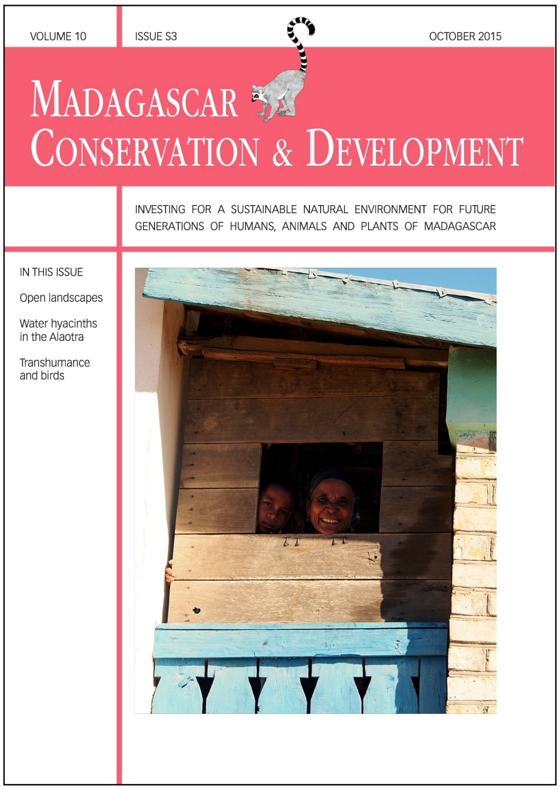
VOLUME 10 ISSUE S3 OCTOBER 2015

MADAGASCAR CONSERVATION & DEVELOPMENT

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

IN THIS ISSUE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Madagascar's open landscapes under the spotlight

Madagascar is known for its rich forests and endemic species, but also, unfortunately, for its ecosystem crises. Forests in Madagascar are diverse, ranging from tropical humid rain forests on the east to dry and spiny forests and thickets in the south and west. Forest biodiversity is high, with over 90% of mammalian species and more than 80% of the bird and amphibian species found in Madagascar existing only in forest habitats (Goodman and Benstead 2005). Thus, it is not surprising that forest ecosystems have attracted most attention in terms of biodiversity research and conservation. Protected areas such as National Parks or nature reserves are one of the most frequently used conservation strategies. Open landscapes and non-protected areas have received less attention although their relevance for Madagascar's biodiversity is indisputable. Madagascar is one of the poorest countries in the world, with more than 80% of the population living below the poverty line of $US 1.25 per day (UNDP 2013). Pressure on the natural ecosystems is high, and unsustainable land use has already resulted in the loss of a significant part of the natural vegetation of the island. Forest ecosystem conversion or disturbance due to deforestation, mining, wood exploitation and invasive species is now a rapid and alarming phenomenon. The high level of habitat destruction in Madagascar has already caused the loss of several species (Harper et al. 2011) and has brought other species to the edge of extinction, for example, the lemurs is now considered as one of the most endangered group of mammals worldwide. There is thus an urgent need for sustainable land management and ecosystem restoration.

Both natural and anthropogenic open landscapes characterize most of the territory of Madagascar, including coastal ecosystems, fresh-water wetlands, grasslands and shrub dominated grasslands in the south. Open landscapes also provide several important ecosystem services that contribute to human wellbeing. For example, wetlands are one of the most undervalued ecosystems but offer several crucial provisional services (Van der Valk 2012), such as fishing, rice farming and raw materials such as reed or cyperus. Furthermore, they filter water and offer a unique habitat for several endemic species. Even several of the grasslands in Madagascar have developed after forest clearing; herbaceous vegetation is crucial for many purposes such as pasture for livestock, land cultivation, pine and eucalyptus plantations, providing useful plants for pharmaceuticals, and emblematic landscapes for tourism.

This special issue consists of six contributions and was initiated at the Open Landscapes Conference – Ecology, Management and Nature Conservation, held in Hildesheim, Germany (29 September–3 October 2013). This special issue presents results covering a broad and representative sample of open landscape contexts in Madagascar. The term 'open landscape' used in this special issue is not as narrow in meaning as the academic sense. Rather, it refers to natural grasslands, lakes, wetlands, coastal ecosystems and open habitats that follow forest conversion.

Wetlands are diverse habitats and include both fresh-water and marine ecosystems (Van der Valk 2012). Madagascar is rich in fresh-water wetlands that are, along with the forests, areas with spectacular wildlife. One good example is the Mahavavy-Kinkony wetlands in western Madagascar. These wetlands hold all the wetland bird species of Western Madagascar, many of which are locally endemic. Another example of a wetland with a large number of locally endemic species is the Alaotra wetlands, which consist of Lake Alaotra and approximately 23,000 ha of fresh-water marshes. Almost 50 bird species have been reported for the wetlands and open grasslands of the region (Pidgeon 1996), eight of them endemic to Madagascar and two of them endemic to Lake Alaotra, although they have been recently extirpated from the region (Hawkins et al. 2000). The Alaotra wetlands are also home to the critically endangered and locally endemic Alaotra Gentle Lemur (*Hapalemur alaotrensis*), the world's only primate species to live exclusively in wetlands. Alaotra is the biggest wetland complex in Madagascar, and many of the local communities depend on its ecosystems for their livelihoods. The lake constitutes the biggest rice and freshwater fish supply for Madagascar (Ferry et al. 2009). Due to increasing population growth and unsustainable land management, the Alaotra wetlands are continuously threatened by the conversion of marshland into rice fields, over-fishing and lake siltation (sediment pollution), caused by the erosion of deforested hills. An ecological investigation of the lake has shown that the lake and its fresh-water marshes are highly degraded, as water levels and oxygen levels are very low (Lammers et al. 2015). The authors state that with an increasing human population, resulting in increased demand for fish and agricultural production, the Alaotra wetlands will undergo further pressures and it is unclear how much more the lake is likely to suffer in terms of alterations in water quality and vegetation in the future. Another problem that has worsened the situation is the invasion of the non-native water hyacinth (*Eichhornia crassipes*, Pontederiaceae), which is the source of various ecological and economic threats, as in many other regions of the world. The encroachment of this plant has been found to be closely correlated with human population density (Rakotoarisoa et al. 2015). Nevertheless, the plant, as well as other introduced species, might also constitute an opportunity as an alternative resource use option. According to these authors, the plant has the potential to improve local livelihoods and alleviate the pressure on the wetland complex by encouraging the use of simple and locally available tools. Given the limited access to credit and technology in the Alaotra region, the most likely use of the water hyacinth is for green manure, fodder, handicrafts, compost and ash as mineral fertilizer.

Grasslands constitute a major part of the open landscapes in Madagascar, especially in the southwest sub-arid ecosystems. As a consequence, the scarcity of resources such as water, arable land, exploited plants and animals may induce complex and unique traditional institutions that contribute to the management of resources and to dealing with conflicts regarding access. In these regions of scarcity, restrictions of access and resource exploitation linked to the establishment of a protected area may lead to severe consequences for the local inhabitants. Therefore, the quality of interactions between protected area managers or

NGOs and local communities is crucial for the success of a project.

In these regions, the climate is particularly harsh and the local populations have developed subsistence strategies and practices (such as transhumance) to cope with these uncertain conditions. As observed in other parts of Madagascar, livestock is also one of the most important elements in the subsistence system, playing a socioeconomic and cultural role. As well as agricultural activities, livestock and pastoralism can have an impact on open landscape ecology and species diversity (although the latter remains unknown). Randriamiharisoa et al. (2015) show that the abundance of birds in the forests of Tsimanampesotse National Park has suffered from the transhumance, while species richness was not affected. Hunting pressure seems to be the main factor affecting the bird communities.

Cattle raids are found to be the main reason for the new transhumance movement, on the one hand, but are also the trigger for emerging socio-institutional constraints on transhumance (Goetter 2015). In her study, the emergence of the new pastoral movement is enhanced by pro-social norms of unconditional hospitality, shared property rights to fodder resources, mental models of kinship and formal indigenous institutions for trust creation. For socio-cultural environments principally ruled by informal indigenous institutions, the study stresses the importance of supportive social norms and fitting shared mental models for determining individual adaptation options.

In Madagascar, in many cases open landscapes are the consequence of forest conversion. Often neglected with regard to conservation policies as they are not considered wild enough, and because they are the direct consequence of deforestation, they nevertheless represent the major landscapes that surround forest protected areas where people have to survive (Carrière and Bidaud 2012). It is now recognised that the conservation effectiveness in the forests strongly relies on the ecological quality of the surrounding anthropogenic open landscapes (Perfecto and Vandermeer 2010). Those landscapes may constitute one of the most suitable places to combine and reconcile human needs, livelihood security and sustainable use of forest species (Carrière and Bidaud 2012). A protected area induces substantial limitations of forest species and reduces access to agricultural lands. Open landscapes around forests play a major role as they are the direct buffer zones. Rural populations may shift from one native and endemic resource use to newcomer species available in their environment, but most of the time they prefer to choose a suitable mix of native and/or endemic species with new introduced ones. They see these species as highly complementary. As the local populations have demonstrated detailed knowledge of the silvicultural traits of a large number of tree species (Lavialle et al. 2015), they are able to manage native and introduced woody species. Alternatives to logging within the protected areas may offer a wider choice of tree species, including native ones. The cultivation of this diverse mix would allow people to take a more active part in the conservation and restoration of the natural capital at landscape scale (Lavialle et al. 2015). The use of non-native plant species is often viewed very critically. Nevertheless, as environmental (and especially soil) degradation is very severe throughout the country, the use of exotic plant species is often the only way to achieve a restoration goal. In addition, fast growing non-native species can lead to rapid habitat improvement.

There is a wide range of exotic species in Madagascar, resulting in the use of exotic and sometimes invasive species by native fauna and especially vertebrates (Kull et al. 2014). They provide food mainly for primates, flying foxes and birds, as well as habitat in open landscapes for all terrestrial vertebrate groups. Although these introduced plants should be viewed with caution due to their potentially invasive behaviour, many can provide services for the native fauna and humans (Kull et al. 2014). These plants could bridge the time lag until native forest regeneration or restoration with native trees has become effective (Gérard et al. 2015).

The situation at Lake Alaotra (as in other wetlands in Madagascar) gives some idea of how to use an open habitat for forest restoration. As soil degradation in the area is relatively high, the surrounding hills that were formerly covered with rainforest are now only covered with grasslands and no reforestation attempts have been initiated. Here, the invasive water hyacinth that covers much of the lake could play an important role as it is possible to make compost out of the plant which in turn could be used to enhance the soil quality and help to initiate reforestation – perhaps starting with non-native plants – or to initiate agroforestry which in turn would have an economic benefit for the local communities.

Sadly, most natural and valuable open habitats are suffering in the same manner as Madagascar´s forests from over-use and habitat destruction. This is alarming as a large part of the population's livelihoods depend directly on these ecosystems, and open landscapes play an important role for forest conservation. Focusing conservation, development and research efforts on open habitats is a necessity, given that actual drivers of land use, economic centers, and political decisions are currently at a crossroads; with the possibility of facilitating land use coordination, which might indirectly alleviate deforestation. Understanding the use of open landscapes by the majority of the rural population can help to provide best practices that preserve the adjacent forests, their biodiversity, ecosystem functions and services. Moreover, considering the current state of open habitats in Madagascar, they might well take a more prominent role in the island conservation narrative.

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ARTICLE

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Effects of transhumance route on the richness and composition of bird communities in Tsimanampesotse National Park

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ABSTRACT

In southwestern Madagascar, livestock (cattle) is a major source of income for the human population and is of tremendous cultural importance. In this subarid region, the farming system faces an extreme climate and has to cope with little food and water resources for several months a year. Local farmers overcome these difficulties in the form of transhumance and roaming of cattle in the forest at Tsimanampesotse National Park. The former strategy uses routes directly through the park twice per year. To assess possible effects of the transhumance and associated human activities on birds, we compared the composition and abundance of birds at one control site and two sites along the trail of transhumance in the forest of Tsimanampesotse National Park from January to May 2012. The results showed that the abundance of birds declined near the trail of transhumance. Ten species of birds were hunted during the transhumance to meet the daily needs of the herders. We interpret the lower density of birds along the trail of transhumance as a consequence of hunting, especially for large and terrestrial birds such as *Coua* spp. Cattle activities (trampling, grazing) do not seem to bird communities.

RÉSUMÉ

Dans le Sud-ouest de Madagascar, l'élevage (zébus, chèvres, moutons) est une source majeure de revenus pour la population et représente une importance culturelle. Dans cette région subaride, le système d'élevage est soumis à un climat extrêmement sec et fait face à un manque de nourriture et d'eau pendant plusieurs mois par an. Pour faire face à ces difficultés, les éleveurs pratiquent la transhumance et laissent divaguer le bétail dans la forêt du Parc National de Tsimanampesotse ; cette stratégie a ainsi ouvert une piste qui traverse le parc. Traditionnellement, à savoir avant l'intensification de vol de bétail sur le plateau Mahafaly, les zébus étaient menés de la plaine côtière au plateau dès le début de la saison des pluies lorsque l'eau était disponible. À la fin des pluies, l'eau devenait rare sur le plateau et les zébus retournaient sur la plaine côtière, en traversant ainsi le parc une deuxième fois. Ce parc est classé parmi les zones abritant une richesse biologique unique, il est la seule aire protégée sur le littoral du Sud-ouest de Madagascar et sur le plateau calcaire Mahafaly. La particularité de la flore et de la végétation du parc se manifeste par différents types d'adaptation à la sécheresse et à la chaleur. La richesse faunique est caractérisée par des espèces à la fois endémiques et menacées avec une diversité d'oiseaux qui pourrait être affectée par des activités anthropiques dans le parc. Pour évaluer les effets possibles de la transhumance sur l'avifaune, la composition et l'abondance des oiseaux, un site de contrôle a été comparé avec deux sites distribués le long de la piste de transhumance dans la forêt du Parc National de Tsimanampesotse de janvier à mai 2012. Les résultats montrent que l'abondance des oiseaux diminue le long de la piste de transhumance alors que la richesse spécifique n'est pas affectée. Dix espèces d'oiseaux sont chassées pendant la transhumance pour répondre aux besoins quotidiens des éleveurs. La densité plus faible des oiseaux le long de la piste de transhumance est interprétée comme un résultat de la chasse, en particulier les oiseaux les plus grands et les terrestres tels les espèces de *Coua*. Le piétinement des zébus qui errent à proximité de la piste durant la transhumance pourrait également affecter le sous-bois, l'habitat de certains oiseaux mais la chasse semble rester le facteur anthropique principal affectant les communautés d'oiseaux dans le parc. La transhumance est une stratégie efficace pour le système d'élevage dans les zones subarides mais elle représente un risque par l'ouverture aux ressources naturelles dans le parc.

INTRODUCTION

Madagascar is one of the world's most important centers of biodiversity (Ganzhorn et al. 2001, Joppa et al. 2013), with exceptionally high species diversity and levels of endemism in all major taxono-

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mic groups including birds (Goodman and Benstead 2005, Raherilalao and Goodman 2011). In southwestern Madagascar the 202,525 hectares Tsimanampesotse National Park was created to protect the unique biological richness of the region and plays a key role in the conservation of the regional bird community, comprising at least 112 species (Goodman et al. 2002). Unfortunately, the remaining natural habitats are under pressure from human activities (Blanc-Pamard and Ramiarantsoa 2003, Primack and Ratsirarson 2005, Brinkmann et al. 2014).

In the region, livestock (zebu, *Bos taurus*, the most common cattle in Madagascar, goats *Capra hircus* and sheep *Ovies aries*) is a major source of income for the human population (Feldt 2015). The area is characterized by an extremely dry climate and shortage of food and water for several months (Raherilalao and Wilmé 2008). Breeders have developed a strategy to overcome those difficulties in the form of transhumance and roaming. Transhumance is defined as seasonal migration of livestock from one pasture to another (Nedelea and Comãnescus 2009). The park is crossed by several routes of transhumance and the forest is used for zebu grazing throughout the cool dry season, from April to October (Projet SuLaMa 2011, Ratovonamana et al. 2013). Transhumance is a traditional farming system in this region which had existed before the creation of the park (Project SuLaMa 2011). In 1927, Tsimanampesotse was created as a Strict Nature Reserve (RNI N. 12 Tsimanampetsotsa) of 42,300 hectares, and became the National Park N. 16 of Tsimanampesotse in 2002, that was extended towards the south in 2009, and extended to a total area of 202,525 hectares in April 2015 (MEEMF 2015). In the traditional transhumance zebus and to a lesser extent also sheep are brought from the coastal plain to the Mahafaly Plateau at the beginning of the wet season (October/November) when water is available on the plateau. By the end of the wet season (March/April), water becomes scarce on the plateau and the zebus are taken back to the coastal plain, thus crossing the park twice. While the transhumance itself only takes about two days (one way), the trails are used to transport a variety of goods throughout the year. Thus, the trails are the source of a variety of possible disturbances for fauna and flora. Humans need firewood and probably collect other forest resources as they are encountered along the trail. Further, livestock roaming in the forest can destroy the undergrowth (Ratovonamana et al. 2013) and thus have a negative impact on habitat quality of birds (Soarimalala and Raherilalao 2008). In order to come to a better understanding of the effects of anthropogenic impacts on Madagascar's native fauna, we are assessing the effects of the transhumance trail through the park on the community composition and density of birds. Our working hypothesis was that bird communities would be affected negatively in the proximity of the trail of transhumance.

METHODS

STUDY SITE. The study was carried out in Tsimanampesotse National Park (E043°46'–43°50', S24°03'–24°12') between January and May 2012 at an altitude between 38 and 114 m on the Mahafaly Plateau. The region is characterized by a sub-arid bioclimate (Cornet 1972) with annual rainfall of 350 mm to 500 mm (Blanc and Paulian 1996, Dewar and Richard 2007). Inventories were carried out in three different sites in the Tsimanampesotse National Park. Site 1 was the control site, located about 1 km away from the transhumance route and characterized by intact vegetation where human disturbances are limited. Sites 2 and 3 were located along the route of transhumance that is used by local people for moving between the plateau and the littoral zone, or for livestock roaming or for transhumance. Site 2 is located at the beginning of the route and Site 3 in the middle (Figure 1). The vegetation types of the different study sites area depend on the type of soil at each site and were classified according to Ratovomanana et al. in 2011 (Table 1).

