochtones de Madagascar, il est indispensable de vérifier rapidement ce qu'il en est de l'identité, de la distribution et de l'impact écologique du *fitoaty*.

INTRODUCTION

The Masoala peninsula is home to one of Madagascar's largest and most remote national parks and contains some of the greatest biodiversity within all of Madagascar (Kremen et al. 1999, Kremen 2003). However, the same geographical features that have played a role in protecting the peninsula's biodiversity from anthropogenic disturbances (i.e., its wet rugged terrain, large size, and relative isolation) have also left it poorly studied. The limited knowledge about carnivoran ecology and population dynamics in northeastern Madagascar (Farris et al. 2012, Hawkins 2012) leaves the status of threatened carnivores on the Masoala peninsula poorly understood. Adequate conservation of the peninsula will also remain limited until the status, threats, and roles of carnivores in regional system dynamics are clarified. Six of the ten carnivore species within the endemic family Eupleridae (Yoder et al. 2003), (*Cryptoprocta ferox* [locally known as: *fôsa*, common name: fosa], *Eupleres goudotii goudotii* [*falanoka*, small-toothed civet], *Fossa fossana* [*tombokantsodina*, Malagasy civet], *Galidia elegans* [*vontsira-*

mena, ring-tailed vontsira], *Galidictis fasciata* [*vontsira-fotsy*, broad-striped vontsira], *Salanoia concolor* [*vontsira-tsavoka*, brown-tailed vontsira]), and three introduced carnivorans, (*Viverricula indica* [*jabady*, small Indian civet], *Canis familiaris* [*amboa*, domestic dog], and *Felis catus* [*bosy*, domestic cat]), are known to exist on the peninsula. This paper calls attention to an animal in the Masoala carnivoran assemblage known as the *fitoaty* (Figure 1). The taxonomic identity of the *fitoaty* is currently unknown. It may be a melanistic feral domestic cat (*Felis catus*), a melanistic wildcat (*Felis silvestris*), or a distinct species unique to the region.

Felis were introduced to Madagascar by the 17th century (Flacourt 1658, Kerr 1792). Both domesticated and wild or feral cats exist on the island today, but whether these represent a single species (*Felis catus*) or two (*F. catus* and *F. silvestris*) remains unknown. The relationship of Madagascar's wild living cats to the African wildcat (*Felis silvestris cafra*) is also unknown. Until further genetic research has been completed, there will continue to be great uncertainty about the taxonomic identity of Madagascar's wild living cats.

The morphology of wild living cats in Madagascar has been described as "easily distinguishable from domestic cats" (Brockman et al. 2008: 137). Their pelage is similar to that of wild living cats elsewhere in the world (Goodman et al. 2003; for a description of typical pelage cf. Daniels et al. 1998) and is characterized by an underlying agouti/tawny brown coat with overlying dark grey tabby patterning, a dark banded tail, and lack of variation in coat pattern (Daniels et al. 1998, Goodman et al. 2003, Brockman et al. 2008). They have also been described as larger than domestic cats (both in overall weight, height, and length), and as exhibiting significant sexual dimorphism (males twice as large as females) (Goodman et al. 2003, Brockman et al. 2008). While most wild living cats around the world have tabby coats, some wildcat (*Felis silvestris*) populations in Scotland exhibit a variety of coat patterns including "primarily black" (Daniels et al. 1998: 237). Hybridization with domestic cats may have been responsible for increasing this color variation, but in Madagascar, differences between wild living cat and domestic cat ranging patterns are thought to "segregate the stocks" (Brockman et al. 2008: 137).

FIGURE 1. Artist's rendering drawn from local Malagasy descriptions and confirmed likeness of a *fitoaty*. © Joel Borgerson

Felis inhabit numerous natural habitats and national parks within Madagascar (e.g., Goodman et al. 1993, Dollar et al. 2007, Brockman et al. 2008, Farris et al. 2012, Gerber et al. 2012ab), but these wild living cats may be more common in the arid western half of the country (Goodman et al. 2003). They have been primarily found in secondary, fragmented, or disturbed forests and in wooded grasslands (Dollar et al. 2007, Gerber et al. 2012b), but can range into deeply forested areas or near villages when crossing them in order to access preferred habitat types (Dollar, unpub. data). They have been variously described as: cathemeral (Gerber et al. 2012a); mostly crepuscular or nocturnal, with some diurnal activity (Dollar, unpub. data); or increasing their diurnal activity only when they have litters (Ratsirarson et al. 2001, Brockman et al. 2008).

Felis has been shown to negatively impact endemic Malagasy fauna in many ways. Elsewhere, wild living cats are solitary, and have an opportunistic diet of birds, small-medium sized rodents, small reptiles, and amphibians (Malo et al. 2004, Lozano et al 2006). Censuses in Madagascar show reduced numbers of understory bird and small rodents within wild living *Felis* sp. ranges (Dollar et al. 2007). *Felis* is known to predate large lemurs such as *Lemur catta* and *Propithecus verreauxi*, when these lemurs descend to the ground (Goodman et al 1993, Ratsirarson et al. 2001, Gould and Sauther 2007, Brockman et al. 2008). *Felis* also negatively impact sympatric native Malagasy carnivorans (Gerber et al. 2012a). In the southeast, *Galidia elegans* is negatively correlated with *Felis* abundance, potentially due to interspecific temporal and dietary competition (Gerber et al. 2012ab), and in the northeast *Salanoia concolor* has been found to be absent at sites where wild living *Felis* occur (Farris et al. 2012). *Felis* may also transmit diseases to *Cryptoprocta ferox* (Dollar 2006).

More research on the little known *fitoaty* is needed, as this animal is currently excluded from discussions on Masoala ecology, yet it may have substantial impact on the Masoala ecosystem. The purpose of this paper is to (i) report preliminary observations on the *fitoaty* collected on the Masoala peninsula, and (ii) describe its distribution and habits based on local knowledge.

METHODS

DATA COLLECTION. This study was conducted over five months in 36 villages on the western portion of the Masoala peninsula by the author and her field assistant Rajaona Delox. Two methods were employed: (i) extensive and detailed semi-structured interviews in a single village; and (ii) rapid indirect assessment survey interviews of village presidents over a broad geographic range.

Single Site Interviews: The author has been working in the region since 2007 and speaks the native dialect of Betsimisaraka. Semi-structured interviews of at least one individual from 100 % of households (n = 32) in the village of Ambodiforaha (population 118) were used, where the author first saw the *fitoaty*.

Interviewees were shown photographs of all known Masoala carnivorans and asked if they: (1) were aware of an animal called *fitoaty*; (2) had ever caught/eaten, or would potentially eat one; (3) if they had or would not, to explain why; (4) if they had ever seen one personally; and if yes, to describe (5) the morphology of the animal; and (6) the location, time, and circumstances of their sighting.

Rapid Indirect Assessment: Village presidents of all known communities bordering the western edge of the Masoala National Park (n = 36) were interviewed by R. Delox, a trained and experienced field assistant native to the peninsula. Interviewees were asked the full set of questions that the author asked about *fitoaty* at single site interviews, as well as the number of villagers who had seen the *fitoaty*. These quick coarse-grain preliminary data were collected to estimate the *fitoaty*'s potential range and may not reflect actual abundance. Village locations, altitude, and population size were also recorded.

DATA ANALYSIS. The relationships between the percentage of people in a community who had seen a *fitoaty* and village characteristics were examined using a Pearson correlation matrix. Percentages were selected over the raw number of villagers to control for the possibility that larger communities may have more people who have seen the *fitoaty* simply because of their size. Four variables were examined as potential predictors of the number of villagers who had seen *fitoaty*: (1) village distance from the Masoala National Park; (2) village distance from the ocean (Antongil Bay); (3) village altitude; and (4) village population size. Village distance from the Masoala National Park was ranked from 1–3, 1 = inside the park, 2 = adjacent to the park (≤ 2 km), and 3 = not adjacent to the park (> 2 km). Two kilometers from the park was selected because this distance is easily travelled to and from by villagers on the Masoala before returning home for a meal (typical practice). Village distance from the ocean was ranked from 1–3, 1 = on the coast, 2 = ≤ 5 km from the coast, and 3 = > 5 km from the coast. Village altitude was ranked from 1–3, 1 = < 400 m above sea level , 2 = 400–700 m a.s.l, and 3 = > 700 m a.s.l.

These four predictor variables were selected because they can be remotely determined with ease by future researchers when determining where to conduct extensive surveys or research on the *fitoaty*. Village distance from the Masoala National Park and the Antongil Bay, population size, and village altitude may also provide preliminary information on *fitoaty* habitat constraints, tolerance for anthropogenic activity and/or disturbance, and/or patterns in *fitoaty* range.

RESULTS

In 2011 the author witnessed a medium-sized melanistic carnivoran crossing a village trail just outside the Masoala National Park boundary. The sighting occurred at approximately 15:00h, in a transitional area of primary and secondary forest, ~1.2 kilometers south of the remote village of Ambodiforaha (at approximately E049°57'35'', S15°43'26''). Further investigation and interviews of local people in 36 villages within the western half of the Masoala peninsula confirmed the existence of a black *Felis* like carnivoran. The animal is widely known throughout the western half of the peninsula, and is called *fitoaty* in the regional dialect of Betsimisaraka Malagasy.

Local people describe *fitoaty* morphology as feline. It is approximately 3–4 kg in size, muscular, lean, with a uniform, short, glossy black pelage. This description is consistent with the author's sighting. It is said to have red-orange eyes. There is apparently a widespread population of this animal on the peninsula, yet its specific taxonomic identity and ecological impact is unknown and requires further investigation.

SINGLE SITE INTERVIEWS. Ninety-four percent of interviewees had heard of an animal called the *fitoaty* and 22 % had seen the animal. The number of sightings per participant ranged from 1–3; sightings occurred 1–25+ years prior to the interview. All were of single animals traveling during daylight. *Fitoaty* have been seen in both remote undisturbed forests and in fragmented forests, but never in or near the village. Most sightings were of the *fitoaty* running across or near a forest trail. Interviewees consistently described *fitoaty* morphology as 'domestic cat-like', with the exception of (1) its larger size, estimated at 3–4 kg, (2) its greater muscularity and leaner build, (3) its uniformly short glossy pelage of solid deep black, and (4) its red-orange eyes. Even people who had repeatedly seen the *fitoaty* considered it rare.

Fitoaty meat is reported to be *mahimbo* (having bad smell). No one interviewed had ever eaten *fitoaty* and 88 % claimed unwillingness to eat the animal, even if they caught it, either because of personal preference or *fady* (complex familial or individual taboo). When asked to explain their disinclination to eat the animal, interviewees described the *fitoaty*'s physical similarity to a domestic cat and the inedibility of the meat (believed to be either poisonous or sickening). Trappers do not build traps to catch *fitoaty* and believe that *fitoaty* outsmart existing carnivore traps targeting the similarly-sized *Fossa fossana* and *Viverricula indica*. Only one trapper reported knowing someone (deceased) who had inadvertently caught the animal.

One participant reported that fifteen years ago, near his remote forest home, *fitoaty* would steal chickens from his land to feed its young. He found a *fitoaty* with four young in a *lalogno* tree hole filled with dried brush two meters above the ground. Throughout the day, the *fitoaty* brought birds (including a *Streptopelia picturata* [*domóhina*, Madagascar turtle dove] and a *Centropus toulou* [*monjo*, Madagascar coucal]) to the tree hole.

RAPID INDIRECT ASSESSMENT. Presidents of 15 of the 36 villages surveyed reported at least one member of their village who had seen a *fitoaty* (Figure 2). Eighty-six individuals were reported to have seen the animal (range = 2–15 individuals per village). Descriptions of the *fitoaty* were consistent with those provided by single-site interviewees. Even in villages where sightings had occurred, they were relatively rare, only 1–20 % of the villagers having seen the animal. *Fitoaty* sightings are not significantly correlated with village size ($r = -0.09$, $P = 0.62$), distance from the ocean ($r = -0.53$, $P = 0.76$), or village altitude ($r = 0.27$, $P = 0.12$). While *fitoaty* were seen by individuals in villages surrounded by both fragmented and primary forests, the percentage of individuals in each village reported to have seen a *fitoaty* was significantly negatively correlated with village distance from the Masoala National Park ($r = -0.39$, $P = 0.018$).

DISCUSSION

This is the first report of a feline-like animal, locally known as the *fitoaty*, on the Masoala peninsula. The name *fitoaty* means seven livers, and originates from a story of a man who unintentionally snared the animal, and upon processing it, discovered seven livers. However, snare trappers interviewed do not actually

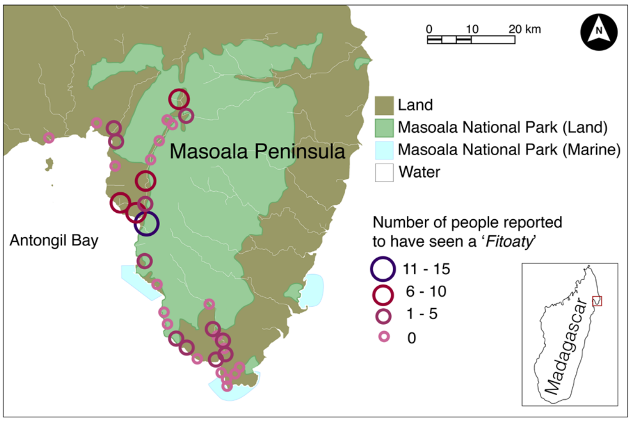

FIGURE 2. Rapid indirect assessment of *fitoaty* sightings on the Masoala peninsula.

believe that *fitoaty* have seven livers and *fitoaty* are currently not hunted or consumed on the peninsula.