BIRD SAMPLING. The composition and abundance of birds were recorded with point counts (Bibby et al. 2000, O'Dea et al. 2004). Points were spaced at 100 m intervals along 900 m transects to minimize the probability of counting the same individual on two successive points (Ravokatra et al. 1998, Raherilalao 2006). At each point, all birds seen and heard were recorded within a radius of 25 m around the point for ten minutes. Transects were placed in parallel and spaced at a 200 m distance to each other. Ten transects were established at Site 1 and five transects were surveyed at Site 2 and five at Site 3. Inventories were conducted from 0530 to 0830h when the activity of diurnal bird is maximal. Each point was surveyed at least five times from January to May 2012. The number of bird species and the number of individuals were averaged per point.

ANTHROPOGENIC IMPACTS. Anthropogenic impacts could either be linked to the activities of zebu (such as trampling, grazing, opening up the forest) or be directly linked to human activities. To measure these impacts, a plot of 10 m x 10 m was placed around each point count at Sites 2 and 3. As a proxy for disturbance by zebus, we counted the number of zebu feces per 100 m² and that are not completely dissolved and not very dry. As measures for human disturbance we recorded the amount of woody debris the number of coarse and fine woody debris > 3 cm in diameter that were on the ground), assuming that people collect dead wood for firewood as they walk along the trail. Information on hunting and the consumption of birds was collected by interviews and direct observations in the villages of Marofijery (E043°37', S24°02') and Efoetse (E043°51', S23°04'). In each village ten people (who have zebu that carried out the transhumance) were interviewed individually.

DATA ANALYSIS. Species similarities between sites were compared based on the presence of species at each site according to the Jaccard index (Magurran 2004). In order to decide on whether or not the Jaccard indices showed a significant difference between sites, we compared the calculated values with values provided by the table for $p = 0.05$ provided by Real (1999).

Single factor analysis of similarities (ANOSIM) (Clarke 1993, Clarke and Gorley 2001) was used to compare the three study sites using 'PRIMER'. Apart from the presence of species, this comparison also includes the number of individuals per species in the calculation of community similarity. First, we compared the bird communities between different sites (Sites 1, 2, and 3) and second, between the reference Site 1 and the combined sites (Sites 2 and 3) along the transhumance.

We used the mean number of species and individuals recorded at each point as the unit of analysis. The number of bird species and individuals did not deviate from normality (Kolmogorov-Smirnov-test: $p > 0.05$). ANOVA was used to compare the number of species and number of individuals between sites. Numbers of bird species and individuals were related to the mea-

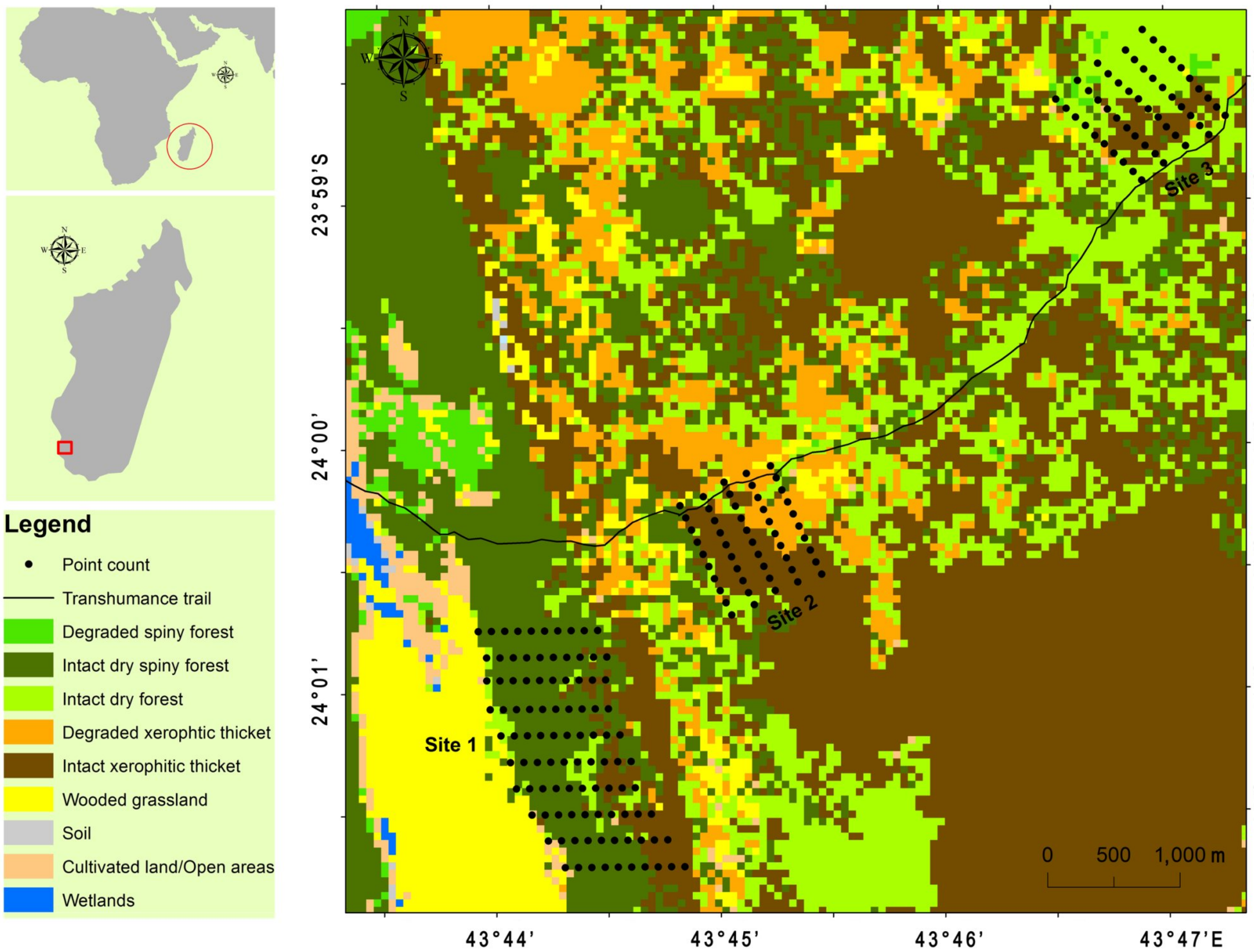

Figure 1. Vegetation types and location of the three study sites in the Tsimanampesotse National Park in subarid southwestern Madagascar. The classification of vegetation follows Ratovonamana et al. (2011).

sures of disturbance by zebu (= number of feces) and humans (= availability of dead wood). The two factors are summarized by the distances to the trail of transhumance using correlations and multiple regression analyses (Waite 2000). SPSS 9.0 (1999) was used to analyze the data. Data on anthropogenic pressure have been log10-transformed to achieve normality.

RESULTS

At all three sites 6,359 individuals of birds were recorded. These were represented by 55 species: 53 species at Site 1, 41 at Site 2, and 39 at Site 3 (Supplementary Material Table S1).

BIRD SPECIES SIMILARITIES BETWEEN SITES. The mean number of species recorded per point did not differ between Sites 1 and 3, but was significantly lower at Site 2 than at Sites 1 and 3 (ANOVA: overall model: $F = 8.80$, $p < 0.001$; Table 2). The mean number of individuals was significantly lower at Site 3 than at either Site 1 or Site 2 according to Scheffe's post-hoc test (ANOVA: overall model: $F = 18.36$, $p < 0.001$). The number of individuals per point did not differ significantly between Sites 1 and 2 according to Scheffe's post-hoc test.

Table 1. Percentage of vegetation types present at the three study sites. Degraded forest is a forest that has undergone disturbance like logging or roaming.

Name	Vegetation	Site 1	Site 2	Site 3
Spiny forest	Intact spiny forest	71%		
Xerophytic thicket	Intact xerophytic thicket	18%	56%	30%
	Degraded xerophytic thicket		34%	
Dry forest	Intact dry forest	11%	10%	38%
	Degraded dry forest			32%

Based on the presence and absence of species at each site, the comparison via Jaccard indices showed that Sites 2 and 3 (0.77) were the most similar. Sites 1 and 3 (0.67) differed most (Table 3). None of these values indicate a significant difference of species similarities between sites (Real 1999).

COMMUNITY SIMILARITIES BETWEEN SITES. Taking the abundance of the various species into account, the ANOSIM analysis indicated that the bird communities of the three sites were significantly different with $p < 0.001$ ($R = 0.76$). Site 1 also differed from the combined sites along the trail used for the transhumance (Sites 2 and 3; $R = 0.82$, $p < 0.001$).

ANTHROPOGENIC IMPACTS. The number of bird species and individuals decreased significantly from the edge to the forest interior at the control site (Site 1; Table 3, Figure 2). In contrast, the number of bird species and individuals increased significantly with increasing distance to the trails of transhumance at Site 2. At Site 3 the number of bird species and individuals also increased with increasing distance to the trail; here, the correlation between the distance to the trail and the number of bird species was significant while the distance and number of individuals were also related positively but the correlation was not significant (Figure 2).

Table 2. Number of bird species and number of individuals per point count at Sites 1–3. (values are means ± standard deviations. At Site 1 each point is based on data from 10 transects; at Sites 2 and 3 each point is based on data from 5 transects per site. Statistics at the bottom of the table are based on Pearson correlations between the number of species or individuals and the distance)

		Site 1		Site 2		Site 3	
	Point	Number of species	Number of individuals	Number of species	Number of individuals	Number of species	Number of individuals
Towards forest interior	P1	11.6±1.7	19.9±2.3	7.6±1.6	10.6±2.2	9.8±1.3	17.0±2.4
	P2	12.6±1.5	21.7±3.9	8.8±0.8	13.5±2.7	10.6±0.9	23.9±5.1
	P3	13.0±1.8	22.2±6.1	8.8±0.9	12.7±1.07	10.9±1.4	20.8±4.4
	P4	11.3±2.4	17.7±5.6	8.9±0.8	12.3±2.6	10.5±1.1	19.6±4.6
	P5	11.6±2.3	17.0±3.1	9.1±1.2	12.9±2.4	10.4±1.7	24.4±7.6
	P6	10.5±1.3	14.8±3.3	9.4±1.5	17.8±3.4	11.4±0.8	26.3±5.2
	P7	10.7±1.3	16.2±2.6	10.2±1.0	18.7±4.3	10.8±1.1	28.1±8.3
	P8	11.8±1.4	17.1±2.0	11.7±0.9	18.1±4	11.0±0.8	23.5±3.9
	P9	10.9±2.5	15.5±3.2	10.4±1.7	15.4±3.6	11.0±1.36	22.5±4.0
	P10	9.3±1.7	13.5±2.2	10.5±2.0	14.9±2.1	11.8±0.8	23.5±4.4
Mean		11.3±1.0	16.4±3.7	9.6±1.2	14.7±2.8	10.8±0.6	18.0±4.8
r		-0.72	-0.85	0.88	0.68	0.72	0.51
p		0.02	0.002	0.001	0.029	0.009	0.13

Indicators for anthropogenic pressure (woody debris, number of zebu feces) were measured only at the points of Sites 2 and 3. Therefore the following analyses had to be restricted to Sites 2 and 3.The number of bird species and individuals recorded per point was correlated significantly with the abundance of woody debris (Species: $r = 0.733$, $p < 0.001$; Individuals: $r = 0.699$, $p < 0.001$, $N = 20$). The number of bird species was uncorrelated with the number of zebu feces ($r = 0.242$, $p = 0.304$) but the number of individuals was correlated significantly with the abundance of zebu feces ($r = 0.482$, $p = 0.031$). Taking site effects into account in analyses of covariance, the abundance of woody debris remained a significant predictor for bird species and individuals while the abundance of zebu feces became insignificant (Table 4).

HUNTING. According to the 20 interviewees from the villages of Marofijery and Efoetsy, about 30–50 zebus carry out the transhumance with at least two people to attend herds. The transhumance across the national park and takes one day and one night. During this time, about two birds are consumed by two or three people. The number and species of birds consumed during transhumance is represented in Figure 3. Seventy percent of interviewees (men and women who had participated in the transhumance) consumed *Coua cursor*, followed by *Numida meleagris* consumed by 50% of the villagers. *Turnix nigricollis* is little used because it is taboo for some villagers, even though all villagers come from the south-west but from several different families. In fact, 5% of the villagers surveyed ate this species. However, bird hunting is not only during transhumance period but during all daily activity of humans. The interviews have also shown that humans hunted birds whenever they are encountered.

Table 3. Pairwise comparisons based on the Jaccard index, and results of the comparison between pairs of sites according to ANOSIM; based on the relative abundance of birds. (values are R-values as calculated by ANOSIM; all comparisons are different with $p < 0.05$)

	Jaccard index		R values (ANOSIM)	
	Site 2	Site 3	Site 2	Site 3
Site 1	0.70	0.67	0.80	0.83
Site 2		0.77		0.66

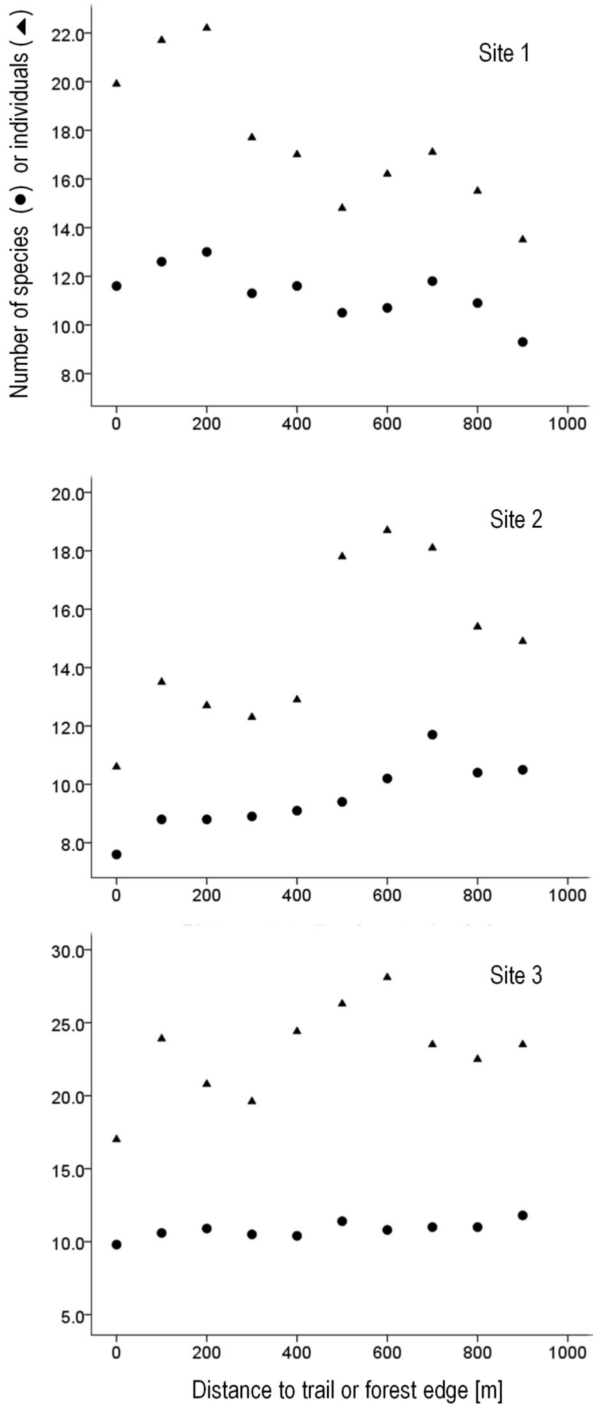

Figure 2. Bird species and individual numbers from the forest edge (Site 1) or the trail of transhumance (Sites 2 and 3) towards the forest interior.

DISCUSSION

In this study we assessed possible effects of the transhumance through Tsimanampesotse National Park on the community composition and density of birds. We used one control site and two sites along the route of transhumance. While densities of different bird species varied between sites, indicating different habitat qualities of the different sites (Collin 1996), the inventories did not reveal any difference in bird species composition between the three sites. The lack of differences in species composition is surprising as the three sites include different vegetation formations, ranging from dry forest to degraded spiny bush (Ratovonamana et al. 2011). The lack of differentiation might be due to our sampling

Table 4. Impact of human activities (measured by the abundance of dead wood) and zebus (measured by the abundance of zebu feces) after corrections for site specific effects at sites 2 and 3. (values are F-values according to analyses of covariance)

	Bird species	Bird individuals
Site	2.25	12.07**
Dead wood	9.21**	5.50*
Zebu feces	0.13	0.06

that was not designed specifically to assess possible differences between vegetation formations or probabilities of bird detection likely varied between points. Alternatively, it could reflect the need of the various bird species to avoid tight habitat specializations in this region that is characterized by unpredictable rainfall and large fluctuations in ambient conditions (Dewar and Richard 2007, Ratovonamana et al. 2011). Similarly to the situation in birds, neither lemurs nor reptiles show pronounced differences in densities or species composition in relation to habitat degradation at Tsimanampesotse (Rakotondranary et al. 2010, Raonizafinarivo 2013).

In contrast to the general characteristics of the bird communities at the three sites, birds responded differently at the two sites along the transhumance than at a site without pronounced human impacts. At the sites of transhumance, bird species numbers and less consistently also their abundance increased towards the forest interior with increasing distance to the trail, while at the protected site, their numbers decreased from the forest edge to the interior (Figure 2). Such an edge effect is to be expected as edges tend to be more productive and allow species with different specializations to overlap (McCollin 1998).