Neither *fitoaty* eye color nor pelage matches that of previously described wild living cats in Madagascar (e.g., Goodman et al. 2003, Brockman et al. 2008). Among mammals elsewhere, the genetic material for different coat patterning often exists, but can be masked (Cieslak et al. 2011). It is possible that the *fitoaty*'s unique coloration is due to a mutant or recessive allele already present in wild living cats, that has either been selected for on the peninsula, or fixed through genetic drift and reduced gene flow. The taxonomic identity of this animal is currently unknown. It may be a melanistic feral domestic cat, melanistic wildcat, or a distinct species unique to the region. Genetic testing is needed to determine the taxonomic identity of this, likely *Felis* sp. in the Masoala, and to clarify the identity of other *Felis* throughout Madagascar. Rigorous methods are also needed to establish the presence or absence of the *fitoaty* throughout the Masoala, and their potential impact on native species.

Unlike wild living cats elsewhere in Madagascar who have been shown to prefer secondary, fragmented, or disturbed forests and wooded grasslands (Dollar et al. 2007, Gerber et al. 2012b), *fitoaty* were most often seen close to the Masoala National Park. This may indicate a relatively low tolerance for forest disturbance and a significant presence of *fitoaty* within the park. Whatever its identity, the *fitoaty* has an unknown impact on the species protected within the Masoala National Park, Madagascar's last remaining lowland coastal rainforest. Considering the Masoala's unique role in Madagascar (summarized in Kremen et al. 1999, Kremen 2003), and the known negative impact of introduced carnivorans on Madagascar's native birds and rodents (Dollar et al. 2007), lemurs (Goodman et al 1993, Ratsirarson et al. 2001, Gould and Sauther 2007, Brockman et al. 2008), and carnivorans (Dollar 2006, Farris et al. 2012, Gerber et al. 2012b), the identity, range, and ecological impacts of the *fitoaty* warrant swift examination. Hopefully, this study will motivate such research.

ACKNOWLEDGMENTS

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SHORT NOTE

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Étude des impacts écologiques du dynamisme spatio-temporel des habitats naturels sur la faune menacée du Complexe Zones Humides Mahavavy-Kinkony, Madagascar

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RÉSUMÉ

Cette recherche menée dans le Complexe Zones Humides Mahavavy-Kinkony a pour but d'évaluer les impacts écologiques du changement des habitats naturels sur les espèces menacées de sa faune. Des outils tels que le SIG, la télédétection ainsi que Marxan ont été combinés avec les études bibliographiques et les travaux de terrains pour (i) identifier les habitats naturels prioritaires pour la faune menacée du site, (ii) évaluer leur changement entre 1950 et 2005, (iii) déceler les causes du changement, (iv) élaborer une prospective des changements en 2050 et (v) évaluer les impacts du changement. Le changement des habitats naturels s'est déroulé au cours des temps mais il n'a pas été assez important au niveau global du site pour transformer radicalement les occupations du sol. Toutefois, le recul des phragmitaies du lac Kinkony et des forêts de Tsiombikibo et de Marofandroboka menace les espèces qui en dépendent. Le suivi du delta de Mahavavy doit être poursuivi et intensifié pour évaluer les menaces qui pèsent sur lui dans le contexte des changements climatiques. La situation de la forêt d'Andohaomby est préoccupante et son avenir menacé en l'absence d'actions concrètes. L'analyse de vulnérabilité à l'érosion du bassin du Kinkony a démontré que les changements physico-chimiques dus à l'érosion dans les quatre bassins au Sud du lac rendent nécessaires des aménagements anti-érosifs. Parmi les espèces de la faune vertébrée, *Amaurornis olivieri*, *Propithecus coronatus* et *Paretroplus dambabe* sont les espèces les plus affectées globalement, mais au niveau du site *Propithecus deckeni*, *Paretroplus kieneri* et *Erymnochelys madagascariensis* sont tout aussi vulnérables. *Pteropus rufus* et *Rousettus madagascariensis* seraient les espèces les mieux protégées.

ABSTRACT

This study of the Mahavavy-Kinkony Wetland Complex (MKWC) assesses the impacts of habitat change on the resident globally threatened fauna. Located in Boeny Region, northwest Madagascar, the Complex encompasses a range of habitats including freshwater lakes, rivers, marshes, mangrove forests, and deciduous forest. Spatial modelling and analysis tools were used to (i) identify the important habitats for selected, threatened fauna, (ii) assess their change from 1950 to 2005, (iii) detect the causes of change, (iv) simulate changes to 2050 and (v) evaluate the impacts of change. The approach for prioritising potential habitats for threatened species used ecological science techniques assisted by the decision support software Marxan. Nineteen species were analysed: nine birds, three primates, three fish, three bats and one reptile. Based on knowledge of local land use, supervised classification of Landsat images from 2005 was used to classify the land use of the Complex. Simulations of land use change to 2050 were carried out based on the Land Change Modeler module in Idrisi Andes with the neural network algorithm. Changes in land use at site level have occurred over time but they are not significant. However, reductions in the extent of reed marshes at Lake Kinkony and forests at Tsiombikibo and Marofandroboka directly threaten the species that depend on these habitats. Long term change monitoring is recommended for the Mahavavy Delta, in order to evaluate the predictions through time. The future change of Andohaomby forest is of great concern and conservation actions are recommended as a high priority. Abnormal physicochemical properties were detected in lake Kinkony due to erosion of the four watersheds to the south, therefore an anti-erosion management plan is required for these watersheds. Among the species of global conservation concern, Sakalava rail (*Amaurornis olivieri*), Crowned sifaka (*Propithecus coronatus*) and *dambabe* (*Paretroplus dambabe*) are estimated the most affected, but at the site level Decken's sifaka (*Propithecus deckeni*), *kotsovato* (*Paretroplus kieneri*) and Madagascan big-headed turtle (*Erymnochelys madagascariensis*) are also threatened. Local enforcement of national legislation on hunting means that MKWC is among the sites where the flying fox (*Pteropus rufus*) and Madagascan rousette (*Rousettus madagascariensis*) are

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well protected. Ecological restoration, ecological research and actions to reduce anthropogenic pressures are recommended.

INTRODUCTION

Les différents écosystèmes de Madagascar ont été affectés par des changements au cours de l'histoire récente (Ricklefs et Miller 1999) que nous appelons « Dynamisme ». Le dynamisme anthropique récent affecte la viabilité des écosystèmes et menace également la pérennité des ressources naturelles d'une région, en mettant ainsi en péril son développement économique. Il est ainsi essentiel de le comprendre afin de pouvoir gérer ses effets dans le temps et dans l'espace.

La gestion des changements, qui se manifestent presque toujours par la dégradation des ressources naturelles, peut assurer le développement d'une région déterminée (FIDA 2001). Le cas du Complexe Zones Humides Mahavavy-Kinkony (connu comme CZHMK et appelé Complexe Mahavavy-Kinkony dans le reste du texte) au Nord-ouest de Madagascar, dans la région Boeny, a été choisi comme site pilote pour mener cette recherche de par la richesse de sa biodiversité et son potentiel en matière de développement économique (Rabenandrasana et al. 2007, BirdLife International et Asity Madagascar 2009, Andriamasimanana et Rabarimanana 2011, Ramsar 2012).