The reversed situation along the trail of transhumance, which can be considered either as equivalent to a forest edge or simply as a linear structure in an otherwise continuous forest, calls for an explanation. According to our original hypotheses and based on the increase of bird species with increasing distance to the trail, we expected some kind of anthropogenic impact along the trail of transhumance. These impacts could either be linked to the presence of zebu or to the presence of humans. The abundance of zebu feces was not linked to bird species or bird individuals in any systematic manner. Thus, zebus during the transhumance do not seem to have any systematic effects on the birds in the vicinity. In

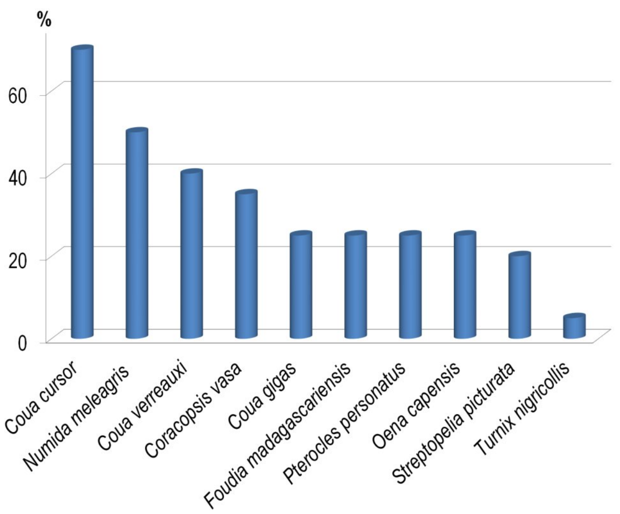

Figure 3. Percentage of people who consumed bird species during the transhumance.

contrast, human presence as indicated by the collection of fire wood (measured as the declining availability of woody debris) seems to have a consistent negative effect on bird species and individual numbers. We cannot provide a causal link between human presence and the reduction of bird abundances. Hunting along the trail may be one component effect on bird species, specifically for birds that are likely to be hunted only in passing, or living around camp sites. The impact of hunting and bushmeat seems to be more important in Madagascar than people had thought. It is a vital part of the rural economy throughout Madagascar (Golden 2009, Sabel et al. 2009, Jenkins et al. 2011) and important also in the Tsimanampesotse area (Walker and Ranfeliarisoa 2012) with profound effects on population densities of Madagascar's native fauna. For the avifauna, large terrestrial birds such as *Coua* spp. are the most hunted in Madagascar (Goodman and Raherilalao 2013). According to the result of interview in this study, *Coua* spp. are also the most consumed by the human population in our study area.

Transhumance and the zebus themselves are unlikely to represent a threat to the native bird community as the duration of the transhumance is short. But the trail is used to commute between the plateau and the littoral for a variety of purposes. Even small effects such as undergrowth destruction might add up over the year and result in the observed pattern of bird distributions. As a further potential threat, herds continue to graze in the park with important consequences for forest regeneration and probably also the negative consequences imposed by people as observed along the trail of the transhumance.

To sum up, bird species number and densities were lower along the trail of transhumance than elsewhere. Ten species of birds were hunted to meet the daily needs of people travelling along the trails of transhumance. Thus, while the transhumance itself does not seem to affect bird communities, hunting associated with the transhumance as well as with other activities may represent one of the threats to birds in particular for the largest and most terrestrial birds such as *Coua* spp.

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

Table S1. Occurences of species at the different sites.

ARTICLE http://dx.doi.org/10.4314/mcd.v10i3s.4

Lake Alaotra wetlands: how long can Madagascar's most important rice and fish production region withstand the anthropogenic pressure?

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ABSTRACT
The Alaotra wetlands represent the biggest lake and wetland complex in Madagascar and are home of several endemic species. The region constitutes the largest rice production area and inland fishery of Madagascar. Rice and fish are the main local sources of income. While the population has increased fivefold during the last 40 years, the growing need for resources is continuously increasing the pressure on the wetland system. In this study, vegetation and water parameters were collected within three sites differing by level of degradation in order to evaluate the current ecological state of the wetland. The results show that high levels of ongoing anthropogenic disturbance are favoring the formation of a new plant community in the fringe area of the marsh belt. This area is now dominated by invasive species such as the water hyacinth (*Eichhornia crassipes*) which shows a mean coverage up to 53% and water ferns (*Salvinia* spp.) with a mean coverage up to 31.4%. Lake water levels were very low and decreased during the dry season to a mean level of only 3 cm in the littoral zone. Signs of eutrophication like hypoxia (mean saturation of only 22%), increased phosphate concentrations (1.18 mg L^{-1}) and black colored, foul smelling water were observed. Under a likely scenario of growing anthropogenic pressures, it remains unclear what the current trends will bring for the wetland's future.

RÉSUMÉ
La zone humide de l'Alaotra représente le plus grand lac et complexe de zones humides de Madagascar hébergeant plusieurs espèces endémiques. La région constitue la première production de riz et de pêche dulcicole de l'île. Le riz et les ressources piscicoles sont les principales sources de revenus locaux. L'effectif de la population humaine locale a été quintuplé au cours des dernières 40 années et les besoins en ressources ont augmenté en conséquence de sorte que les pressions sur la zone humide ont été exacerbées. Dans cette étude, des paramètres portant sur la végétation et l'eau du lac ont été collectés dans trois sites qui diffèrent par le niveau de dégradation pour évaluer l'état écologique actuel de la zone humide. Les résultats montrent que le niveau élevé des perturbations anthropiques favorise la formation d'une nouvelle communauté végétale sur la ceinture du marais. Cette zone est dominée par des espèces de plantes envahissantes à l'exemple de la jacinthe d'eau (*Eichhornia crassipes*) dont la couverture moyenne est de 53% et de la fougère d'eau (*Salvinia* spp.) avec une couverture moyenne de 31,4%. Les niveaux du lac sont bas et diminuent jusqu'à 3 cm de moyenne dans la zone littorale pendant la saison sèche. Des signes d'eutrophisation comme l'hypoxie (saturation moyenne de 22%), l'augmentation de la concentration de phosphate (1,18 mg L^{-1}) et la présence d'eau de couleur noire et nauséabonde ont été observés. Dans un possible scénario avec une augmentation des pressions humaines, les tendances actuelles restent difficiles à comprendre pour l'avenir de la zone humide.

INTRODUCTION
Wetlands are diverse ecosystems, including both fresh water and marine habitats (sensu Van der Valk 2012). They build the transition zone between land and water and fulfill various ecological functions such as nutrient and groundwater retention and supply, flood control and flow regulation, sediment retention, erosion and salinity control, water purification and climate stabilization. Wetlands further provide crucial ecosystem services to humans such as water, fish, natural products (e.g., construction material, crafts and medicinal plants) and resources for agriculture, cattle farming and energy production, game, wood and services like facilitation of transport and recreation (Dugan 1990, Roggeri 1995, Mitsch and Gosselink 2000, Turner et al. 2000, Junk 2002).

The Alaotra wetlands, situated on the northeastern part of the Madagascar highlands, are formed by the Lake Alaotra (less than 20,000 hectares of open water body), and by 23,000 ha of fresh water marshes (Bakoariniaina et al. 2006, Copsey et al. 2009a). The surrounding 120,000 ha of rice fields constitute Mada-

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gascar's biggest rice production area with an annual yield of ca. 300,000 tons (Plan Régional de Développement 2005). In addition, Lake Alaotra supplies the country with 2,500 tons of freshwater fish annually (ibid).

The wetland complex provides habitat for a variety of plant and animal species. At least three vertebrate taxa are microendemics: the Alaotra gentle lemur (*Hapalemur alaotrensis*) is Critically Endangered with an estimated population of less than 2,500 individuals in 2005 (Ralainasolo et al. 2006, Ratsimbazafy et al. 2013), the Madagascar rainbowfish *Rheocles alaotrensis* (Bedotiidae) (Reinthal and Stiassny 1991) and a recently described small carnivore *Salanoia durrelli* (Eupleridae) (Durbin et al. 2010).

Although declared as a Ramsar site of international importance in 2003 and 'Nouvelle Aire Protégée' since 2007, the wetland system experiences continuous anthropogenic pressures and degradation (Peck 2004). During the last 50 years, the human population in the two lake districts has increased fivefold from some 110,000 inhabitants in 1960 (Pidgeon 1996) to over 560,000 inhabitants (INSTAT 2013) leading to a steadily increasing demand for natural resources and agricultural land. While the fresh water marshes are shrinking due to burning and conversion into rice fields, the lake suffers from massive overfishing. Further problems include the invasion of non-native fish and plant species. Among invasive plant species, the water hyacinth (*Eichhornia crassipes*) is one of the most problematic while it causes several ecological, social and economic problems; water loss due to increased evapotranspiration, oxygen loss, decreased phytoplankton productivity (associated with changes in the food web) due to decreasing light conditions, loss of biodiversity and clogging of waterways (Masifwa et al. 2001, Rommens et al. 2003, Mangas–Ramirez and Elias–Gutierrez 2004, Andrianandrasana et al. 2005, Villamagna and Murphy 2010).

Water loss and the decreasing open water surface represent serious problems in the area since Lake Alaotra is a shallow lake with a maximum depth of four meters. Sedimentation, transformation of water and streams for agricultural irrigation and environmental degradation have already reduced the lake to 20–30% of its original size (Bakoariniaina et al. 2006, Kusky et al. 2010). Shallowness and tropicality imply that physical aspects of water depth and water temperature are the determining features in the environmental regulation of the lake system (Talling 2001). Shallow lakes show a higher sensitivity towards rapid changes in those two parameters. While wetlands in tropical Africa seem to be well documented (e.g., Lake Chilwa (two meters depth, Howard-Williams 1975), Lake Chad (four meters depth, El-Shabrawy and Al-Ghanim 2012), Lake George (2.4 m depth, Ganf 1974), Lake Naivasha (four meters depth, Gaudet 1977), Lake Nakuru (four meters depth, Vareschi 1982), there is a lack of research on freshwater lakes in Madagascar. For Lake Alaotra, studies have mainly focused on population biology, distribution and behavior of vertebrate species, especially on *Hapalemur alaotrensis*, as well as on bird and fish species (Wilmé 1994, Mutschler et al. 1998, Hawkins et al. 2000, Nievergelt et al. 2002, Waeber and Hemelrijk 2003, Ralainasolo 2004, Ralainasolo et al. 2006, René de Roland et al. 2009, Guillera–Arroita et al. 2010). There are few studies only including ecological data and interactions, e.g., studies focusing on different trophic levels and on the consequences of environmental changes on habitat quality and biodiversity. The last comprehensive study about the ecological state of the lake dates back to some 20 years (Pidgeon 1996). The marsh vegetation is important in terms of habitat and food source for terrestrial and aquatic communities. Changes in vegetation heterogeneity and composition are therefore important attributes to assess ecosystem functioning. Physico-chemical features of the water (e.g., water level and temperature, dissolved oxygen, pH, luminosity, conductivity and nutrient content) are determining ecological parameters for aquatic communities (Lévêque 1997, Prepas and Charette 2003, Ekau et al. 2010). However, the terrestrial system relies on the aquatic system as well. This article will present an update of the lake's water quality and vegetation parameters in order to draw some general conclusions on the current wetland conditions.

METHODOLOGY

STUDY AREA. The study was conducted at Lake Alaotra (E048° 26', S17° 31'), Madagascar (Figure 1). The lake is situated 750 m above sea level and lies in a tectonic basin encompassing an area of 685,500 ha (Andrianandrasana et al. 2005, Ferry et al. 2009, Kusky et al. 2010). The lake is shallow with water depths of 1.5 to 2 m on average and a maximum of 4 m during the rainy season (Pidgeon 1996). The lake obtains water from infiltration, runoff and flooding (Ramsar 2007). Four main rivers feed the Lake Alaotra: the Anony and the Sahamaloto in the north and the Sasomangana and the Sahabe in the south. The Maningory in the northeast constitutes its effluent (Chaperon et al. 1993). The Alaotra region is characterized by a tropical climate. Mean annual temperature is 20.6 °C, but ranges from 11.1 °C in July to 28.4 °C in January (Ferry et al. 2009). The basin is characterized by an annual precipitation of 900 to 1,250 mm with a maximum of 250 mm in January during the warm rainy season (November–March).

The freshwater marshes of Lake Alaotra are dominated by sedges and grasses. The higher strata is presented by common reed (*Phragmites australis*), cyperus (*Cyperus madagascariensis*) and the Convolvulaceae, *Argyreia vahibora*, while the lower strata is settled by *Cyperus latifolius*, *Leersia hexandra*, the fern *Cyclosorus interruptus*, *Persicaria glabra* and *Echinochloa pyramidalis* (Mutschler and Feistner 1995, Pidgeon 1996, Ranarijaona 2007). At least three invasive species have colonized successfully the shallow areas of the lake: the invasive *Eichhornia crassipes*, and the water ferns *Salvinia molesta* and *Azolla* spp. (Andrianandrasana et al. 2005).

STUDY SITES. Three different sites were chosen for this study in terms of location at the lake, human population density

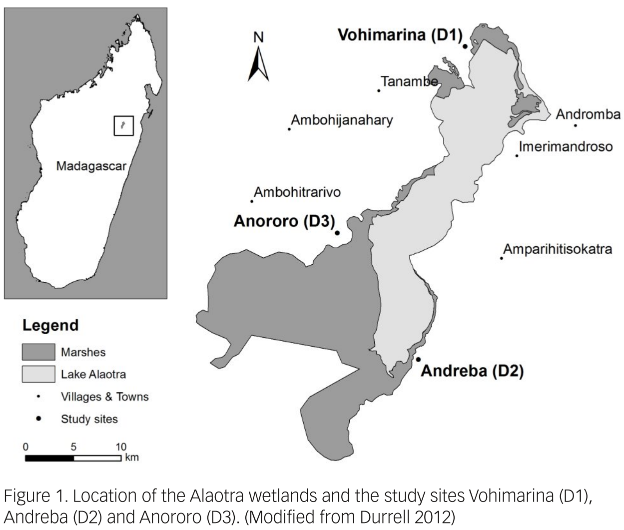

Figure 1. Location of the Alaotra wetlands and the study sites Vohimarina (D1), Andreba (D2) and Anororo (D3). (Modified from Durrell 2012)

and level of degradation: Andreba, Anororo and Vohimarina (Figure 1). The level of degradation was defined a priori by (i) protection status and existence of local management units for the marshes, (ii) abundance of the invasive *Eichhornia crassipes*, (iii) intensity of fishery activities, (iv) presence of sanitation and (v) water level. Evaluation of the criteria was based on information from the *fokontany* (smallest administrative unit in Madagascar) and direct observations. Vohimarina, on the northern side of Lake Alaotra (E048° 32' 59.7", S17° 20' 02.4", 761 m a.s.l.) has a population of less than 500 inhabitants and encompasses 300 ha of marshes (Andrianandrasana et al. 2005); its marshes are defined as low-degraded (D1). It is described by a low water level, a village with low fishery activities and a low *E. crassipes* occurrence as well as the presence of sanitation and a community-based association (VOI, *Vondron' Olona Ifototra*) for the management of the marshes. Andreba, on the east side of the lake (E048° 30' 08.0", S17° 37' 51.7", 739 m a.s.l.) has 4,800 inhabitants and 235 ha of marshes (Andrianandrasana et al. 2005). Its marshes are intermediate-degraded (D2). Like Vohimarina, Andreba has a sanitation and a VOI but differs in terms of increased fishery activities and higher abundance of *E. crassipes*. Anororo, on the west side of the lake (E048° 26' 01.4", S17° 30' 44.0", 724 m a.s.l.) has a population of 8,000 inhabitants (Copsey et al. 2009b) and entails 9,850 ha of marshes (ibid). Water levels are higher than in the other sites. Its marshes are considered as highly-degraded (D3) because of a high occurrence of *E. crassipes* combined with high fishery activities, no sanitation and the absence of the VOI in 2012/13.

DATA SAMPLING. Environmental parameters were assessed in the marsh vegetation and open water of the lake across all three sites from November 2012 to April 2013. For each study site, 9 line transects (each of 220 m length and 1 m width) were established along the lake shore (Figure 2a, b). At all three locations, a canal represents the main connection between the village and the lake. Through the canal, municipal and agricultural wastewater is discharged directly into the lake. Further, the canal and its surroundings are subjected to mechanical disturbance by frequent boat traffic, fishery and cultivation activities. To detect habitat changes along a nutrient and mechanical disturbance gradient, four transects were placed on both sides of the canal and one transect was located near the canal (10 m). The ecological state of Lake Alaotra was assessed by sampling vegetation and water parameters. Vegetation parameters were assessed in all transects, whereas the water parameters were determined in the core-transects only (Figure 2a, b).

WATER PARAMETERS. The water depth (cm) was determined using a measuring rod. Water quality was assessed by measurements of conductivity (µS cm^{-1}), pH, temperature (°C) and dissolved oxygen (mg L^{-1} and %). All water quality measurements were performed with a digital multi-meter (WTW, Multi 350i). Luminosity (lux) was recorded with a digital lux-meter (PHYWE, model: 07137-00). Water quality and depth were sampled along the four core-transects. Daily physicochemical fluctuations were accounted by sampling the water parameters during four periods: 0700–1000h, 1000–1300h, 1300–1600h and 1600–1900h. The temporarily low water levels of the lake during the dry season made it difficult to reach the plots by boat and thus measurements were restricted to n= 20 per day. To detect seasonal changes, data were collected during the period of lowest lake water levels at the on

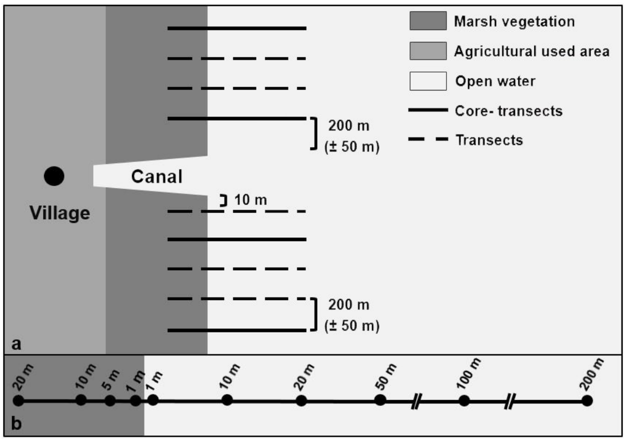

Figure 2. Direction and location of transects and plots in the littoral zone of Lake Alaotra. (a) Four transects were set out on each sides of the canal. One transect was additionally installed near the canal (10 m distance). (b) In each transect, a total of ten 1 m²-plots were installed, four in the lake shore vegetation – 20, 10, 5 and 1 m from the water edge – and six plots in the open water – 1, 10, 20, 50, 100 and 200 m from the lake shore vegetation. (The geographical coordinates of all plots were determined using a UTM, WGS 84 GPS)

set of the rainy season in 2012 (December 2012–January 2013; it only started raining in February; for brevity, it will be termed 'dry season' for the remainder of this manuscript) and during March–April 2013; this will be termed 'rainy season'. Sampling during the dry season was performed in surface water (0–10 cm depth) of the open water plots (10–200 m); due to higher water levels in the rainy season, analyzes were additionally done in plots within vegetation (20 and 10 m) and within deep water (1.5 m depth). In total n= 240 measurements were performed during the dry season versus n= 672 measurements in the rainy season.

Nutrient concentrations were measured during midday in two core-transects per site using a photometer (WTW, Photoflex Turb). Samples to detect nitrite (NO_2^-), nitrate (NO_3^-) and phosphate (PO_4^{3-}) were taken in the surface water (0–10 cm depth). For these measurements, open water plots (10 m to 200 m) during the dry season (December 2012–January 2013, n = 30) and the rainy season (March–April 2013, n= 30) were sampled. Ammonia (NH_4^+) could not be measured due to the high air temperatures at the study sites and the missing option for cooling.

VEGETATION PARAMETERS. The lake shore vegetation was described using plant diversity, species abundance and composition as well as vegetation structure. Data were collected from February until March 2013 in all plots (n= 270). Plant species richness, total plant cover per plot and cover of each species were determined. Plant cover estimations were obtained in percentage for each plant species applying Londo's decimal scale (Londo 1976) and completed by open water and dead organic material cover estimates in percentage. Plant species were determined in the herbarium of the Parc Botanique et Zoologique de Tsimbazaza, Antananarivo, Madagascar. Vegetation structure was measured in all plots and was defined by vertical density of the vegetation, visually estimated as percentage in the plot (1 m section) for defined height intervals.

DATA ANALYSES. All statistical tests were done with the software SPSS for Windows (IBM, version 21). The comparison of data was performed with the nonparametric Mann-Whitney U-test for independent samples (*two-tailed*). Because of multiple comparisons α level (α = 0.05) was lowered using the sequential Bonferroni correction (Bland and Altmann 1995, Abdi 2010).

To detect site specific differences of plant species cover, plots without vegetation cover (100% open water surface) were excluded resulting in a sample size of n = 175. For the comparison of plant species abundance related to human disturbance, transects near the canal (200 m and 10 m) were compared with the ones located in a greater distance (400 m, 600 m, 800 m). Water parameters were analyzed with respect to seasonal changes, site specific differences, differences between deep and surface water, vegetation and open water. Water parameters within vegetation plots were analyzed separately because only sampled during the rainy season. Nitrite, nitrate and phosphate contents of the water were analyzed in order to detect seasonal changes and differences between the low-, the intermediate- and the high-degraded site.

RESULTS

Conductivity: The concentration of dissolved material present in ionic form was generally low for all the study sites (Table 1). During the dry season, mean values ranged from 79 µS cm^{-1} in Vohimarina (D1) to 98 µS cm^{-1} in Andreba (D2). In contrast, during the rainy season mean values decreased significantly ($p \leq 0.001$, n = 160) to a range between 50 µS cm^{-1} for Anororo (D3) and 81 µS cm^{-1} for Vohimarina (D1).

pH: During the dry season, mean values of pH measured in the surface water ranged between 6.8 in Andreba (D2) to 7.0 in Anororo (D3). In the rainy season, the pH ranged from around 6.4 (D2 and D3) to 7.4 (D1) (Table 1). Minimum pH ranged between 5.6 and 6.1 in the dry season and 6.0 to 6.5 in the rainy season (Table 2).

Water level: The water level of Lake Alaotra was subjected to high seasonal fluctuations (Table 1). During the dry season, the water level in the littoral zone ranged from 14.6 cm (D3) to 11.7 cm (D1) and was extremely low in Andreba (D2) with a mean level of three centimeters (Figure 3a, b). In the rainy season it raised up significantly ($p \leq 0.001$, n = 160) ranging between 182 cm in Andreba (D2) and 205 cm in Vohimarina (D1).

Table 1. Mean ($\bar{x}$), standard deviation (SD) and range (Min., Max.) of the water parameters at the three study sites with different level of degradation. (Vohimarina, D1 = low, Andreba; D2 = intermediate, Anororo; D3 = high. Presented are data measured within the open water in the dry season (surface water) and the rainy season – surface water and deep water – determined during four periods a day: 7000–1000h, 1000–1300h, 1300–1600h and 1600–1900h. Asterisks shown with the values of the dry season (surface water) indicate statistical significant differences between dry and rainy season (n = 160). Asterisks presented with the values of the rainy season (deep water) indicate statistical significant differences between surface and deep water (n = 160); significance level: p ≤ 0.05 = *, p ≤ 0.01 = **, p ≤ 0.001 = ***)

		Water parameters	D1 (n= 80)				D2 (n= 80)				D3 (n= 80)			
			$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	Min.	Max.
Surface water (0-10 cm)	Dry season	Conductivity (µS cm^{-1})	80***	12.1	65	131	98***	20	67	156	89***	14.6	62	116
		DO (mg L^{-1})	5.0	1.6	0.1	7.4	3.7	1.9	0.1	7.7	6.3***	1.1	2.3	8.0
		DO (%)	70	21	1.2	99	52	28	1.6	135	92***	18.9	30	123
		pH	6.9***	0.2	5.6	7.3	6.8***	0.3	6.2	7.9	7.0***	0.3	6.1	7.6
		Temp (°C)	29.6***	3.0	21.9	36.4	30.8	4.4	21.3	41.3	29.8***	3.7	23.2	36.8
		Max. Water level (cm)	11.7***	4.6	0.5	23	3.0***	2.3	1.0	10.0	14.6***	4.4	7.0	22
		Light (lux)	919**	699	46	2839	326***	263	14.3	1272	1826***	1407	23	6350
	Rainy season	Conductivity (µS cm^{-1})	64	2.4	60	81	81	9.7	66	109	50	6.1	31	62
		DO (mg L^{-1})	5.3	0.7	3.9	6.6	3.4	2.1	0.2	7.5	3.1	1.5	0.5	8.0
		DO (%)	69	9.4	44	89	50	32	2.3	117	42	22	6.7	110
		pH	7.4	0.3	6.5	8.3	6.4	0.2	6.1	6.8	6.4	0.3	6.0	7.0
		Temp (°C)	25.7	0.9	24.0	29.1	29.6	2.7	26.0	35.3	25.7	1.3	23.5	29.4
		Max. Water level (cm)	205	6.9	195	220	182	9.2	170	205	195	4.9	185	200
		Light (lux)	530	419	10.0	1779	149	143	0.0	525	1066	1422	0.0	6830
Deep water (150 cm)	Rainy season	Conductivity (µS cm^{-1})	64	1.3	58	69	95***	11.3	74	122	50	5.3	41	59
		DO (mg L^{-1})	5.4	0.7	3.2	6.8	2.1*	0.4	1.2	3.1	3.1	0.9	1.7	5.0
		DO (%)	72	9.0	47	89	28**	5.0	16.6	43	41	12.2	22	65
		pH	7.4	0.4	6.5	8.3	6.3***	0.1	6.1	6.6	6.4	0.2	6.0	7.0
		Temp (°C)	25.1***	0.6	23.8	26.6	26.8***	0.7	25.8	28.2	25.0**	0.7	22.4	26.8
		Max. Water level (cm)	205	6.9	195	220	182	9.2	170	205	195	5.0	185	200
		Light (lux)	0.0***	0.0	0.0	0.0	3.8***	16.4	0.0	99	0.0***	0.0	0.0	0.0

Table 2. Mean ($\bar{x}$), standard deviation (SD) and range (Min., Max.) of nitrate, nitrite and phosphate at the three study sites with different level of degradation. (D1 = low, D2 = intermediate, D3 = high. Measurements in the dry season and in the rainy season are presented. Samples were taken during midday (1300h) in the surface water (depth = 0–10 cm). Asterisks shown with the values of the dry season indicate statistical significant differences between dry and rainy season; significance level: p ≤ 0.05 = *, p ≤ 0.01 = **, p ≤ 0.001 = ***)

		Water parameters	D1 (n= 10)				D2 (n= 10)				D3 (n= 10)			
			$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	Min.	Max.	$\bar{x}$	SD	Min.	Max.
Surface water	Dry season	Nitrite (mg L-1)	0.13***	0.02	0.11	0.16	0.04*	0.02	0.02	0.06	0.11***	0.06	0.04	0.17
		Nitrate (mg L-1)	4.36*	2.01	2.70	9.40	2.04***	0.77	1.30	3.60	2.88***	1.24	1.10	4.70
		Phosphate (mg L-1)	1.10	0.52	0.74	2.50	1.18	0.86	0.41	2.50	0.95**	0.23	0.61	1.36
	Rainy season	Nitrite (mg L-1)	0.06	0.01	0.05	0.09	0.07	0.04	0.03	0.15	0.06	0.03	0.03	0.13
		Nitrate (mg L-1)	5.31	0.44	4.70	6.20	5.32	0.77	4.50	6.70	4.96	0.32	4.30	5.30
		Phosphate (mg L-1)	0.97	0.67	0.22	1.07	0.63	0.30	0.29	1.06	0.45	0.25	0.33	2.50

Temperature: Temperatures in the surface water were generally high in the dry season with mean values around 30 °C and an extreme value of 41.3 °C measured in Andreba (D2), the study site with lowest water levels (Table 1). In the rainy season, the mean temperature of the surface water at site D1 and D3 was significantly lower ($p \leq 0.001$, n = 160) than in the dry season with 25.7 °C. No seasonal difference was determined at site D2 with a mean of 29.6 °C in the rainy season (Figure 3c, d). A significant temperature decline (D1, D2: $p \leq 0.001$, n = 160; D3: p = 0.006, n = 160) regarding the water depth occurred within all three sites.

Oxygen: The highest concentrations of dissolved oxygen (DO) in the dry season were measured in Anororo (D3) with a mean of 92% (6.3 mg L^{-1}) implicating supersaturation of oxygen prevailing around midday in Anororo: 43% of the measurements exhibited DO concentrations higher than 100% (Figure 3e, f). Lowest oxygen concentrations during the dry season were measured in Andreba (D2) with a mean of 52% (3.7 mg L^{-1}).

Results of the rainy season showed a moderate decrease of DO at D1 and D2 compared to the dry season, while marked seasonal changes occurred in the highly-degraded site D3. Here the DO concentration dropped significantly ($p \leq 0.001$, n = 160) from 92% (6.3 mg L^{-1}) in the dry season to 41% (3.1 mg L^{-1}) in the rainy season (Figure 3e, f). The degraded sites D2 and D3 were characterized by exceeding low oxygen concentrations within the mornings in the rainy season. The low-degraded site D2 showed a mean of only 22% (1.4 mg L^{-1}), the highly-degraded site D3 a mean of 26% (2.0 mg L^{-1}). Significant differences of oxygen concentrations between the marsh vegetation and the open water were only detected for the low-degraded site D1. Here, DO of the deep water within the vegetation (57%, 4.3 mg L^{-1}) was significantly lower ($p \leq 0.001$, n = 112) than in the open water (72%, 5.4 mg L^{-1}).

Luminosity: The highest luminosity within the surface water in the dry season was measured at D3 with a mean of 1,826 lux (Table 1). The lowest mean value was measured at D2 with 326 lux. A brown coloration of the water during the dry season (lower water levels) was observed more frequently, which was likely related to sediments stirred up by fishes. During the rainy season, a significant decrease of luminosity was observed for all sites with lowest light penetration of 149 lux within the water column in D2 ($p \leq 0.001$, n = 160) and highest luminosity of 1066 lux in D3 ($p \leq 0.001$, n = 160). Low light penetration in the rainy season was often accompanied by a black colored, foul smelling water.

Nutrients: The average nitrate content ranged between 2.04 mg L^{-1} at D2 and 4.36 mg L^{-1} at D1 during the dry season (Table 2). Nitrate rose up to mean values around 5.31 mg L^{-1} and was very similar in all three sites during the rainy season (Table 2).

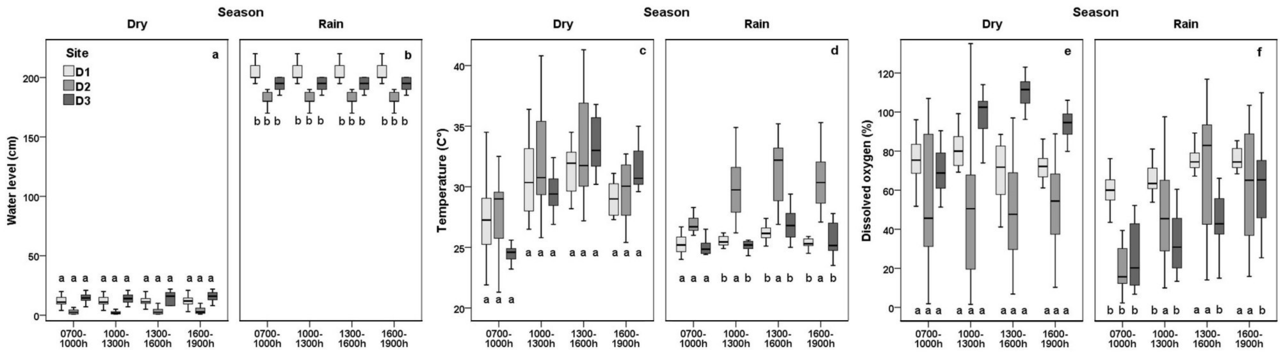

Figure 3. Box–whisker plots (showing median, upper and lower quartiles, and minimum and maximum values) of the daily range of water level (a, b), temperature (c, d) and dissolved oxygen (e, f) at the Lake Alaotra during the dry (left) and the rainy season (right) within the open water of the three study sites shown. (D1 = Vohimarina, D2 = Andreba, D3 = Anororo. Letters indicate statistical significant differences between dry and rainy season (n = 160) analyzed with Mann-Whitney U-Test and corrected by sequential Bonferroni method; significance was determined as p = ≤ 0.05)

Phosphate concentrations showed no site specific differences. PO_4^{3-} ranged between 0.95 mg L^{-1} at D3 and 1.18 mg L^{-1} at D2 during the dry season. PO_4^{3-} ranged from 0.45 mg L^{-1} at D3 to 0.97 mg L^{-1} at D1 during the rainy season (Table 2). Nitrite concentrations differed significantly ($p \leq 0.001$, n = 20) between the sites in the dry season with values between 0.04 mg L^{-1} (D2) to 0.13 mg L^{-1} (D1).

Plant diversity and abundance: A total of 22 plant species were identified within the lake shore vegetation at all three sites. Most of the species are either native or naturalized (reproduce by themselves) (Supplementary Material 5). *Echinochloa pyramidalis* (mean cover = 11.5%), *Phragmites australis* (mean cover = 2.9%), the Polygonaceae *Persicaria glabra* (mean cover = 2.1%) and the Onagraceae *Ludwigia stolonifera* (mean cover = 6.2%) were the most abundant species within this group. Two endemic species were identified: *Argyreia vahibora* (mean cover = 2.2%) and *Cyperus madagascariensis* (mean cover = 0.7%). Two invasive species were the most abundant plant species: *Eichhornia crassipes* appeared with a mean cover of 25% followed by *Salvinia* spp. with 15.6%. While the number of species within the genus *Salvinia* is not yet clarified, it is assumed that at least one invasive species, *Salvinia molesta*, can be found at the lake.

Site specific plant composition: *Eichhornia crassipes* and *Salvinia* spp. were the most abundant plant species within the marsh vegetation bordering the open water. However, there was a high variation in species occurrence and cover between the three sites (Figure 4). The abundance of *E. crassipes* increased with level of degradation: it dominated 53% of the lake shore vegetation at D3 followed by D2 where it had a cover of 24%. At D1, *E. crassipes* was nearly absent with a mean cover of 0.4% and a maximum of 10% cover which differed significantly to the other sites (D1/D2: $p \leq 0.001$, n = 120).

Salvinia spp. characterized the intermediate-degraded site D2 with a significant higher mean cover compared to D1 and D3 (D1/D2: $p \leq 0.001$, n = 120; D2/D3: p = 0.001, n = 114). In D1, the native grass *Echinochloa pyramidalis* was the most abundant plant species with a significant higher cover than in D2 (p = 0.010, n = 120) and D3 (p = 0.014, n = 116). Hydrophytes occurred mainly in the most intact site D1: the water lily *Nymphaea nouchali* covered 8.6% of the open water. Its abundance was significantly lower in the intermediate-degraded site D2 (p = 0.017, n = 120) where *N. nouchali* was rare and in the highly-degraded site D3 (p= 0.009, n= 116) where it was absent. The Menyanthaceae *Nymphoides indica* appeared only in D1.

Total cover: In Vohimarina (D1) and Andreba (D2) the mean vegetation cover within the marsh belt accounted for 72% (SD = 33%, n = 36) and 74% (SD = 34% n = 36). The rest was represented by open water surface (D1: mean = 26%, SD = 32%, n = 36; D2: mean = 23%, SD = 31%, n = 36). In Anororo (D3), the vegetation accounted for only 45% (SD = 27%, n = 36) while the open water surface covered 53% (SD = 29%, n = 36).

Species abundance in relation to human disturbance: At the low-degraded site D1 the species abundance in transects near to the canal (CN) and transects far from the canal (CF) showed no statistical significant difference. At D2 the Onagraceae *Ludwigia stolonifera* had a significantly higher abundance in CN (CN: mean cover = 14.6%, SD = 19.1%; CF: mean cover = 5.3%, SD = 10.8%; p = 0.012, n = 59). Although, *Eichhornia crassipes* exhibited also a

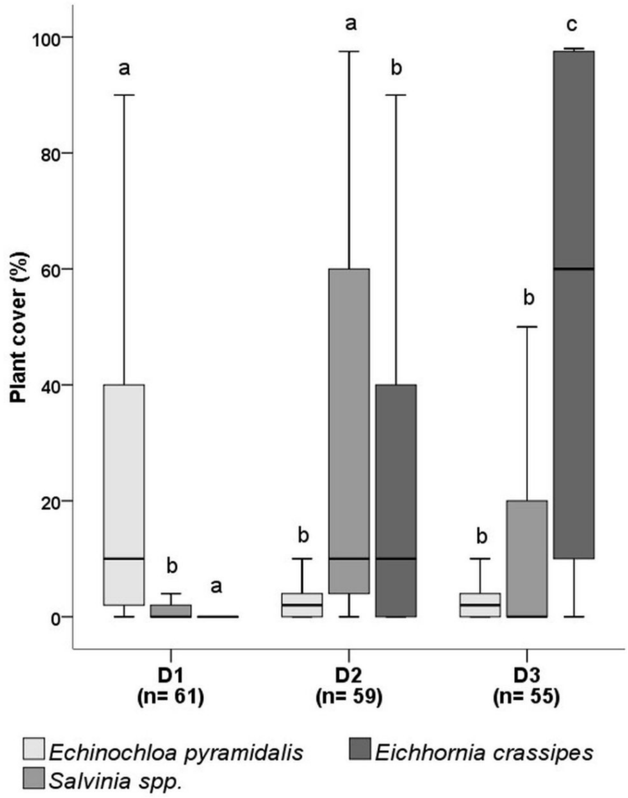

Figure 4. Box–whisker plots (median, upper and lower quartiles and minimum and maximum values) of the three most abundant plant species within the lake shore vegetation of Lake Alaotra. (D1 = Vohimarina, low-degraded; D2 = Andreba, intermediate-degraded; D3 = Anororo, highly-degraded. Differences between sites were analyzed with the Mann-Whitney U-Test using Bonferroni correction. Different letters above columns indicate significant differences; significance was determined at p = ≤ 0.05)

higher abundance in CN at D2 the differences were not significant to CF. At D3, *E. crassipes* and *L. stolonifera* had a significantly higher cover in CN whereas *Salvinia* spp. was significantly less abundant. *E. crassipes* had a mean cover of 85.4% (SD = 28.3%) in CN and a significantly lower ($p \leq 0.001$, n = 55) cover of 34.4% (SD = 35.3%) in CF. *L. stolonifera* occurred with a significantly higher (p = 0.004, n = 55) mean cover of 12.9% (SD = 13.4%) in CN compared to CF (mean cover = 3.5%, SD = 7.73%). In contrast, *Salvinia* spp. were significantly less abundant (p = 0.036, n = 55) in CN (mean cover = 18.8%, SD = 4.6%) than in CF (mean cover = 29.0%, SD = 15.6%).