La cible de cette étude est la biodiversité. Seules les espèces menacées de la faune vertébrée ont été prises en compte pour constituer l'échantillon d'espèces représentatives de l'ensemble de la biodiversité de la région. Ce choix repose sur l'hypothèse impliquant qu'en protégeant les espèces les plus menacées, toutes les autres espèces de la région profiteraient également de cette protection (Roberge et Angelstam 2004). L'objectif est de chercher à comprendre comment les habitats naturels des espèces de la faune menacée dans la région évoluent au cours du temps et quelles sont les causes et les impacts de leur évolution. L'information récoltée servira aux décideurs de la région afin qu'ils puissent adopter les bonnes stratégies pour assurer une gestion pérenne des ressources naturelles. Pour atteindre cet objectif, nous avons (i) identifié les habitats naturels prioritaires pour la faune menacée du site, (ii) évalué leur dynamisme entre 1950 et 2005, (iii) recherché les causes de ce dynamisme, (iv) proposé une prospective des changements en 2050 et (v) évalué les impacts de ce futur dynamisme.

MÉTHODOLOGIE

La hiérarchisation des habitats naturels des espèces menacées a été réalisée de façon automatique et logique grâce au programme Marxan (Ball et al. 2009). La lecture des rapports d'inventaire biologique et des rapports de suivi écologique disponibles au niveau du Programme de BirdLife à Madagascar a permis de disposer de points d'observation pour les 19 espèces cibles appartenant aux groupes des oiseaux, des primates, des chauve-souris, des poissons et des reptiles du complexe Mahavavy-Kinkony.

Pour procéder à l'analyse, la région d'étude a été divisée en unités de planification de forme carrée de 625 m de côté. La distribution des espèces cibles a ensuite été cartographiée sur la couche d'unités de planification. L'objectif de conservation a été fixé à au moins 25 % des habitats pour toutes les espèces cibles et pour chaque unité de planification. Une autre couche portant sur le coût de la conservation a été élaborée à partir de la couche des unités de planification. Les coûts ont été définis de manière à ce que les unités de planification ne présentant que des habitats naturels comme des forêts, des lacs, des rivières ou des mangroves aient des coûts plus bas. Plus les unités de planification présentaient des habitats dégradés comme la forêt dégradée ou les zones herbeuses, plus le coût était élevé. Le dernier fichier nécessaire pour exécuter Marxan définissait la longueur des limites. Un coefficient 1 à été attribué à cette limite lorsque les unités de planification étaient adjacentes afin de favoriser des solutions compactes.

Marxan été programmé pour faire 100 exécutions avec un million d'itérations. Comme l'algorithme a une composante de randomisation, de multiples configurations ont été identifiées lors de chaque exécution. Les interprétations utilisent les valeurs en pourcentage de l'unicité de chaque unité de planification. Les résultats identifient le nombre de fois qu'une unité de planification a été choisie au cours des 100 exécutions. Plus une unité de planification se rapproche de la valeur 100, plus elle est précieuse et donc irremplaçable. L'analyse a été menée pour savoir quelle proportion de la zone d'occupation de chaque espèce menacée était incluse dans la solution Marxan.

Pour évaluer le dynamisme à l'échelle du site entre 1950 et 2005, les données topographiques des cartes FTM de 1949 ont été numérisées. Les images satellite géoréférencées et corrigées géographiquement prises par Landsat en juillet 1973 à une résolution de 60 m, en septembre 1999 et en avril 2005 à une résolution de 30 m ont été utilisées pour estimer l'évolution et la tendance des changements dans le temps ainsi que pour élaborer une prospective des changements en 2050. La méthode suivie fut celle de la classification supervisée, méthode basée sur la connaissance préalable des occupations du sol du site de recherche (Bouveyron et Girard 2009). Des sites d'entrainement ont alors été libellés dans les zones les mieux connues des images géoréférencées. L'occupation du sol d'après les images de 2005 a été validée avec les points de référence relevés sur le terrain des habitats naturels prioritaires pour la faune menacée du site. L'indice Kappa (Gwet 2002) a été utilisé pour vérifier la similarité entre les résultats du traitement des images satellitaires et les habitats naturels de la faune sur le terrain. Les analyses ont été réalisées à deux niveaux, sur le site d'abord puis au niveau de chaque habitat naturel prioritaire identifié.

Les points d'occurrence des cibles de conservation ont été placés sur la carte validée d'occupation du sol, et réalisée à partir des traitements des images satellitaires de 2005. Les aires d'occupation ainsi modélisées ont été confirmées par les biologistes travaillant dans le programme de BirdLife International à Madagascar. Les aires d'occupation des espèces constituent les données de base essentielles pour le processus du programme Marxan.

La prospective a utilisé l'outil de modélisation du changement d'occupation du sol de l'Idrisi Andes (Eastman 2006). Il s'agissait de faire un essai de modélisation entre 1973 et 2005, dates au cours desquelles les occupations du sol étaient connues. La prospective de l'occupation du sol en 2005 a été soumise à des tests statistiques et comparée à l'occupation réelle des sols à cette date. Les facteurs déterminant les changements ont été identifiés lors de cette étape, en se basant notamment sur les références bibliographiques et les observations de terrain. La performance de la prospective de l'occupation a été estimée. La prospective de l'occupation du sol en 2005 et la réelle occupation du sol en 2005 ont été croisées pour estimer la valeur de l'association V' de Cramer (Cramér 1999) ainsi que la valeur de similarité Kappa (Carletta 2004) entre les deux images.

Pour évaluer la performance du modèle prospectif, nous l'avons testé avec le module ROC ou *Relative Operating Characteristic* (Paladino et Pontius 2004) jusqu'à obtention de valeurs satisfaisantes. Si de telles valeurs ne pouvaient être obtenues, les facteurs de changement ont été modifiés avant de répéter le processus. La chaîne de Markov (Eastman 2006) a été utilisée pour modéliser l'occupation du sol.

La méthode adoptée pour évaluer la vulnérabilité des espèces face au changement repose sur une théorie de la diversité spécifique : la relation entre une espèce et son domaine vital selon l'équation $S = c.A^z$, dans laquelle 'S' est le nombre d'espèces, 'A' la surface, et 'c' et 'z' sont des constantes. La constante 'c' représente le nombre d'espèces dans la plus petite zone d'échantillonnage, et 'z' la pente de la droite dans un espace log-log formé par le nombre d'espèces (Preston 1962). La valeur de l'exposant z est approximativement égale à 0,25 qui est une valeur généralement retenue pour les taxons insulaires ; le nombre d'espèces augmente avec la taille de la zone échantillonnée (Borda-de-Água et al. 2002). En interprétant cette théorie, nous avons admis que la probabilité de présence d'une espèce dans un espace donné diminue avec la taille de cet espace et la probabilité de présence de chaque espèce augmente avec la surface de son habitat (Connor and McCoy 1979). Lorsque nous considérons un habitat spécifique à une espèce, si cet habitat disparaissait, l'espèce qui en dépend tendra à disparaître et deviendrait ainsi vulnérable, tout en réduisant la diversité du site. L'analyse a ainsi consisté à comprendre comment les habitats avaient évolué dans le temps et dans l'espace et quelles espèces les utilisent. Les espèces qui dépendent d'habitats en cours de disparition sont les espèces vulnérables qui ont tendance à disparaître.