Vegetation structure: Vegetation structure varied between the three study sites and vegetation density increased with level of degradation. At D3 mean density was 76.5% at the ground level (0–3 cm) whereas it was only 25.9% at D1 (Supplementary Material 6). However, regarding the vertical vegetation density profile (Figure 5a, b) the sites differed especially in the open water. Within the lake shore vegetation (Supplementary Material 7) density declined from 78.3 % (0–3 cm) to 39.6% (50–100 cm) at site D3, 53.5% (0–3 cm) to 19.4% (50–100 cm) at D2 and from 33.2% (0–3 cm) to 17% (50–100 cm) at D1. In the open water (Supplementary Material 8) vegetation density ranged between 73.6% (0–3 cm) and 5.0% (50–100 cm) at site D3, 48.8% (0–3 cm) to 3.4% (50–100 cm) at D2 and 15.3% (0–3 cm) to 0.3% (50–100 cm) at D1. Regarding the vegetation height, at D1 and D2 vegetation reached a maximum height of 300–500 cm while the maximum height measured at D3 was only 200–300 cm (Supplementary Material 6). Accordingly, D3 was characterized by lower but denser vegetation whereas the intermediate- and low-degraded sites showed higher and more open vegetation.

DISCUSSION

CLASSIFICATION OF LAKE ALAOTRA. Talling and Talling (1965) classified the African lakes based on their conductivity. Lake Alaotra with its low conductivity (50–98 µS cm^{-1}) belongs to Class I, characterizing lakes depending largely on rain and run-off or rivers of low salt content (Talling and Talling 1965, Payne 1986, Talling 2009) (e.g., Lake Victoria, Lung'ayia et al. 2001; Lake Tana, Kebede et al. 2006; and Lake Malawi, Chale 2011). Low conductivity is common for lakes fringed by marshes (Howard–Williams and Lenton 1975) like Lake Alaotra, as the vegetation absorbs and accumulate ions when inflow is passing through. Consequently, the overall low conductivity leads to a low buffer capacity (alkalinity) of Lake Alaotra (cf. Talling and Talling 1965). Although highly vulnerable to acidification, Lake Alaotra still has a neutral pH (6.8–7.0) with partly slight acidic values around 6.0. Pidgeon (1996) described an acidic character of the open lake water (4.3–7.4). Current results are more similar to measured pH values (6.8–7.3) in the 1970s (Moreau 1980). Studies by Arhonditsis et al. (2003) and Araoye (2009) confirmed the spatial and temporal heterogeneity of pH in a lake system, which are derived mainly from photosynthetic and respiratory processes as well as nutrient loads (decomposition of organic matter and pollution). Measurements over a restricted time or of a small sample size are therefore highly influenced by daily, seasonal and regional patterns.

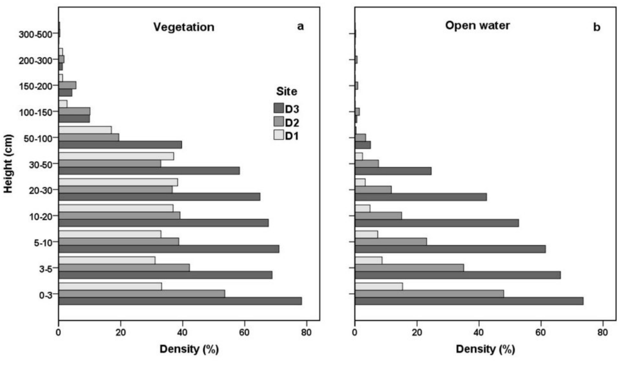

Figure 5. Vertical vegetation density (mean density in %) of the plots presenting the lake shore vegetation (a) and the open water (b) of the three study sites. (D = degradation level; 1 = low, 2 = intermediate, 3 = high)

WATER LEVEL. Recent studies show that Lake Alaotra has lost ca. 5 km² of open water surface over the past 30 years (Bakoariniaina et al. 2006). The cumulative effect of multiple factors can further aggravate this situation and eventually lead to the disappearance of the lake, these include: (i) erosion of surrounding hills leading to sedimentation and siltation downhill, (ii) higher evaporation due to vegetation clearance, and (iii) a lower water recharge into the lake due to rainwater percolation in fractures and faults and transformation of water and streams for agricultural irrigation (ibid). Besides a reduction in water surface, a diminution in its water depth as a main driver for the alteration of the abiotic conditions is crucial. Although no specific data is available for the evolution of the depth during the last century, the brownish red coloration of the rivers discharging into Lake Alaotra indicate the lake clearly as a sink for sediments (especially during the rainy season).

WATER TEMPERATURES AND OXYGEN LEVEL. The low water levels of Lake Alaotra imply high water temperatures due to quick heating of the water column. Average temperatures around 30 °C were reached in the surface water with a maximum of 41.3 °C measured in Andreba (D2). Other shallow lakes in the tropics show similar high temperatures in the upper water layers. The surface water of Lake George in Uganda for example reached temperatures of 36 °C (Ganf 1974).

The combination of low water levels and high temperatures can lead to a precarious decrease of dissolved oxygen in the water (Lévêque 1997). During the dry season, the low water column of the Lake Alaotra is heated up rapidly leading to very low solubility of dissolved oxygen (1.2%, 0.1 mg L^{-1}). A high oxygen demand from decaying organic material can deplete the level of oxygen as well (ibid). Typically for seasonal flooded wetlands such as the Alaotra wetlands, large amounts of organic matter and nutrients are carried into the lake when the first rains arrive (sensu Payne 1986). Additionally, the lower parts of standing vegetation are subjected to decomposition when water level rises. The considerable drop of the luminosity in the rainy season accounts for the deposition of suspended material in the lake. The marsh vegetation is normally acting like a buffer zone between the lake and surrounding agricultural areas because of its high nutrient uptake (Fisher and Acreman 2004). The high human population at sites D2 and D3 increases the pressure on the marshes. Large parts of the marshes have been converted into agricultural area minimizing their buffer capacity. This is aggravated by an increased nutrient load due to use of fertilizers and pesticides, decaying rice straws after rice harvest and direct wastewater discharges into the lake because of absence or lack of sanitation. Consequently, hypoxic conditions (1.4–2.0 mg L^{-1}) occurred at the more degraded sites during morning periods of the rainy seasons.

POSSIBLE RESPONSE OF AQUATIC COMMUNITIES TO HYPOXIA. It is assumed that dissolved oxygen is becoming a determining factor for aquatic organisms in the Lake Alaotra. The shallow waters in the littoral zone represent habitat for aquatic invertebrate communities as well as foraging and nursery ground for fish species (Gilinsky 1984, Schramm and Jirka 1989, Petr 2000) and will be particularly affected. However, high water temperatures and low oxygen concentrations in the littoral of Lake Alaotra allow only zooplankton, macroinvertebrate and fish species with morphological, physiological and behavioral adaptations to resist such conditions (Marcus 2001, Ekau et al. 2010, Chang et al. 2013). Lake Alaotra's zooplankton is dominated by the water flea family Daphniidae (Pidgeon 1996). Several studies have proved a high hypoxia resistance of species belonging to the Daphniidae (Larsson and Lampert 2011, Smirnov 2013) while zooplankton abundance and distribution is generally negatively affected (Stalder and Marcus 1997, Qureshi and Rabalais 2001, Roman et al. 2012, Chang et al. 2013). The aquatic macroinvertebrate taxa in Lake Alaotra are represented mainly by molluscs (Limnaea), mosquitoes (Culicidae), dragonflies (Coenagrionidae), mayflies (Baetidae), water-bugs (Heteroptera) and diving beetles (Dytiscidae) (Pidgeon 1996). Although, invertebrates exhibit a wide range of adaptations (Grieshaber et al. 1994, Verberk et al. 2008a, b) depleted oxygen levels can at least contribute to the near absence (Efitre et al. 2011). The fact that hypoxia tolerance is species- and stage-specific and varies widely (Miller et al. 2002) makes it difficult to predict changes in species composition, trophic pathways and productivity without further identification of the macroinvertebrate and zooplankton species of Lake Alaotra.

The ichthyofauna of Lake Alaotra is nowadays dominated by the hypoxia tolerant invasive *Tilapia* spp. and the snakehead fish *Channa maculata* (Moreau 1979, Pidgeon 1996, Wallace et al. 2015). Snakeheads are able to uptake atmospheric oxygen (Yu and Woo 1985) while the aquatic breathing *Tilapia* spp. have hemoglobin with higher affinity to oxygen and can cope with hypoxia up to 2 $mg.L^{-1}$ (Dusart 1963, Philippart and Ruwet 1982, Verheyen et al. 1985). The native Anguillidae is less tolerant to hypoxia than *Tilapia* spp. (Hill 1969) and the tolerance range of oxygen concentration of the only left endemic fish species of Lake Alaotra, *Rheocles alaotrensis* (Batoidae) is not yet documented. In the near future those invasive species may outcompete completely the remaining native and endemic fish species due to their highly adapted metabolism to oxygen poor environments.

INTACT MARSHES VERSUS DEGRADED MARSHES. Regarding oxygen levels, three site-specific differences can indicate the important role of marshes. (i) Vohimarina exhibited permanent normoxic levels whereas prolonged hypoxia occurred in the perturbed waters of Andreba and Anororo in the rainy season. A lower nutrient discharge into the lake and a higher nutrient uptake by the marsh belt is assumed at the low-degraded site. (ii) The open water of Vohimarina exhibited significant higher oxygen levels in comparison to the marsh belt. The water column of marshes is naturally characterized by lower oxygen concentrations than the open water based on its high primary production resulting in an increased oxygen demand from decomposition processes (Gaudet and Muthuri 1981, Howard-Williams and Thompson 1985, Lévêque 1997). In the degraded sites equalized oxygen conditions within the open water and the marshes might be the result of marsh clearance. (iii) At the highly-degraded site, a wide seasonal range of oxygen concentration has been observed. While hypoxic conditions were frequent in the rainy season, supersaturation arose in the dry season. An intact marsh belt seems to prevent near-shore areas from strong seasonal changes, since it can remove high amount of nutrients passing through at the beginning of the rainy season (Howard-Williams and Gaudet 1985). Related to nutrient discharge, supersaturated as well as hypoxic water could be a sign of eutrophication, which is nowadays widespread in tropical water bodies (Dudgeon et al. 2006).

EUTROPHICATION. Eutrophication of lakes causes rapid growth of phytoplankton and aquatic plants with severe implications for water quality, food web, biotic community structure, biogeochemistry and littoral plant communities (Schindler 2006, Smith et al. 2006, Moss et al. 2011, Søndergaard et al. 2013). Due to the complexity of nutrient dynamics a high frequency of measurements over a long period is still necessary to enable drawing a representative statement about the trophic state of Lake Alaotra. Nevertheless, the current measurements allow to sketch first trends.

Although surrounded by large cultivated areas, the nitrate and nitrite values for Lake Alaotra are comparatively low. Both are far below the guideline values for drinking water with 50 $mg.L^{-1}$ for nitrate and 3 $mg\ L^{-1}$ nitrite (WHO 2011). However, a comparison to nitrate measurements 20 years ago (Pidgeon 1996) manifests a doubling of the nitrate content in the Lake Alaotra.

Generally, low nitrogen contents are common for African lakes (Talling and Talling 1965). Nitrogen often occurs in its reduced form (ammonia) or bound in living plant stocks and sediments (Gaudet and Muthuri 1981, Payne 1986). The overall increase in nitrate during the rainy season can be explained by (i) nutrients (agricultural and natural origin) that were accumulated in the soil and washed out in the rainy season and (ii) large amounts of organic matter that reaches the lake with the first rain.

Elevated phosphate concentrations (1.18 $mg\ L^{-1}$), denote a beginning eutrophication. Samples taken in the 1970s (Moreau 1980) and in the 1990s (Pidgeon 1996) indicated lower concentrations. The origin of the phosphate might be from the release from anoxic sediments (internal loading) of Lake Alaotra and from external sources like pesticides, fertilizer and leaching from the weathered hills. Algae blooms (red or brown algae), observed in calm and shallow waters during the dry season at D2 could be directly related to the higher phosphate concentrations measured at Andreba (D2). Internal loading is accelerated by high water temperatures (Søndergaard et al. 2001) and therefore favorably occurs in quickly heated up shallow waters, during periods of high air temperatures and anoxic conditions.

Enhanced phosphate concentrations, algae blooms, black colored and foul-smelling water and hypoxia are strong signs of eutrophication (Stahl 1979, Lamers et al. 1998, Lamers et al. 2002, Prepas and Charette 2003).

PLANT COMMUNITY CHANGES. In our study a total of 22 plant species were identified, considering the littoral zone of Lake Alaotra. Pidgeon (1996) found a similar number of 23 plant species when he sampled this zone. A comparison of the plant composition points out the changes in species dominance within the fringe area of the marsh belt. Twenty years ago *Cyperus madagascariensis* and *Cyclosorus interruptus* were highly abundant within the lake shore vegetation, whereas nowadays they are continuously being reduced. *Cyperus madagascariensis* stands are used by local people for houses and mats (Mutschler 2003, Rendigs et al. 2015) and burned to extend the agricultural areas, pasture or open areas for fishing (Andrianandrasana et al. 2005). *Cyclosorus interruptus* was mainly observed inside of intact marsh vegetation of Lake Alaotra although it is known to occur in floating fringe areas of the marsh belt exposed to the sun (Hill et al. 1987, Geron et al. 2006). The growing anthropogenic impacts through cultivation, wastewater, biomass harvesting, fire, grazing and fishery is leading to the formation of new plant community types at Lake Alaotra. The most affected zone is the fringe area of the marsh belt due to its easy accessibility. Nowadays, fast growing species like *Ludwigia stolonifera*, *Echinochloa pyramidalis*, *Eichhornia crassipes* and *Salvinia* spp. characterize the vegetation fringing the water body. *Eichhornia crassipes* and *Salvinia* spp. also dominate the open water vegetation while the water lily *Nymphaea nouchali*, which covered once large parts of the lake before 1950 (Pidgeon 1996), seem to disappear and is only found where human activities are low.

The distribution pattern of the plant species at Lake Alaotra reflect the ongoing changes in species composition and show trends determining plant species abundance and composition in the future: (i) spread of invasive species: *Eichhornia crassipes* shows highest abundance where disturbance is most developed: in Anororo (D3) where intensive clearance has reduced lake shore vegetation to around 50% and in canal adjacency (D2 and D3), where nutrient load and mechanical disturbance tends to be highest. (ii) Raise of disturbance-tolerant native species: the native *Ludwigia stolonifera*, known as a plant with intense vegetative growth and rapid expansion (Sheppard et al. 2006, Lambert et al. 2010, Thouvenot et al. 2013), has become one of the prevailing species within the last twenty years (Pidgeon 1996) with a significant higher abundance in areas close to the canal. A study of Njambuya and Triest (2010) at Lake Naivasha (Kenya) has shown the ability of *L. stolonifera* to prosper in the presence of the *E. crassipes*. (iii) Plant species restriction to low disturbed sites: the wide spread of *Nymphaea nouchali* and *Echinochloa pyramidalis* exclusively at the low-degraded site (Vohimarina) denotes their sensitivity toward disturbance which is most likely physical damage by boat traffic and the dense mats of *Salvinia* spp. and *E. crassipes* which may restrict them from light and pressing them physically down.

EFFECTS OF THE VEGETATION SHIFT ON AQUATIC AND TERRESTRIAL COMMUNITIES. According to Huston (1979) only species capable of rapid recolonization and growth will persist to increased disturbance levels. Moreover, increased nutrient loads promote the dominance of a few highly competitive species and restrain other species (Pausas and Austin 2001). Changes in plant species composition and abundance during the last two decades and current spatial distribution pattern of plant species at Lake Alaotra highlight trends that will determine the plant community and abundance in the future. The spread of invasive and disturbance-tolerant native species as well as the disappearance of natural species communities occurring still at intact sites will be the main processes in vegetation changes affecting Lake Alaotra on an ecological and economic level (cf. Rakotoarisoa et al. 2015).

Eichhornia crassipes and *Salvinia molesta* have worldwide altered biodiversity, ecosystem functioning and services in wetlands (Mailu 2001, Calvert 2002, Charles and Dukes 2007). Many African lakes are nowadays invaded by invasive species (Ogutu-Ohwayo et al. 1997, Mailu 2001). Direct effects of the *E. crassipes* are modification of water clarity, monopolization of light, increased sedimentation, higher evapotranspiration rates, decrease of dissolved oxygen, nitrogen, phosphorous, heavy metals and other contaminants, changes in key habitat structure and waterway clogging (Toft et al. 2003, Jafari 2010, Villamagna and Murphy 2010, Katagira et al. 2011). Particularly the high evapotranspiration rates and sedimentation by the rotting mats (Sambasiva Rao 1988, Villamagna and Murphy 2010) pose a problem for Lake Alaotra due to its shallowness. Sediment deposits due to decomposition of dead plant material of floating *E. crassipes* mats will most likely play a minor role for the water depth and siltation of the lake as the sedimentation from the eroded hills has a strong impact on the lake.

The effects of *Eichhornia crassipes* on other aquatic communities are disparate: the abundance and diversity of epiphytic zooplankton and aquatic invertebrates are supported by the structural complexity of the *E. crassipes* roots and the increased habitat heterogeneity while the decreased food availability (phytoplankton) restricts their occurrence (Villamagna and Murphy 2010). At Lake Naivasha (Kenya) *E. crassipes* provides refuge for many invertebrates (Adams et al. 2002). Similarly, Pidgeon (1996) found higher species diversity in *E. crassipes* mats compared to aquatic grassland at Lake Alaotra. Thus, Pidgeon (1996) assumed that invertebrate abundance in the lake does not depend on diversity but density of aquatic plants.

Fish might benefit from a high abundance of epiphytic invertebrates, breeding grounds provided by *E. crassipes* and reduced predation risk (Mailu 2001, Villamagna and Murphy 2010) as it was the case in Lake Victoria in the 1990s (Mailu 2001, Njiru et al. 2002). However, the low phytoplankton biomass and oxygen concentration under the dense mats can affect negatively planktivorous fish and hypoxia sensitive species (Villamagna and Murphy 2010). Gichuki et al. (2012) documented the alteration of fish communities at Lake Victoria by *E. crassipes* promoting anoxia tolerant species. Hence, hypoxia-tolerant species of Lake Alaotra could benefit from the oxygen poor conditions under *E. crassipes* mats.

The terrestrial fauna might be affected by the higher density of *E. crassipes* modifying the habitat structure and heterogeneity. Harper et al. (2002) noted that foraging for the fish eagle is impeded by the *E. crassipes* mats covering Lake Naivasha (Kenya). Villamagna et al. (2012) suspected that changes in the seasonal waterbird community on Lake Chapala (Mexico) were related to *E. crassipes* cover. In Anororo the monospecific and dense *E. crassipes* mats have already caused wide changes in vegetation structure that can have a considerable bearing on the Lake Alaotra waterfowl and other terrestrial communities. Whether *E. crassipes* negative or positive influence prevails seems to depend on the size of the mats formed by *E. crassipes*, original communities and geographic distribution (Bailey and Litterick 1993, Villamagna and Murphy 2010, Chowdhary and Sharma 2013).

CONCLUSION

The results of this study demonstrate the continuously growing anthropogenic pressure on the Alaotra wetlands altering both water body and vegetation. Our major conclusions are that: (i) Low water levels in the dry season raising the water temperatures and favoring hypoxic conditions. (ii) A disturbed buffer function of the marshes results in depleted oxygen concentrations. (iii) A low buffer capacity makes the lake vulnerable to acidification. (iv) Signs of eutrophication such as foul smelling water, algae blooms and increased phosphate concentrations call for further long-term investigations of the trophic state of Lake Alaotra. (v) Anthropogenic activities on the lake and the surrounding marshes promote invasive plant species and disturbance tolerant species and repress native species. (vi) The encroachment of invasive species is highly correlated with human population density.

With a growing human population, resulting in increased demand for fish and agricultural products, the Alaotra wetlands will undergo further pressures. However, it is unclear how much more the lake can buffer in terms of water quality and vegetation alteration. If erosion, sedimentation, marsh clearance and nutrient load proceed unchecked, the cumulative effects may lead to an entire collapse of the Alaotra wetlands.

This article provides an insight in the current ecological state of Lake Alaotra. In consideration of the given facts about the demographic trends it is crucial to close gaps in knowledge about the ecological processes and functions of the lake to enable targeted management strategies and interventions. Further research should therefore (i) focus on the influence of the Alaotra marshes on the dissolved oxygen content in the water to estimate the minimum marsh belt width, which can guarantee its intact buffer function. For this purpose, the nutrient uptake and retention as well as the oxygen gradient from the fringe to the inner marshes has to be analyzed. (ii) To give a better understanding of nutrient sources and cycles, and the eutrophic state of Lake Alaotra, additional parameters like ammonia, total nitrogen and phosphorus as well as chlorophyll-a concentrations, lake turbidity using a Secchi disk and the biological oxygen demand are highly needed. Moreover, an investigation of the exchange processes between the sediment and the open water column and their role in nutrient cycling would clearly lead to a better understanding of the ongoing chemical processes within Lake Alaotra. (iii) As the Lake Alaotra plant community composition and structure undergoes notable changes and the knowledge about the flora of the lake is incomplete and outdated, a plant inventory is needed to identify the occurring species and to know about their abundance. (iv) Further, studies regarding the disturbance tolerance of the plant species of Lake Alaotra can help to understand the alteration of the local plant community composition.

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

Table S1: Mean, standard deviation (SD) and range (Min., Max.) of the water parameters at the three study sites with different level of degradation.

Table S2: Mean, standard deviation (SD), and range (Min., Max.) of the water parameters measured within the open water at Vohimarina during the four daily periods.

Table S3: Mean, standard deviation (SD), and range (Min., Max.) of the water parameters measured within the open water at Andreba during the four daily periods.

Table S4: Mean, standard deviation (SD), and range (Min., Max.) of the water parameters measured within the open water at Anororo during the four daily periods.

Table S5: Plant species, growth forms, site specific and plant species cover in %.

Table S6: Shown are means and standard deviation of the vertical vegetation density at the three sites.

Table S7: Shown are means and standard deviation of the vertical vegetation density of the lake shore vegetation at the three sites.

Table S8: Shown are means and standard deviation of the vertical vegetation density on the open water at the three sites.

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Water hyacinth (*Eichhornia crassipes*), any opportunities for the Alaotra wetlands and livelihoods?

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ABSTRACT
Species invasions are one of the world's most severe conservation threats. The invasive water hyacinth (*Eichhornia crassipes*) is one of the most troublesome plants in the world. It appears in over 50 tropical and subtropical countries. This plant species causes several ecological and socioeconomic problems affecting ecosystems and local livelihoods. The water hyacinth occurs in the Alaotra wetlands encompassing the largest lake of Madagascar. The Alaotra region is renowned as Madagascar's bread basket as it is the biggest rice and inland fish producer. The current study collected socioeconomic data from the Alaotra wetland stakeholders within three locations around Lake Alaotra to contextualize local livelihoods and to identify the drivers and barriers for the utilization of this plant. Methods of control seem to be unrealistic due to institutional and financial limitations in Madagascar. Using the plant as fertilizer, animal fodder or for handicrafts seems to represent a feasible alternative to improve the livelihood of the local population. However, local concerns about livelihood security may hinder acceptance of such new alternatives. Providing information as well as financial and technical support to local stakeholders may help encourage the use of the water hyacinth in the Alaotra region.

RÉSUMÉ
Les espèces envahissantes ont été récemment identifiées comme l'une des principales menaces pour la protection de la biodiversité. La jacinthe d'eau (*Eichhornia crassipes*) est l'une des plantes envahissantes les plus problématiques au monde. Elle est connue dans plus de 50 pays tropicaux et subtropicaux. Cette plante est la source de nombreux problèmes écologiques et économiques et affecte par conséquent les écosystèmes ainsi que les moyens de subsistance des populations humaines des régions concernées. Elle est rencontrée au niveau des zones humides de l'Alaotra englobant le plus grand lac de Madagascar, le premier grenier à riz de l'île et qui tient une place importance pour la pêche. Les méthodes pour contrôler la prolifération des jacinthes d'eau semblent ne pas pouvoir être appliquées à cause des limitations institutionnelles et financières de Madagascar. L'utilisation de la jacinthe d'eau, comme fertilisants, fourrage ou dans la production artisanale, pourrait représenter une alternative pour améliorer les moyens de subsistance de la population locale. Au cours de cette étude, des données socioéconomiques touchant les parties prenantes des zones humides de l'Alaotra ont été collectées dans trois localités qui se différencient au niveau de la dégradation de l'habitat naturel (Anororo, Andreba et Vohimarina). Les objectifs de cette recherche consistent d'une part à décrire des différents moyens de subsistance locale et d'autre part à identifier les moteurs et barrières de l'utilisation de la jacinthe d'eau. Le contexte général affectant la sécurité des moyens de subsistance pourrait bloquer l'acceptation de l'utilisation de cette plante. Cependant l'information ainsi que des supports financiers et techniques pour les parties prenantes locales sont des moteurs importants pour encourager l'usage de la jacinthe d'eau au niveau du lac Alaotra.

INTRODUCTION
The water hyacinth (*Eichhornia crassipes*, Pontederiaceae) is an aquatic plant, originating from the Amazon Basin. It is listed by IUCN as one of the "100 most invasive species" in the world (Lowe et al. 2000) due to its high reproduction rate, the complex root structure and the formation of dense mats with up to two million plants per hectare (Gopal 1987, Villamagna and Murphy 2010). The water hyacinth is to date recognized as invasive in over 50 tropical and sub-tropical countries on five continents (Africa, Australia, Asia and America and for Europe in Portugal) (Gopal 1987, Villamagna and Murphy 2010). The spreading of the plant can lead to great ecological, social and economic problems (Kull et al. 2014). The plant can reduce light and oxygen leading to deteriorating water quality, increase water loss due to high evapotranspiration and thus negatively affect the flora and fauna. Moreover it can hinder transportation, fishing and block intakes for hydropower and irrigation schemes affecting therefore the livelihood of local communities (Calvert 2002). Furthermore, the water hyacinth represents a microhabitat for disease vectors (snails for bilharzia or *Anopheles* sp. for malaria) and therefore constitutes a threat to

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human health (Masifwa et al. 2001, Plummer 2005).

Globally, a number of methods are used to manage and control the water hyacinth: the manual and mechanical control requires high expenses. In China, removing water hyacinth comes at a cost of more than US$ 12 Million per year (Jianqing et al. 2001). Chemical control, using 2,4-D or glyphosate, is seemingly a more economically feasible option. In the USA, chemical control is estimated to cost US$ 183 per hectare (Charudattan et al. 1996). However, in many countries public opinion is strongly against the use of chemicals in water bodies, which are oftentimes used for drinking purposes (ibid). Biological control, though less widely applied, uses the weevil species *Neochetina eichhornia*, *N. bruchi* and the moth *Sameodes abligutallis* which adults feed on water hyacinth leaves and the larvae tunnel in petioles (Coetzee et al. 2009). Pathogens can also be used to control the water hyacinth. In Egypt, the fungus *Alternaria eichhornia* was condensed in cottonseed oil emulsion and spread on the water hyacinth killing 100% of the plants seven weeks after application (Shabana et al. 1995). Biocontrol is economically feasible and environmentally viable but requires several years of implementation (Charudattan et al. 1996).

As an alternative to mechanical, chemical or biological controls, the economic utilization of this invasive plant has to be considered. Globally, the water hyacinth is used in China, Indonesia, India, Malaysia, Bangladesh, Sri Lanka, Thailand, Philippines and in some African countries such as Kenya and Nigeria for producing fertilizers, handicrafts, paper, biogas, fodder, briquettes, furniture and to clean industrial waste water by phytoremediation (Jafari 2010, Ndimele 2011, Patel 2012). However, in remote poor regions in developing countries the use of water hyacinth is hindered by absence of electricity, lack of technology and poor infrastructure (e.g., Gunnarsson and Petersen 2007).

The water hyacinth (vernacular name: *tsikafona* or *tsikafoka*) occurs in Madagascar's largest wetland, located in the Alaotra-Mangoro region encompassing about 23,000 ha of freshwater marshes. Lake Alaotra is the largest freshwater lake in Madagascar (20,000 hectares of open water); with an average depth of 1–1.5 m, it is a very shallow lake (Ferry et al. 2009). The natural freshwater marshes fringing the lake are dominated by common reed (vernacular name: *bararata*) (*Phragmites australis*) and cyperus (vernacular name: *zozoro*) (*Cyperus madagascariensis*). The marsh vegetation supports endemic species such as the Alaotran gentle lemur (vernacular name: *bandro*) (*Hapalemur alaotrensis*) which is the only permanent swamp living primate in the world (Andrianandrasana et al. 2005, Ralainasolo et al. 2006, Guillera-Arroita et al. 2010, Waeber et al. In press). The water hyacinth occurs in both the open water where it is freely floating and moved by winds as well as in the marsh vegetation.

The water hyacinth has been introduced to Madagascar at the beginning of the twentieth century as ornamental plant (Binggeli 2003) and was identified later as serious threat by Perrier de la Bathie (1928). Goarin (1961) reported that the plant was already present in the Lake Alaotra during the period of French colonization.

Lake Alaotra is home to over 560,000 people who live along its shores (INSTAT 2013). Rice cultivation and fishing constitute the main income in the region, resulting in an increasing pressure on the marshlands (Ralainasolo et al. 2006, Copsey et al. 2009). To support a steadily growing human population in the region, many marshlands have been converted into rice fields during dry season when the water level is low (Ranarijaona 2007). The surrounding hills are dominated by open grasslands and subject to continuous erosion. This leads to the reduction of the lake water surface by sedimentation (Raharijaona-Raharison and Randrianarison 1999, Wright and Rakotoarisoa 2003, Bakoariniaina et al. 2006). In the last 30 years, Lake Alaotra has lost 5 km^2 in size (Bakoariniaina et al. 2006). Fish catches (4,000 tons in 1960 to 2,000 tons in 2004) are declining due to overfishing. Rice production decreased by approximately 40% in recent years due to deposits of sand and infertile laterite in poorly maintained irrigation systems and deterioration of fertile soils (Pidgeon 1996, Rakotonierana 2004, Razanadrakoto 2004, Bakoariniaina et al. 2006). Consequently, reduced incomes are further exacerbating the pressures on the remaining marshlands.

According to Lammers et al. (2015), the water hyacinth is found everywhere on Lake Alaotra, building occasionally thick and dense mats spanning hundreds of square meters. The plant, however, is barely used in the region; a few people occasionally use it to produce compost, to feed pigs and geese and for installing fish traps on the mats. It is currently unclear to what degree the water hyacinth in the Alaotra region is affecting local livelihoods (sensu Chambers and Conway 1991), or whether the plant could be used systematically and economically by a wider range of stakeholders. The objective of this study is to identify the potential drivers and barriers to the use of water hyacinth by depicting the socioeconomic conditions of the concerned local stakeholders. The basic assumption is that the plant has negative ecological and economic impacts. Using the plant as an additional source of income could potentially benefit a wider range of stakeholders; this could alleviate its possible impacts and diminish pressure on the marshland ecosystem. A typology of the main stakeholders of the Alaotra wetlands is provided to describe the qualitative and quantitative features of local livelihoods. An assessment of the local population's perception and knowledge of water hyacinth as well as current and potential usages are discussed.

METHODOLOGY

Field work was conducted from November 2012 to April 2013 in the Lake Alaotra region. Three study sites were chosen according to the level of marsh degradation (cf. Lammers et al. 2015): Vohimarina (E48° 32′ 59.7″, S17° 20′ 02.4″, 761 m), situated on the north shore of the lake, with about 500 inhabitants, entails 302 hectares of intact marsh vegetation. Anororo (E48° 26′ 01.4″, S17° 30′ 44.0″, 724 m) on the western coast of the lake has over 8,000 inhabitants, and encompasses over 9,850 hectares of marshland vegetation. Andreba Gare (E48° 30′ 08.0″, S17° 37′ 51.7″, 739 m), located in the eastern part with 4,000 inhabitants, contains 235 hectares of marshes (Andrianandrasana et al. 2005).

Qualitative and quantitative data focusing on socioeconomic conditions and the use of water hyacinth were collected using two methods: group surveys and semi-structured interviews. Oral information from the village heads (*chef fokontany*) was considered to identify and select the main local stakeholders (sensu Reed 2009) of the Alaotra wetland system. Group surveys (cf. McNamara 2003) were conducted to assess the socioeconomic conditions for each of the households of the four stakeholder groups (rice cultivators, fishers, vegetable farmers and cattle breeders). Twelve meetings representing each of the four resource user groups were organized in the three study sites with a total of 120 stakeholders. The survey covered livelihood characteristics such as the individual daily income, the description of targeted resources (e.g., fish or rice), the type and use of equipment and application of respective techniques as well as time allocation, associated investments, costs and benefits and the encountered daily livelihood challenges (cf. Supplementary Material).

Semi-structured one-on-one interviews (Bernard 2005) were conducted to assess the potential drivers and barriers of the use of the water hyacinth. Again, a total of 120 stakeholders (others than the ones engaged in the survey) were interviewed (rice cultivators, fishermen, vegetable farmers and cattle breeders). The interview was subdivided into (i) personal perception of resources and value system; (ii) assessment of personal attitudes through the depicting of possible future resource use scenarios; (iii) awareness and potential use of the water hyacinth as an alternative source of income (cf. Supplementary Material).

All data were analyzed using MAXQDA 2011, a qualitative data analysis software. This software is designed to facilitate qualitative data analysis by coding and categorizing the answers expressed by each interviewee.

RESULTS

STAKEHOLDER TYPOLOGY. The main stakeholders at Lake Alaotra were fishermen and rice cultivators. A majority, however, had several activities (e.g., vegetable farming and breeding) and depend on the marshes for arable land and for obtaining several plant species for their livelihoods. Cyperus (*Cyperus madagascariensis*) is the most widely used plant species in this region, and together with the common reed (*Phragmites australis*), are deeply rooted in Sihanaka tradition and used for constructing houses, fences, animal shelters, handicrafts, fish traps as well as during traditional ceremonies (Rendigs et al. 2015).

Across the three study sites, 38% of the stakeholders interviewed (n=46) earn less than US$ 2.5 per day (exchange rate MGA/USD=2,884), 60% (n=72) earn US$ 2.5 to US$ 5 and 2% represented by retired officials (n=2) earn more than US$ 5. In contrast, 60% (n=72) of the stakeholders stated that they cannot make ends meet, 30% (n=37) could but only without mishaps, 8% (n=9) with difficulties and 2% represented by the same retired officials (n=2) do not have problems to ensure their livelihoods. Most individuals therefore are already under severe economic stress.