Six facteurs ont été utilisés pour modéliser la carte potentielle de transition entre l'état de la forêt en 1973 et celui de 1995. Ils ont été catégorisés entre facteurs statiques et dynamiques. Les facteurs statiques, qui ne changent pas au cours des temps, sont les distances par rapport aux rivières et des pentes du relief. Les facteurs dynamiques, qui changent au cours des temps, sont les distances par rapport aux zones d'habitation, des routes ou pistes praticables ou encore l'interpolation de la population par unité administrative (*fokontany*). La distance des changements entre 1973 et 1995 a aussi été créée. Cette couche d'informations inclut tous les autres facteurs de changements locaux.

RÉSULTATS

L'interprétation des images de 2005 a permis de distinguer sept classes d'habitat, dont la forêt dense sèche (37 %), une formation herbeuse (26 %), des zones humides continentales (18 %), la mangrove (4 %), le sable (7 %), des zones de culture (7 %) et le tan (1 %). La surface totale de la zone de recherche est de 299 000 ha.

La solution finale du programme Marxan a été superposée sur les occupations de sol du complexe Mahavavy-Kinkony en 2005. Les occupations de sol importantes pour la faune sont la forêt, la mangrove et la zone humide. Plus particulièrement les forêts de Tsiombikibo, de Marofandroboka, d'Antsilaiza, d'Anjohibe et d'Andohaomby, la mangrove du delta de la Mahavavy et de Marambitsy, le lac Kinkony abritant une phragmitaie et le lac Tsiambarabe (Figure 1). Avec les 363 points de référence, le test statistique a donné une valeur de l'indice de Kappa positive de 0,78 pour la forêt, 0,22 pour la mangrove, et de 0,60 pour le plan d'eau. En retenant ces habitats en priorité, les valeurs de l'unicité de Marxan variaient de 35 à 98 % avec une valeur moyenne globale de 70 %.

Au niveau du site, des analyses statistiques ont donné une valeur V de Cramer de 0,57 entre 1973 et 2005. La valeur positive de l'indice de Kappa était de 0,61. Les analyses au niveau de chacun de ces habitats ont montré que les habitats naturels prioritaires pour la faune menacée avaient diminué en superficie, en particulier les phragmitaies du lac Kinkony et les forêts d'Andohaomby, de Marofandroboka et de Tsiombikibo. D'autres habitats se sont étendus comme les forêts d'Anjohibe et d'Antsilaiza. Les habitats qui ont gardé la même superficie sont les mangroves de Marambitsy et de Mahavavy (Tableau 1). Avec un intervalle de confiance de 95 % et un degré de liberté de 7, la valeur du test t de Student effectué sur la différence entre les surfaces des habitats prioritaires en 1949 et 2005 est de 0,76, bien inférieure à celle de la table de distribution qui est de 2,37 et qui a permis de conclure une différence non significative avec une erreur acceptée de 5 %.

Les changements de chaque habitat ont été corrélés avec le temps (en année) pour considérer l'évolution temporelle. Les forêts d'Anjohibe et de Tsiombikibo ont les valeurs maximales, des coefficients de corrélation 0,90 et -0,87 respectivement, suivies des forêts d'Andohaomby et de Marofandroboka avec des coefficients avoisinant -0,60. La forêt d'Antsilaiza et les mangroves de Mahavavy et de Marambitsy avaient des valeurs inférieures à 0,4. Les changements des forêts d'Anjohibe, d'Antsilaiza et la mangrove de Marambitsy étaient en corrélations positives avec le temps. Ceux des forêts de Tsiombikibo, d'Andohaomby, de Marofandroboka et la mangrove de Mahavavy étaient en corrélations négatives avec le temps (Tableau 1).

La distance des changements entre 1973 et 1995 a atteint un taux d'exactitude de 100 % avec 872 itérations. La carte de transition élaborée a été utilisée pour proposer une prospective de la couverture de la forêt en 2005 qui, cartographiée, a été validée avec la carte forestière extraite du traitement d'images satellites de 2005. La valeur de la caractéristique de *Relative Operating Characteristic* par le test de validation de 0,87 a été

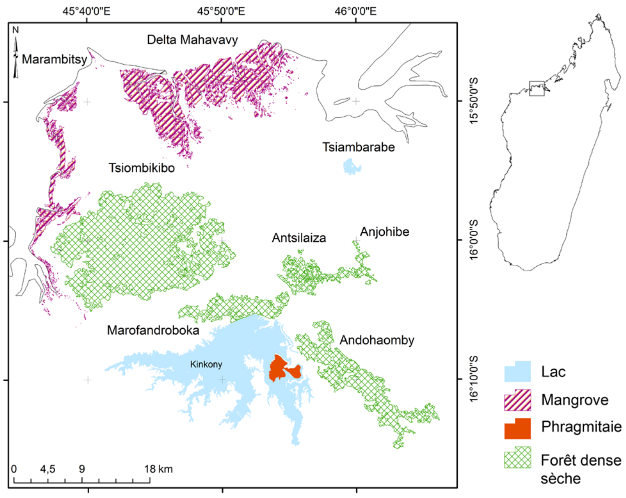

FIGURE 1. Les habitats prioritaires pour la faune menacée du complexe Mahavavy-Kinkony.

TABLEAU 1. Évolution dans le temps des superficies des trois habitats naturels considérés dans le complexe Mahavavy-Kinkony.

		Superficie (ha)		
Type d'habitat	Localité	1949	2005	2050
Mangrove	Delta Mahavavy	15,310	14,960	12,030
	Marambitsy	2,490	2,700	2,110
	sous total	17,800	17,660	14,140
Phragmitaie	Lac Kinkony	540	70	
Forêt sèche	Andohaomby	9,740	7,750	4,330
	Tsiombikibo	27,960	23,490	20,730
	Marofandroboka	5,800	3,430	3,170
	Anjohibe	290	760	700
	Antsilaiza	2,370	2,650	1,970
	sous total	46,160	38,080	30,900
	TOTAL	64,500	55,810	45,040

jugé satisfaisant (Pontius et al. 2000). La même carte de transition a été utilisée par le programme pour construire la carte prospective en 2050.

Les forêts d'Andohaomby et d'Antsilaiza seraient les plus menacées avec une diminution de leur superficie d'environ 44 % et 26 % respectivement en 2005. La forêt de Tsiombikibo a été réduite de 12 %, celles d'Anjohibe et de Marofandroboka de près de 7,5 %. Les deux mangroves du complexe Mahavavy-Kinkony pourraient perdre 20 % de leur superficie pour le Delta de Mahavavy et 22 % pour Marambitsy. La surface de la forêt d'Anjohibe a presque triplé entre 1945 et 2005 alors que celle d'Antsilaiza n'a augmenté que de 11 %. (Tableau 1).