FISHERMEN. Only practiced as source of local subsistence a century ago, fishing in the Alaotra developed gradually with the introduction of fishnets and opportunities created by the railroad for selling fish outside the region (Moreau 1979). Several types of fishing tools exist at Lake Alaotra; their use depends on the targeted species and on the season. The fishing nets are generally used year-round and target various fish species according to the mesh size. The fishing rods (*fintana*), spears, sticks (*jorira*) and fish traps are mainly used during the rainy season as long as high water levels allow their usage. Fish traps and fishing nets are the most common tools. A single fish trap and one kilometer of fishing reel sell for US$ 0.75 and US$ 3.5, respectively. Depending on the size a canoe sells for US$ 35–100. Fish catch is now reserved mainly for cash income rather than subsistence. The fish price depends on the season (and peaks during the period of rice harvesting), the buyers (local or national collectors) and the targeted species (Copsey et al. 2009). The common carp (vernacular name: *besisika*) (*Ciprinus carpio*) is the most expensive fish followed by *Tilapia spp.* (vernacular name: *lapia*) (Cichlidae) and the Asian snakehead (vernacular name: *fibata*) (*Channa maculata*). A full ten liter bucket (ca. 16 kg) of common carp costs US$ 25, while tilapia or Asian snakehead brings US$ 18 and the Alaotra rainbow fish (vernacular name: *katrana*) (*Rheocles alaotrensis*) sells for US$ 10 on the local markets. Official fishing activity requires a license from the fisheries state department which can be obtained for an annual fee of US$ 5. Fishermen are organized in federations encompassing several associations. The federations control the mesh size diameter and fishing activities during the period of fishing closure (15 November to 15 January) during which only subsistence fishing is allowed. A majority of fishermen, however, do not have permits and many do not respect the fishing closure due to a lack of alternative income.

RICE CULTIVATORS. Rice represents the most important crop production in the Alaotra region and therefore constitutes the main subsistence and source of income of the farmers (Ducrot and Capillon 2004). In general, a rice field can be under traditional irrigation systems or modern systems of irrigation with dams and canals (*mailles*) allowing reliable water control and supply. Rice cultivation occurs mainly in lowland parcels (*rizières*) and occasionally in upland parcels (*tanety*) and forest plots during the rainy season (January–June, *vary taona*) and in former marshes converted into rice fields during the dry season (July–December, *vary jebo*); cf. Ducrot and Capillon (2004) for detailed farming typology. The first investments required for rice cultivation are the acquisition (or leasing) of land, seeds, pesticides and tools. Planting one hectare of rice requires 15 kg of seeds costing between US$ 3.5–5; currently, there are more than ten different types of rice in use (Ducrot and Capillon 2004). The most common tools used in rice cultivation are spades (*angady*, US$ 4), ploughs (US$ 150), small tractors (*kibôta*) (US$ 4,500), carts for transporting the harvest ($US 500), and weeders (US$ 10). Rice cultivation consists of various activities such as irrigating and ploughing the soil, direct seeding or transplanting the sprouts, irrigating the fields and discarding the weeds manually or with chemicals. The daily salary for workers in the rice fields ranges from US$ 1.5–3. The rent of land can either be paid in cash or in part of harvest: the landowner usually earns one ton of rice per hectare without working with the lender or 1.5 tons when working with the lender. The tenure contract also includes responsibilities for both lessee and lessor regarding input, labor and equipment (Jacoby and Minten 2007). One hectare of rice field produces about three tons of rice. The yield is attributed more for self-subsistence than for cash income. One kilogram of rice on local markets costs about US$ 0.4. Water supply and control represent the main issues of rice cultivation in the Alaotra (Ducrot and Capillon 2004).

VEGETABLE FARMERS. Though negligible compared to rice cultivation in terms of cultivated surface and production, vegetable farming produces enough vegetables for the Alaotra region and supplies for other regions of Madagascar (Monographie Régionale 2003). In contrast to rice, vegetables are produced mainly for cash income. Collectors from the cities buy and export vegetables to the islands around Madagascar. The main investments for planting vegetables are the seeds (3 sachets for US$ 1), tools (e.g., spade), cow dung (US$ 4.5 per one cart) and to have a well built for the water (US$ 60). Compost is rarely used compared to the cow dung because it needs extra preparation. However, cow dung is relatively rare and expensive (US$ 4.5 per cart). One hectare of field needs ten carts of cow dung. Therefore it is combined with industrial fertilizers and pesticides. Vegetables are planted in the lake shore during the dry season (May to November). However, onions, beans and peanuts are still planted during the rainy season. As for the rice cultivation, the rent of land can be paid in cash or in part with the harvest.

BREEDERS. Breeding represents a food and income source as safety net against stress and shock for the Alaotra farmers. The majority of breeders have zebus, pigs and poultry (e.g., chicken, ducks and geese); only few are breeding sheep and goat. During day time, the animals (except pigs) are let free and kept inside shelters in the villages during night hours because of eventual thieves (*dahalo*). Zebu in the Alaotra region represents, as in other parts of Madagascar, a banking system (Kaufmann and Tsirahamba 2006); they are used for milk production and work (e.g., pulling a plough for rice production). A zebu is butchered or sold on the local market only in circumstances where money is needed, e.g., for cultural purposes such as marriage or funerary tradition *famadihana*. A male adult zebu costs between US$ 250–400, an adult pig costs about US$ 200. The lack of income decreases the investments into animal care such as vaccines and proper supply of animal food.

DRIVERS AND BARRIERS OF WATER HYACINTH UTILIZATION. In order to assess possible drivers and barriers for using water hyacinth in the Alaotra region, a survey with five questions was administered.

(i) What are the most invasive plant species in the Alaotra wetlands? This question intended to unveil the stakeholders' knowledge related to the marshland ecosystem. Due to the ambiguity of the term 'invasive' (Kull et al. 2014) it was presented as plant species that spread rapidly in the area and with potentially negative impacts on the livelihood of local stakeholders. Accordingly, water ferns (vernacular name: *ramilamina*) (*Salvinia spp.*) (40%) and the water hyacinth (36%) are considered as most abundant and harmful species for rice cultivation and fishing in the Alaotra wetlands (Table 1). A few participants (4%) affirm that there is no invasive plant species in the wetlands.

(ii) What are the current negative impacts caused by the water hyacinth in the Alaotra region? Nineteen percent of the stakeholders stated not to be affected by the water hyacinth. All impacts listed by the participants represented mainly visible clues such as waterway clogging (63%) and invasion of rice fields (14%). The rest of opinions (4%) were the bad smell generated by decaying water hyacinth, decrease of space for fishing occupied by the plant, reduction of fish catches due to waterway clogging and destruction of fish nets by the plant and water flows decrease due to thick mats of water hyacinth.

(iii) How do you use the water hyacinth in your daily life? This question intends to assess the awareness for this plant in the region. Most of the stakeholders have never used this plant (89%). This is accentuated in particular in Vohimarina, the least degraded site with lowest abundance of water hyacinth (Lammers et al. 2015), where more than 93% of the stakeholders have never used water hyacinth. The rest of the stakeholders occasionally used the plant for fish trapping, pig farming or compost production (Table 2).

(iv) How can the water hyacinth be used? This question assesses the stakeholders' knowledge on potential benefits deriving from this plant. 67% of the respondents would use water hyacinth either as a source for composting, mulch, fodder, handicraft and water purification (Table 2). Local composting consists of mixing fresh water hyacinth with cow dung. Mulching this plant consists in spreading chopped fresh water hyacinth before planting rice in the fields. Pigs and geese feed on this plant. Pigs eat the whole plant except the roots whereas geese feed only on the leaves. Handicrafts are made with dry water hyacinth stems. Thirty-three percent of the stakeholders do not see any possible use of this plant.

(v) What would you do if the entire lake would be covered with water hyacinths? This question intends to test the creativity and willingness of resource users to using the plant in an extreme scenario. Only 16% of the interviewees would use the water hyacinth as compost and handicrafts; in contrast, all other proposed activities are either laborious and/or financially costly and without any economic gain for the stakeholders (Table 3).

Table 1. Plant species in the marshes identified by respondents (n=120) as covering large areas and having negative impacts within the three study sites.

Harmful and widespread plants species at Lake Alaotra	English names	Malagasy names	Percentage of respondents
Salvinia spp.	Water fern	Ramilamina	40
Echhornia crassipes	Water hyacinth	Tsikafona	36
Echinochloa pyramidalis	Antelope grass	Karangy	10
Phargmites australis	Common reed	Bararata	5
Leersia hexandra	Southern cutgrass	Vilona	3
Argyreia vahibora	Vine	Vahankelana	2

DISCUSSION

POTENTIAL THREATS. Extensive use of chemical fertilization for agricultural production around wetlands leading to an increase of nutrient concentrations of water bodies (eutrophication) and combined with high solar energy (Ndimele et al. 2011) represent favorable conditions for the spread of the water hyacinth (Charudattan et al. 1996). These conditions are found at Lake Alaotra (Pidgeon 1996). High water temperatures peaking more than 41°C have been measured in the littoral zone of the lake (Lammers et al. 2015) and are further favoring the spread of water hyacinth and depleting dissolved oxygen (Gratwicke and Marshall 2001).

The thick mats of water hyacinth lead to a decrease of phytoplankton (due to light deprivation), an increase in water turbidity (due to the constant rotting of the mat base) and a decrease of dissolved oxygen (due to the high oxygen consumption of rotting plant biomass) (Masifwa et al. 2001, Rommens et al. 2003, Mangas-Ramírez and Elías Gutiérrez 2004, Perna and Burrows 2005, Villamagna and Murphy 2010). Collectively these effects may negatively impact animal and plant species at Lake Alaotra. The impacts of water hyacinth on invertebrate communities are variable: A greater number of invertebrates is observed in the transition

Table 2. Current and Potential usage of water hyacinth expressed by stakeholders during interviews (n=120) within the three study sites (Vohimarina, Andreba and Anororo). Current uses do not reflect the potential uses.

Uses of *Eichhornia crassipes*	Percentage of respondents
Current uses	
No uses	89
Support for fish trap	5
Fodder	4
Compost	2
Potential uses	
No possible usage	33
Compost	32
Fodder	23
Raw material for handicraft	10
Water purification / Shelter for fish and crab / keep humidity	2

Table 3. Proposed management actions in case of total invasion of the Lake Alaotra by the water hyacinth (n=120) within the three study sites (Vohimarina, Andreba and Anororo). The majority of the actions do not generate economic benefits.

Proposed management actions	Percentage of respondents
Dry and kill *Eichhornia crassipes*	33
Kill *E. crassipes* using chemicals	18
No solution	17
Compost / handicraft	16
Alert the government	7
Ashes as fertilization / Convincing people to get rid of it / Build fence to contain the plant	6
Invest only in agriculture	3

zone from *E. crassipes* stands to open water due to increased structural diversity as compared to open water zones (Masifwa et al. 2001). However, the total amount of invertebrates decreases because of the overall reduced availability of phytoplankton (Toft et al. 2003, Midgley et al. 2006). The decrease of invertebrates reportedly leads to reduced fish diversity (Howard and Harley 1998, Gratwicke and Marshall 2001). As with the invertebrate communities, the impacts of the water hyacinth on waterbirds are ambivalent: The positive effects of the water hyacinth on the invertebrate communities could lead to higher diversity and density of waterbirds whereas dense mats of water hyacinth or the low dissolved oxygen under the mats could physically hinder waterbird access to prey or impact negatively the abundance of the prey species (Villamagna and Murphy 2010). At Lake Alaotra, several bird species such as the white backed duck (*Thalassornis leuconotus insularis*) suffer from the spread of the water hyacinth (Nicoll and Langrand 1989). Due to its strong competitiveness regarding light and nutrient acquisition, the water hyacinth is able to out-compete and displace submerged vegetation (Mitchell 1985). The impact of the water hyacinth on the local lemur *Hapalemur alaotrensis* remains up to now understudied. However, since *H. alaotrensis* needs tall vegetation (cyperus) to cross water channels (Ralainasolo 2004), the potential isolation of tall vegetation patches due to further spread of large water hyacinth mats might hinder genetic exchange between the populations of *H. alaotrensis*. Interestingly, *H. alaotrensis* was reported to feed on the stems and flowers of the water hyacinth at Lake Alaotra (Birkinshaw and Colquhoun 2003).

As discussed by Rendigs et al. (2015), the cumulative effects combined with the spreading of water hyacinth can lead to further loss in fish and increasing the vulnerability of fishermen in the Alaotra region. Regarding the impact of water hyacinth on the fishing activities at Lake Alaotra, 63% of the stakeholders considered waterway clogging as the main problem caused by the plant on their livelihood since it decreases fish catches and destroys fishing material such as fishnets. The floating thick mats of water hyacinth are moved around by winds. These can also invade rice fields; suppressing rice crop, inhibiting rice germination and interfering with rice harvest. These negative impacts have been shown to cause important losses of rice paddies in West Bengal (EEA 2012, Patel 2012). At Lake Alaotra, this phenomenon can be observed frequently due to inefficient water control. The risk of production loss due to the water hyacinth can become more prevalent in the near future; the water scarcity at the lake, combined with badly maintained irrigation systems are pushing the rice fields closer into the marshlands.

Another factor adding to the water issue is the high evapotranspiration demand of this invader, which can exceed by ten times the one by open water bodies (Gopal 1987). Increased water loss by the water hyacinth leads especially in shallow lakes such as Lake Alaotra to a drop in water level. In turn this can add an additional stress to the hydrologic balance in the region (Ferry et al. 2009), which constitutes another factor further stressing the rice production in the wetlands. A reverse effect could happen during periods of heavy rain or cyclones. By clogging waterways the water hyacinth can slow down the water flow up to 95% leading to severe flooding (Jones 2009).

The management of the water hyacinth requires prior estimations of the current state of invasion to evaluate the costs. Shackleton et al. (2007) created models about invasive species characterized by the time since invasion, abundance and level of cost and benefits. The models can be used as a tool to guide interpretation and future management of invasive species and simultaneously assessing vulnerabilities of local populations toward the invasive species. According to classifications and procedures used in the model and combined with our findings from the Alaotra in this study, the water hyacinth can be defined as a "undesirable, strongly competitive species" Shackleton et al. (2007: p 124). Regarding time since invasion, the water hyacinth invasion in the Alaotra seems to be in 'phase 2': rapid spreading thanks to its competitive nature. Awareness of the water hyacinth increases as it becomes first a nuisance, and later on a significant hindrance to local livelihood activities and options (e.g., rice cultivation and fishing activity in the Alaotra). The future costs (ecological, aesthetic, harvesting, and control) are increasing rapidly thus reducing the productivity of other resources; hence, the vulnerability of the livelihood of local population is further increasing (Shackleton et al. 2007).

POTENTIAL OPPORTUNITIES. Some invasive plants have been in the landscapes for several generations, and instead of being controlled or eradicated, they became part of the livelihood and the well-being of human communities. In South Africa, for example, the prickly pear (*Opuntia ficus-indica*) is a source of food (jam and the fruit itself), used for beverages (beer and syrup) or for medicine and income for local traders (Beinart and Wotschela 2003, Shackleton et al. 2011). In Nepal the invasive climbing weed *Mikania micrantha* is used by the local population as fuel wood and fodder (Rai and Scarborough 2013). In India, due to the unsuccessful attempts to eradicate the tickberry (*Lantana camara*), the local communities addressed as adaptation strategy the use of this plant as source of income. In Madagascar, the use of the water hyacinth as a source of raw material for handicrafts was initiated through the collaboration between the Government of Madagascar and the Embassy of Indonesia (Rakotomalala 2014).

In the Alaotra wetlands, composting based on water hyacinth could represent a realistic possibility due to attributes such as its relative short period of maturation (about 30 days), its ability to retain nitrogen (N), phosphorus (P) and potassium (K) and thus to improve soil structure and nutrient contents (Polprasert et al. 1980). The plant should be chopped into 5 cm long pieces and put into piles with cow dung and other leaves before composting in order to enhance microbial access (Dalzell et al. 1979, Polprasert et al. 1980). Due to its high moisture content (90%), Elserafy (1980) stated that composting water hyacinth does need only little amount of water but should be covered or performed in pits to avoid excessive water loss in compost pile. Since composting requires time and workload investments, local stakeholders from the Alaotra region prefer to use directly cow dung instead. Despite the relative 'short' duration of maturation of water hyacinth compost, this is already perceived as a long term investment for the interviewees and thus represents a potential barrier to its adoption. In comparison to developed countries where farmers often possess health and production insurance (cf. Fisher et al. 2002), the rural poor farmers of the Alaotra region are less resilient to eventual shocks such as drought, floods, landslides, crop pests, market collapse, health problems and accidents (affecting households and individuals). Especially the direct dependence on rice and fish production as main source of food or cash income leads to increased vulnerability due to the unpredictability of production and price fluctuations, with the latter depending oftentimes on outside drivers such as the national demands for the products or the season influencing the road conditions. As an adaptation to these high uncertainties, mutual aid groups give relative insurance and flexibility to the Alaotra farmers especially during hard times (Ducrot and Capillon 2004). However, the dissolution of mutual aid group can be traumatic for poor-equipped farmer (ibid). The high exposure to risks for the local farmers can reduce or inhibit investment in time demanding innovations and prevent long term perspectives. This is supported by our results; only 16% of the stakeholders showed an opportunistic attitude towards the water hyacinth. Another limitation for composting in developing countries is probably the intense workload for transporting large amounts of fresh water hyacinth (Gunnarsson and Petersen 2007). According to a vegetable farmer "(…) the only possibility to involve people [in the Alaotra region] to use the water hyacinth as compost is to process it via a small factory where people can work and compost can be sold".

An alternative to composting could be the use of green manure out of water hyacinth to reduce the labor requirements due to the usage of dried material (Gunnarsson and Petersen 2007). Green manuring consists of spreading plant material (with high nitrogen content) on the fields or working it into the soil (Stopes et al. 1995). The green manure could be the most feasible alternative for farmers in the Alaotra region. Due to its high ash content (40% of dry weight, Thomas and Eden 1990), the water hyacinth can also be burnt and used as mineral fertilizer. Ashes from water hyacinth could be applied in the fields to provide minerals, mainly phosphorus (P) and potassium (K). The ash spreading would require a relatively low labor input; however, the effects and application rate must be investigated (Gunnarsson and Petersen 2007).

Thanks to its high content in crude protein (20%) (Abdelhamid and Gabr 1991), the water hyacinth is excellent as fodder for ruminant animals (Tag El-Din 1992). However, the air filled tissues of water hyacinth lead to high consumption of water by the animal, therefore decreasing the nutritional value of the diet. The calcium oxalate occurring in its tissues represents a potential harm for the animal digestive tract in case of low amount of digestive acid (Bolenz et al. 1990). The water hyacinth should be chopped into pieces to reduce air and negate water absorption. The material should be pressed, centrifuged and washed with acid to eliminate the calcium oxalate (Bolenz et al. 1990). Some Alaotra farmers are already feeding their pigs with this plant, but at current stage it is unclear to what degree it is used. However, including water hyacinth in the diet of pigs and geese could at least reduce the cost of animal food.