DISCUSSION

Le test de validité entre les points de référence obtenus sur le terrain et l'occupation du sol montre des indices de Kappa élevés et positifs indiquant une bonne attribution des classes pour la forêt et le plan d'eau à partir des images satellitaires. Les différences entre des valeurs trouvées (0,78 pour la forêt et 0,60 pour le plan d'eau) et la concordance parfaite (1,0) pourraient être expliquées par une erreur d'interprétation des images par le logiciel de traitement mais aussi par les changements d'occupation du sol entre la date de la prise de vue de l'image (2005) et la date à laquelle la vérité terrain a été effectuée (2008). Néanmoins, les bonnes concordances indiquent une interprétation fiable des images pour ces deux classes. L'indice assez bas obtenu pour la mangrove est expliqué par la difficulté d'accéder à ce milieu sur le terrain.

L'extension des forêts d'Anjohibe et d'Antsilaiza pourrait s'expliquer par la faible valeur agricole des terres de la région et l'éloignement des centres urbains, de sorte qu'un corridor a fini par relier ces deux forêts.

La forte corrélation négative avec le temps de la forêt de Tsiombikibo indique que *Propithecus deckeni* pourrait devenir encore plus vulnérable dans un avenir proche au niveau du complexe Mahavavy-Kinkony. En observant les résultats de la prospective des changements au niveau du site, la forêt d'Andohaomby serait la forêt la plus menacée. En revanche, deux espèces de chauve-souris, *Pteropus rufus* et *Rousettus madagascariensis,* seraient favorisées par le changement positif des forêts d'Antsilaiza et d'Anjohibe. Le principal changement au niveau des forêts est le résultat d'une agriculture traditionnelle sur brûlis appelée « hatsaka » et au prélèvement par les villageois qui exploitent le bois de chauffe et d'autres bois.

La mangrove du complexe Mahavavy-Kinkony ne semble pas souffrir de la pression anthropique dans l'état actuel, fait qui est vraisemblablement en relation avec la capacité de dispersion et d'avancée sur la mer de ce type de forêt. Il convient cependant de suivre l'évolution de la mangrove avec l'élévation du niveau de la mer annoncée par le changement climatique global (Barber et al. 2004). Les oiseaux d'eau menacés, hormis *Amaurornis olivieri*, pourraient profiter de l'avancée de la mangrove.

Le changement du lac Kinkony est davantage d'ordre physico-chimique (Andriamasimanana et Rabarimanana 2011). La réduction considérable de sa phragmitaie résulte des feux incontrôlés et de la conversion des marais en rizières. La phragmitaie est l'unique habitat d'*Amaurornis olivieri* qui en dépend aussi pour la nidification, sa disparition entrainerait la disparition de ce râle endémique. La végétation flottante du lac Kinkony est aussi une zone de frai pour le poisson *Paretroplus dambabe* (BirdLife International Madagascar Programme 2006). La diminution de ce type de végétation toucherait alors l'écologie du poisson en perturbant sa reproduction. L'espèce de tortue aquatique *Erymnochelys madagascariensis* utilise en revanche les embouchures au sud du lac Kinkony (Andriamazava 2005). Les agriculteurs opérant dans ces zones du lac pratiquent la culture du riz en suivant la décrue des eaux sur les rives du Kinkony, pratique qui fait reculer le plan d'eau. Les surfaces occupées par la riziculture avancent ainsi chaque année. La diminution du plan d'eau avec la forte turbidité constituerait une réelle menace pour ce reptile aquatique (Andriamasimanana et Rabarimanana 2011). Les effets combinés du changement qualitatif et quantitatif pourraient être néfastes aux espèces qui en dépendent.

L'approche développée ici pour établir une prospective de changement des habitats naturels a été basée sur les facteurs identifiés dans le passé et suppose que les contextes socio-économiques de la région resteraient stables. La prospective dévierait nettement s'il y avait de profonds changements dans les stratégies de développement régional. Il s'agirait en particulier des grands projets d'exploitation minière ou pétrolière qui modifieraient considérablement les données socio-économiques de la région.

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MATÉRIEL SUPPLÉMENTAIRE.
DISPONIBLE EN LIGNE UNIQUEMENT.

TABLEAU S1. Répartition des espèces menacées dans les habitats naturels prioritaires du Complexe Zones Humides Mahavavy-Kinkony, Madagascar.

ESSAY

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Madagascar's nascent locally managed marine area network

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ABSTRACT

Since 2004, the creation of locally managed marine areas (LMMAs) in Madagascar has exponentially increased, highlighting the need for improved information sharing between communities and between support organizations. Until recently, however, these LMMAs operated in relative isolation, with little communication or coordination between LMMA community associations. Madagascar's first national LMMA forum was held to address this need in June 2012 in the village of Andavadoaka, on Madagascar's southwest coast. The forum brought together 55 community members from 18 LMMAs throughout Madagascar, representing a total of 134 villages. A principle outcome of this meeting was the formation of a national LMMA network named MIHARI, a Malagasy acronym that translates into 'local marine resource management'. The nascent MIHARI network is an informal network that was inspired by the success of the LMMA Network in the Indo-Pacific region. MIHARI aims to facilitate peer-to-peer learning amongst coastal communities, improve communication, raise the profile and expand the use of the LMMA approach and serve as a unified lobbying platform for the interests of Madagascar's traditional fishers. The creation of MIHARI represents a significant development towards uniting community-led approaches to conservation in Madagascar and highlights the significant role LMMAs can play in marine conservation on a national scale. This is of particular significance in Madagascar, a country with little capacity or financial resources to oversee large-scale marine conservation efforts, a problem compounded by both the vast coastline and geographical isolation of many fishing communities. Madagascar's new LMMA network is leading the way for coastal community conservation in the western Indian Ocean and aims to serve as the basis for a wider regional LMMA network.

RÉSUMÉ

Depuis 2004, la mise en place d'Aires Marines Gérées Localement (AMGL) à Madagascar suit une augmentation exponentielle, soulignant la nécessité d'améliorer le partage d'informations entre les communautés et les organisations partenaires. Néanmoins, jusqu'à récemment, ces AMGL opéraient de façon isolée en ne profitant que d'une faible communication ou coordination entre les différentes AMGL et les associations communautaires. Afin de combler ce besoin, le premier forum national sur les AMGL à Madagascar s'est tenu en juin 2012 dans le village d'Andavadoaka. Le forum a rassemblé 55 représentants de communautés provenant de 18 AMGL différentes de Madagascar, représentant un total de 134 villages. Un des aboutissements phares de ce rassemblement fut la création d'un réseau national d'AMGL, dénommé MIHARI, un acronyme malgache qui se traduit par 'gestion locale des ressources marines'. Ce réseau naissant MIHARI est un réseau informel qui s'inspire du succès de son homologue dans la région Indo-Pacifique. MIHARI a pour objectif de faciliter l'enseignement entre pairs au sein des communautés côtières, d'augmenter la communication, d'accroitre la visibilité, d'encourager et de faciliter le recours à l'approche AMGL et de servir de plateforme commune de lobby dans l'intérêt des pêcheurs traditionnels de Madagascar.

La création de MIHARI représente un développement conséquent en vue de l'unification des approches communautaires pour la conservation à Madagascar, et met en lumière le rôle important que jouent les AMGL dans le domaine de la conservation marine à l'échelle nationale. Cela a une importance primordiale à Madagascar, un pays où les ressources en termes de capital et de compétences sont insuffisantes pour la supervision d'initiatives de conservation marine à grande échelle ; une problématique elle-même exacerbée par l'étendue des zones côtières et l'isolation géographique de nombreuses communautés de pêcheurs. Le nouveau réseau d'AMGL de Madagascar fait figure de chef de file pour la conservation communautaire dans l'océan Indien et compte bien servir de socle pour un réseau AMGL régional.

LOCALLY MANAGED MARINE AREAS

Fishing communities have been managing marine resources in a number of ways for hundreds of years. However, in recent decades traditional fisheries (sensu FAO No date) around the world have come under increasing pressure from the effects of both indirect and direct threats, such as global climate change (Cinner et al. 2012), population growth (Harris et al. 2012) and overfishing (Harris 2011). The result has been that fishing communities are finding that once abundant resources are dwindling. Locally managed marine areas (LMMAs) have emerged as effective solutions to challenges of small-scale fishery management in tropical low-income countries (Govan et al. 2008, Obura and Samoilys 2011). LMMAs are defined as "areas of near-shore waters and coastal resources that are largely or wholly managed at a local level by the coastal communities, land-owning groups, partner organisations, and/or collaborative government representatives who reside or are based in the immediate area" (Govan et al. 2008: 2). The main impetus for the creation of LMMAs is a "community desire to maintain or improve livelihoods, often related to perceived threats to food security or local economic revenue" (Govan 2009: 86).

Using LMMAs, communities are able to tailor and blend traditional and modern management practices to best suit their needs (Govan 2009). This community-based approach has proven to be a cost-effective, resilient and a more socially acceptable alternative to traditional top-down management of natural resources in places such as southwest Madagascar (Harris 2007). In addition, LMMAs have shown promise at addressing coastal poverty and issues of food security by mitigating overfishing and implementing temporary and permanent reserves (Govan 2009, Obura and Samoilys 2011). Although Govan (2009) suggests caution when implementing income-generating projects within LMMAs and cite a lack of evidence of success, some LMMAs have succeeded in incorporating supplementary livelihoods projects, such as aquaculture farms (Robinson and Pascal 2009, Harris 2011). The LMMA approach also places community members at the forefront of decision-making, ensuring that those who are most affected by conservation decisions are responsible for those choices and the subsequent enforcement of any resource regulation (Gutiérrez et al. 2011). This means LMMAs also build institutional capacity through developing managerial and problem solving skills in community leaders, thus improving local adaptability to climate change. The LMMA approach ensures greater incentive and support for conservation projects than traditional top-down approaches (Obura and Samoilys 2011) by utilising local management structures that better understand the nuanced relationship between marine resource users and their environment.

Communities and their supporting non-governmental organisation (NGO) partners have created thriving national and regional networks in the Indo-Pacific region; over 600 villages participate in 420 LMMAs (Tan and Parras 2011), collectively known as the LMMA Network. This network has proved invaluable for information sharing and scaling up of the LMMA approach and has provided inspiration for the further expansion of LMMAs as a resource management tool.

THE EXPANSION OF LMMAS IN MADAGASCAR

Sustainable fishery management in Madagascar is a key development priority and vital to ensuring food security for coastal communities (Le Manach et al. 2012). Marine fisheries contribute 7 % of GDP and 20 % of export earnings and play a significant role in food security and job creation (FAO 2008). Additionally, the sea plays a central role in the cultural heritage of geographically isolated, traditional fishing communities along Madagascar's 5,500 km coastline. However, Madagascar is politically volatile and economically unstable (Ploch and Cook 2012, Randrianja 2012a, b), with decreasing indicators of social well-being (World Bank 2011) and inadequate capacity and financial resources to effectively oversee complete management of its traditional fisheries (Harris 2011). Community-based conservation is often the most effective substitute for, or supplement to, national fisheries management. Furthermore, it builds heavily upon Madagascar's goal, known as former President Marc Ravalomanana's 2003 Durban Vision, to triple its protected areas through the effective involvement of local communities in natural resource management (Norris 2006).

Since 2004, Madagascar has witnessed an exponential increase in the number and popularity of LMMAs. The development of Madagascar's first LMMA followed the launch of the first temporary octopus fishery closure in 2004 in the village of Andavadoaka in southwest Madagascar (Harris 2007). The initial seven-month closure of a designated octopus fishing site, led by the local fishing community with guidance from the Wildlife Conservation Society and Blue Ventures, allowed octopus stocks to recuperate and resulted in a noticeable increase in catch upon reopening (Harris 2007, Obura and Samoilys 2011). The quick pay-off from this initial closure allowed fishers to see the immediate benefits of resource management interventions and quickly led to the spread of the temporary octopus closure model to surrounding communities. Today, seven years of data (2004–2010) proves that octopus closures improve fisher income through a 461 % increase in median recorded catches per closure and lead to an enhancement in catch per unit effort (CPUE) of up to 120 % following the reopening (Benbow and Harris 2011). The data also demonstrate that the economic benefits of the closures outweigh any potential negative effects (Benbow and Harris 2011).

As the number of temporary closures surrounding Andavadoaka grew with repetition and replication, the need for a broad management body to regulate and coordinate closure activities became apparent. In 2006 this led to the creation of the Velondriake LMMA and its governing body, the Velondriake Association. Velondriake, meaning 'to live with the sea', covers approximately 680 km^2 and encompasses 25 villages (Peabody and Jones 2012).

The temporary octopus closure model was quickly recognised as an effective tool for shifting community attitudes towards participation in conservation (Langley et al. 2006, Cinner et al. 2009a), and in 2007 was supported and promoted by the *Projet d'appui aux communautés des pêcheurs* (PACP), a government project funded by the African Development Bank. PACP worked along Madagascar's southwest coast, from south of Toliara to Morombe, to fund local NGOs committed to working with communities to establish new marine reserves. PACP and local NGOs used Andavadoaka as a training base for communities interested in learning about the temporary octopus fishery closure model, and soon communities throughout the southwest adopted the approach. Now, as a result of community exchange trips to the southwest, and with support from Conservation International, closures have spread to northern Madagascar and internationally to the Mauritian island of Rodrigues. The spread of the closure model led many communities throughout Madagascar to emulate the Velondriake LMMA and create their own LMMAs. Several LMMAs also grew organically, according to each area's specific needs.

Peer-to-peer learning has proven highly effective at initiating new conservation initiatives, passing on local conservation knowledge (Obura and Samoilys 2011) and maintaining momentum within the communities responsible for implementing LMMAs. However, the ability of LMMA leaders to communicate regularly and exchange information remained limited to isolated instances; there was no single structure used to facilitate discussion and most collaboration amongst LMMAs was restricted to intermittent communication between NGO partners or between LMMAs supported by the same NGO. The rapid geographic expansion of LMMAs throughout the country, combined with the lack of regular opportunities for LMMA coordination and cooperation, spurred discussions amongst partner NGOs about the need for an inaugural national LMMA forum.

FROM FORUM TO NATIONAL NETWORK

Madagascar's first national LMMA forum took place in Andavadoaka in June 2012. Fifty-five representatives from 18 of Madagascar's LMMAs attended the forum, which was hosted by Blue Ventures and the Velondriake Association. The 18 LMMAs in attendance represented approximately 134 villages from Madagascar's coastal regions, including Atsimo-Andrefana, Menabe, Melaky, Analanjirofo and Diana. Additionally, eight NGOs and LMMA partner institutions were in attendance: Blue Ventures, Cellule des Océanographes de l'Université de Tuléar, which is Madagascar's National Marine Institute, Cetamada, Conservation International, Honko, the Wildlife Conservation Society, and the World Wide Fund for Nature.

The forum provided a platform for Madagascar's LMMA representatives to discuss common challenges their communities face in managing marine resources sustainably, and share the innovative solutions many have developed to overcome these challenges. Participants gave comprehensive overviews of their LMMA's governing structure, management techniques, activities within the LMMA, conservation project implementation strategies, and accomplishments and challenges. LMMA representatives discovered that nearly all LMMAs had previously implemented either a permanent or temporary reserve, or both.

A second part to the forum was organised in Toliara, directly following the trip to Andavadoaka. In Toliara, the forum included government representatives from all of the relevant regional agencies, as well as two representatives of the Ministry of Fisheries in Antananarivo and one representative from Madagascar's protected areas system (SAPM). This meeting provided an opportunity for dialogue and information exchange between the LMMA leaders and government agencies. Most importantly, it allowed LMMA representatives to discuss the challenges they face in local management and identify opportunities for improved government support.

The forum ultimately led representatives to recognise the importance for continued communication and the significance of a united LMMA coalition. This led them to establish Madagascar's first national LMMA network, named MIHARI, with the goal of creating a structure to continue dialogue. MIHARI is an acronym that translates into 'local marine resource management'. Informal networks like MIHARI have proven effective at facilitating information sharing and peer-to-peer learning amongst coastal communities in other regions (Obura and Samoilys 2011), and MIHARI seeks to emulate the efforts made by the LMMA Network in the Indo-Pacific region.

The growing MIHARI network will provide opportunities for further collaboration amongst Madagascar's LMMAs and continue to raise awareness among regional and national government officials of the scale of the LMMA movement, and the scope of marine area currently under local management. This united front of LMMAs will be able to better voice concerns and ideas and leverage their interests concerning national policies and official marine protected areas. The creation of the network also marks a significant addition to the work undertaken by Madagascar National Parks to promote local marine management thus far, and represents a notable step towards Madagascar's ambitious goal to triple the coverage of its protected areas (Norris 2006, Harris 2011).

DINA

The creation of MIHARI is particularly beneficial considering the high level of commonality across Madagascar's LMMAs shown at the forum. The LMMAs represented almost universally use *dina* to enforce marine management resolutions. *Dina* are local laws based upon a traditional social code (Cinner et al. 2009b). Although *dina* are created and enforced by communities (ibid), they can be recognised by regional courts, enabling *dina* to be administered as law (Rakotoson and Tanner 2006, Andriamalala and Gardner 2010). During the forum, LMMA leaders specifically requested support from regional authorities for assistance with enforcement of *dina*, but highlighted the importance of community-based decision-making and consensus before any consultation with public authorities on *dina*-related matters. Community leaders agreed they face difficulties with providing adequate evidence to regional courts in litigation cases and proposed that public authorities provide technical support and capacity building to members of the community involved in the creation and extension of *dina*; this would ensure more effective application in the future.

While *dina* are typically focused on specific local issues (Andriamalala and Gardner 2010), certain themes, such as banning the use of destructive fishing gears like beach-seine nets, were common across all LMMAs represented. Despite this, the proposal of a 'national *dina*' was deemed impractical by government authorities during the Toliara forum. According to the officials, the creation of such a *dina* would essentially amount to the creation of new fisheries laws, an extensive process that must occur through national government channels. Government representatives did suggest, however, that if certain destructive fishing practices are widely banned by multiple LMMAs it could provide a strong basis for an official nationwide ban. This would expand on sub-regional government bans in existence, such as Arrêté 18680/2006, which bans the use of mosquito netting for fishing in Antongil Bay (Government of Madagascar 2006).

ONGOING DEPENDENCE ON EXTERNAL SUPPORT

During the LMMA forum, the leaders also discussed ongoing reliance on support from partner NGOs, particularly in terms of financial and technical assistance, as well as for the development of viable alternative livelihood activities. Participants expressed the desire to diversify sources of income, but pointed to the inaccessibility of private seafood sector collectors and the need for assistance from NGOs in identifying and evaluating the feasibility of potential activities, providing training and capacity building, and connecting communities to international markets. For example, in the Velondriake LMMA, a community-based holothurian aquaculture project is beginning to generate significant income for local communities (Harris 2011). However, the project remains reliant on the regular field presence of Blue Ventures as well as a successful partnership with a seafood collection company that provides juvenile sea cucumbers from an industrial factory and purchases and exports the adults to lucrative Asian markets (Harris 2011).

LEGAL CLARIFICATIONS

At the Toliara forum, community representatives united to request clarification from regional authorities on a number of issues. Firstly, they raised concerns over potential overlap of community marine resource management and future mining and oil exploration permits. Government officials identified exploitation of Madagascar's natural resources as part of the country's development strategy, but underlined the importance of integrating local management efforts into national zoning plans and protected areas systems to avoid future conflict.

Leaders also highlighted the continued lack of clarity regarding the ways in which community groups can legally generate income in order to sustainably finance LMMA initiatives. The implications of community associations' status as a non-profit entity (as stipulated by Malagasy Law 60 133) remain ambiguous. In some instances, government officials have interpreted this non-profit status to mean that community associations cannot perform income-generating activities and therefore cannot fundraise, aside from charging LMMA member fees. This presents a significant barrier to the long-term financial sustainability of LMMAs; NGO project funding cycles are inherently short-term, and community associations must eventually inherit LMMA operating costs. This matter will need further clarification, as it appears that there is not currently a common understanding of how LMMA associations are allowed to generate income under Malagasy law.

CONCLUSION

The creation of the MIHARI network is a major milestone towards more effective community-based marine conservation in Madagascar. The establishment of MIHARI sets the stage for further replication of the LMMA approach, as well as more frequent dialogue amongst coastal fishing communities. Moving forward, a top priority for partner organizations will be continued support for the nascent MIHARI network through the formation of a robust and functional communications plan and the standardisation of social and ecological evaluation methodologies. Additionally, improving internal management capacity of community associations, as well as communication between communities, government representatives and private sector stakeholders will be crucial to ensure the long-term sustainability of management efforts, as well as a gradually decreasing role of NGOs and other supporting organisations.

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