Water hyacinth can be used as part of fish diet (*Tilapia* spp., *Cyprinus carpio*) (Igbinosun et al. 1988, Mohapatra and Patra 2013); this however, showed limited application with low proportion of water hyacinth in the diet (15–23%). Sixty years ago, fish farming was introduced by the Department of Forests and Water in the Alaotra with 85,000 ponds (each pond about 235 m2) covering an area of 2,000 ha and collapsed to 10,000 ponds in 1984 (Pidgeon 1996). In comparison during the same period integrated rice-fish culture within villages covered only some 400 ha (Kiener 1963). Nowadays for the Alaotra region, fish breading has lost its importance (Anonymous 2010). Currently, only one private company in Anosiboribory produces alevin of *Tilapia niloticus* and *Cyprinus carpio* to supply the very few pisciculturists around Lake Alaotra (Bary-Jean Rasolonjatovo, pers. comm.). The limiting factor for pisciculturists is the water supply in the Alaotra. The low proportion of water hyacinth in fish diet and the negligence of pisciculturists in the region limit the use of the plant as fish food. However fish farming may gain momentum given the lake fish catches have dropped by about half (i.e., by about 2,000 t) within the last fifty years while human population has increased more than five times in the same period (Razanadrakoto 2004).

Water hyacinth can be used as raw material for making handicraft and furniture (Ndimele 2011). Long stems of water hyacinth (≥ 70 cm) are collected and sun-dried. The stalks should be completely dry (Jafari 2010). However, the only use of the stem does not allow successful infestation reduction and the market for these products is far too small to have any impact on water hyacinth populations (UNEP 2013). Nonetheless, it could improve cash income at least for the handicraft makers of the Alaotra. The reduction of sedges and reeds utilization for handicraft can alleviate pressure on the critically endangered lemur *H. alaotrensis* feeding mainly on those plant species (Ratsimbazafy et al. 2013, Waeber et al. In press).

Due to its high moisture content (90%) and its high ash production (40% of dry weight) using water hyacinth as charcoal is unattractive because its incineration produces only 1.3 kJ/m3 in comparison to 9.8 kJ/m3 for firewood (Thomas and Eden 1990). However, briquettes out of this plant produce 8.6 kJ/m3 which is comparable to charcoal (9.6 kJ/m3) (ibid). In the Philippines, a company supplies local restaurants with briquettes (Laguador et al. 2013). The process of making briquettes is relatively simple but requires material (burning, briquetting and drying machines) (ibid). Meier (2008) concluded that using water hyacinth briquettes at Lake Alaotra is not efficient since it produces too much ash and smokes therefore reducing its calorific performance and representing a threat for human health. Also, it does not suit to the local used cooking oven and requires more preparation time and effort in comparison to the charcoal. Moreover a mechanical press machine is needed to reduce those latter cited preparations but it would not be likely affordable for the local population (from US$ 2,000).

Water hyacinth can be used to produce ethanol, methane and sludge. The ethanol is produced by hydrolyze and fermentation of water hyacinth. However, pretreatment is necessary due to the lack of yeast fermentable sugar within the plant (Thomas and Eden 1990). In China, the plant is mixed with pig manure to produce biogas (Lu et al. 2010). Biogas is generated by the degradation of organic material through anaerobic biological process. Due to high content of lignin in water hyacinth tissues, thermochemical pretreatment such as addition of ions is needed (Gunnerson and Stuckey 1986, Patel et al. 1993). The remaining sludge can be used as fertilizers due to its high concentration of nutrients (Hons et al. 1993). The transportation of the sludge would represent important labor force requirements due to its high water content (Gunnarsson and Petersen 2007). Producing ethanol, biogas and sludge out of the water hyacinth in the Alaotra wetlands is limited by technical and financial requirements since they need important transfer of technology and infrastructure.

Madagascar belongs to the category of low human development countries with a HDI (Human Development Index) of 0.483, ranked as 36th poorest country in the world (UNDP 2013). In a system where input credit, crop production and health insurances are not sufficient or missing, stakeholders adopt their own strategies to manage covariant and idiosyncratic risks (e.g., weather uncertainty or illness, respectively) (Devereux 2001). Peasants in the Alaotra region depend mainly on fishing and rice cultivation; however, diversification of activities, land tenure flexibility and mutual aid are used to buffer uncertainties effects (cf. Ducrot and Capillon 2004). Governmental administrations in collaboration with NGOs should increase effort to help poor farmers to increase their capabilities to improve their assets and to cope with risks, stress and shocks affecting their livelihood. In the near future, fish and rice production will likely drop continuously with increasing anthropogenic pressures and degradation in the Lake Alaotra. Investing into new technologies or adoption of new resource use could represent additional buffers and increase resilience of farmers to an uncertain future. However, this would require increased and concerted educational efforts to raise the awareness for environment and its potentials such as the usage of water hyacinth (cf. Reibelt et al. 2014).

CONCLUSION

The livelihoods of local stakeholders can benefit from using water hyacinth but only to some degree. Based on limited access to cash and technology, the most feasible uses are green manure, animal fodder, handicrafts, compost and ash as mineral fertilizer. Using water hyacinth as fertilizers could be implemented to promote conservation agriculture by improving and maintaining soil fertility and therefore reducing pressures on the marshlands. Water hyacinth could be combined with local craft materials improving cash income. However, access to information, financial and technical supports as well as markets for handicrafts constitute important but currently missing aspects. This is also the case in other wetland regions of Madagascar where the plant occurs (e.g., Lake Ravelobe within Ankarafantsika National Park, Betsiboka basin, Imerina and Betsileo regions, northern rivers of Madagascar and Pangalanes Canal) (Binggeli 2003). Additional cost/benefit and risk analyses are needed to assess potential utilization of the water hyacinth. The most significant barrier to local adoption of new water hyacinth uses seems to be uncertainty linked to long term investments and planning.

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

S1. Questionnaire for stakeholders' typology in the Alaotra.

S2. Questionnaire regarding the identification of the drivers and barriers of using the water hyacinth at Lake Alaotra.

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Complementarity of native and introduced tree species: exploring timber supply on the east coast of Madagascar

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ABSTRACT

In Madagascar, nature conservation and human livelihood security both appear as crucial imperatives. The degraded secondary forest remnant of Analalava, on the east coast, near Foulpointe, is a protected area since 2006. The long-term conservation of the site's biodiversity can only be guaranteed by local support. Given that access to timber from native trees within the protected area is restricted, management of tree resources outside of the protected area represents a critical nexus between biodiversity conservation and human benefits linked to ecosystem services. We investigated and characterized the local farmer's use of available tree species, to provide a basis for satisfying the dual objectives of biodiversity conservation and sustainable and equitable rural development.

Our results showed that local people are interested in various types of trees for timber, both native and introduced. Furthermore, they demonstrated detailed knowledge about silvicultural traits of a large number of tree species. Regarding the important complementarity of properties and uses recognized for native and introduced species we conclude that free distribution of nursery seedlings of fast-growing introduced tree species should not be the only alternative to logging within the protected forest fragment offered to local people. Instead, a larger choice of tree species, including native ones, should be proposed. The cultivation of this diverse mix would allow people to take a more active part in the preservation and restoration of natural capital at the landscape scale and could enlarge the range of benefits obtained from trees that they plant.

RÉSUMÉ

À Madagascar, il est crucial de répondre au double impératif de protéger la nature et d'assurer des moyens de subsistance aux populations. Analalava, où se situe un fragment de forêt secondaire dégradée de la côte Est, à côté de Foulpointe, bénéficie d'un statut de protection depuis 2006. La conservation à long terme de la biodiversité de ce site ne peut être garantie sans la participation des populations. Étant donné l'accès restreint des populations à l'intérieur de l'aire protégée pour l'exploitation du bois, la gestion des sources d'approvisionnement en bois de construction à l'extérieur du site représente un trait d'union entre la conservation de la biodiversité et les bénéfices fournis aux Hommes par les services écosystémiques. Nous avons déterminé et caractérisé les relations entre ces populations locales et les espèces d'arbres qu'elles utilisent. Cette étude pourrait constituer une base à la mise en place d'une coopération qui satisferait à la fois aux objectifs de conservation de la biodiversité et de développement rural durable et équitable.

Nos résultats montrent que pour les populations locales, le bois de différentes espèces d'arbres, indigènes ou introduites, présente un intérêt pour la construction. En outre, les personnes interrogées ont montré une connaissance détaillée des traits sylvicoles d'un grand nombre d'espèces. Devant la complémentarité des espèces indigènes et introduites en termes de propriétés et d'usages, nous concluons que la distribution gratuite de plantules d'espèces introduites à croissance rapide ne devrait pas être la seule alternative offerte aux populations locales à l'exploitation du fragment de forêt protégée. Au lieu de cela, un choix plus large d'espèces d'arbres, y compris d'espèces indigènes, devrait être proposé. La plantation d'un mélange de diverses espèces permettrait ainsi aux populations de prendre part de manière plus importante à la préservation et la restauration du capital naturel à l'échelle du paysage, et pourrait étendre la gamme de bénéfices qu'ils retirent des arbres plantés.

INTRODUCTION

In an effort to conserve Madagascar's biodiversity, natural reserves were first established in the early 1900s. Since then, Madagascar's protected areas network (Système des Aires Protégées

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de Madagascar, SAPM) is growing. In 2003, former President Marc Ravalomanana launched a program to triple the SAPM from 17,000 km² to over 60,000 km² (i.e., from 3%, to 10% of Madagascar's total land area). With help from various funders and NGOs, progress on achieving this goal was continuous until the coup d'état that threw the country into turmoil, in January 2009. Nevertheless, as of December 2013, 70,000 km² (11.77% of the country) of land of high conservation value has been earmarked for possible inclusion in the SAPM network, and many of these areas have been accorded a 'temporary protection' status (Ministère de l'Environnement et des Eaux et Forêts et al. 2012). While the original network of protected areas is managed by Madagascar National Parks, the recently created reserves are, for the most part, run by NGOs.

It appears clearly that two imperatives coexist in the landscapes surrounding protected areas in Madagascar. On the one hand, local people have crucial needs for economic development and access to the resources on which they depend. Indeed, rural Malagasy remain partially dependent on native tree resources for income and subsistence (Blanc-Pamard and Ralaivita 2004, Carrière et al. 2005). In many cases, the establishment of protected areas restricted local people's access and curtailed their access to natural resources (Marie et al. 2009), especially to wood obtained from native tree species. On the other hand, these special areas are critical for biodiversity conservation (Carrière and Bidaud 2012, Birkinshaw et al. 2013), and threatened: ongoing landscape fragmentation is harming and reducing habitat and inhibiting successful seed dispersion in many cases (De Wilde et al. 2012).

One response to the loss caused by the establishment of protected areas has been the introduction of fast growing species, since the beginning of the twentieth century; these species now play an important role in satisfying the needs of rural Malagasy populations (Pfund 2001, Carrière et al. 2008). More than 70% of introduced flora is considered as being useful (Kull et al. 2012). *Eucalyptus* spp. (Myrtaceae) cultivation furnishes a profitable income in particular as timber and fuel wood, and has become crucial for economic development (Aubert et al. 2003, Carrière and Randriambanona 2007). Kull et al. (2013) described the large range of ecosystem services supplied, i.e. introduced tree species: provisioning service by edible parts of the plant, regulation services through carbon sequestration, habitat service for native bird species (cf. Martin et al. 2009). Despite the invasive potential of some introduced tree species, they are clearly part of rural people's subsistence strategy and are, arguably, complementary to native species, in terms of services and as an alternative to native timber extraction (Carrière et al. 2008, Kull et al. 2013).

The protected area of Analalava is located on the east coast of Madagascar (E0 49°27'22", S 17°42'26"), seven kilometres west of Mahavelona-Foulpointe, a small town of 8,000 inhabitants, which is also a well-known seaside resort frequented by both Malagasy and foreigners. This region is characterized by a tropical humid climate with almost no dry season, and low rainfall during winter – although several weeks without rainfall can occur unpredictably at any time of the year. Mean average annual rainfall is 2,500 mm, with ca. 200 rainy days per year. Monthly average temperatures in Analalava range from 23 to 33°C. Most people in the villages studied belong to the Betsimisaraka. Originally farmers living in the forest with a subsistence economy, these people are now actively engaging in trade. Population growth, successive migrations, and migration of new people into the region in recent decades has led to logging and extensive land clearing for agriculture. The degraded secondary forest of Analalava has high conservation value because of its numerous endemic and endangered plant species (Rakotoarinivo et al. 2010, Missouri Botanical Garden 2011), and also because there is no other large fragment of lowland humid forest left in the vicinity. In the past 35 years, this forest has suffered from damage and isolation due to logging, slash-and-burn agriculture and related wild fires occurring each year in the area (Lehavana and Birkinshaw 2006). It has seen its area reduced by 47 ha, as compared to 250 ha in 1979. Since 2004, the conservation site is under management of the Missouri Botanical Garden (MBG), together with the local community. Economic alternatives are developed through an association of local stakeholders: ecotourism, fish-farming, introduced fast-growing species seedlings distribution.

The predominant landscapes around the protected area are characterised by: (i) irrigated rice fields; (ii) fields of cassava root and other crops often in association with fruit trees such as jackfruit, breadfruit and other trees such as *Harungana madagascariense* Lam. Ex Poir (Clusiaceae), *Albizia lebbeck* Benth. (Fabaceae), and *Litsea glutinosa* Lour. (Lauraceae); (iii) uncultivated woody grassland (or *savoka* in Malagasy) dominated by the native *Ravenala madagascariensis* Sonn (Strelitziaceae), the introduced *Eucalyptus robusta* Sm. and various ferns; and (iv) young secondary forest fragments and thickets in which *Ravenala madagascariensis* and other native trees, as well as various non-native, invasive shrubs and trees co-occur.

Improving the ecological resilience of these landscapes is vital. To answer this specific issue, we focused on tree species because of the diversity of ecosystem services they provide for local communities and also in view of their importance to conservation objectives. The goal of this study was to explore the knowledge and uses farmers have of the different tree species they use for timber in the largely agricultural landscapes surrounding the Analalava protected area (0–10 km radius). We sought to elucidate the appreciation by local people of different tree species' characteristics, and the relative importance of these characteristics. Our study is qualitative, and it aims to describe the relationships between a specific group of people and the tree species that are part of their lives and livelihoods. This is an illustration of the global call to take into account local environmental knowledge for more sustainable protected area management (Lescuyer 2008, Binot 2010). We expected that the substitution of a large range of native forest species by a few introduced ones imagined by government and NGOs to reduce deforestation and pressure on natural resources is not a sufficient response. We hypothesized that interest and attachment for some native tree species does exist among local people in our study area and that this aspect could be more usefully integrated in conservation and sustainable development strategies.

METHODS

DEFINITIONS AND CONCEPTS. The following key concepts were used in this study: 'Forest fragment' as defined by Urech et al. 2012: "The whole contiguous natural forest, including larger forest patches of more than 500 ha, has been classified as a forest massif. All natural forests smaller than 500 ha, surrounded by agricultural land or fallows and therefore not connected to the massif are considered forest fragments". 'Ecosystem services' are defined as the goods and services from ecosystems and its native biodiversity perceived as direct or indirect benefits by humans (Millennium Ecosystem Assessment 2005). Following de Groot et al. (2009), we consider five types of ecosystem services: provisioning, cultural, supporting, regulating, and habitat. Species type terminology comes from Convention on Biological Diversity (2001) and Richardson et al. (2000). 'Native species' are species that occur naturally at a given location or in a particular ecosystem. They can either be endemic (found only within a particular region) or indigenous (found both within the region and elsewhere). 'Introduced species' are species in a given area whose presence there is due to intentional or accidental introduction as a result of human activity (synonyms: exotic species, alien species, non-native species, non-indigenous species). 'Naturalized species' are introduced species that reproduce consistently and sustain populations over many life cycles without direct intervention by humans. 'Invasive species' are naturalized species that produce reproductive offspring at considerable distances from parent plants.

SURVEY METHOD. The study took place from April to August 2013. The four villages studied were chosen within those the Missouri Botanical Garden works with because they were the administrative centers of *fokontany*, accessible by rural path and located on the outskirts of the Analalava reserve, less than 10 km from the protected area's edge. In what follows, the letters A, B, C, and D will designate the groups within the villages of Bongabe, Ambodivoarabe, Ambatobe and Morarano respectively.

The first author conducted 36 individual semi-structured interviews with the help of a translator, with random people from those four villages. The methodology used was the one developed by Olivier de Sardan (2003) based on participative observation, semi-open questions, conflict case study and information triangulation. These interviews coupled with observations of day-to-day life served to collect information on the trees present in farmers' fields, and their common use. As a result of these interviews, among local people timber was found to be the most appreciated of the services provided by the Analalava forest before it became protected. That is why the first author conducted afterwards four group surveys on timber sources and their uses. For the group surveys, each lasting one to two hours, we used the SAS2 method (Chevalier et al. 2013), known as 'Scoring tips'. This method is in turn based on the Rapid Rural Appraisal technique (FAO 2002). Each group was comprised of ten men, men being the only ones concerned by timber collecting. No distinction of age classes was made, and all participants were volunteers and received no incentives. Each group survey took place in one of the four villages, each village being composed by a lineage, or unilineal descent group. The objective of doing a group survey was to gather collective knowledge.

First, people were asked to list the tree species x_i they would use for timber, assuming they were locally available. Second, we asked people to list the different criteria y_i under which they would choose to plant a tree for timber use. These criteria were for example intrinsic timber qualities such as 'wood hardness' and also 'rot resistance' (to humidity or insects), the latter of which correlates with the material lifespan of cut timber. All respondents also cited silvicultural qualities such as 'growth rate' and 'upright growth form' as selection criteria. Third, we asked people to classify the different tree species according to the criteria of their choice. The different tree species were rated for each criteria y_j, using a total of $N(y_j)$ beans as markers. Finally, the different criteria were weighted, from the least to most important: the group was asked to put a number of beans $a(y_j)$ on each criterion (represented by a symbol on their sheets of paper), in proportion to its relative importance. A total number of M beans were used. Table 1 illustrates the method.

DATA ANALYSIS. We divided the score given to the species or to the criteria by the number of beans used in order to smooth out the ranking differences between groups. These data allowed us to classify each tree species according to their criteria, and also to highlight which criteria were the most important ones for each group.

Local vernacular names of trees were used during the exercise, to be assigned to their scientific name based on either Schatz (2001), the botanical inventories of the Analalava forest (Missouri Botanical Garden 2006) and on the expertise of one of the co-authors (C. M.).

RESULTS

A total of 35 tree species were cited, among the four groups, as being appreciated for their timber. These included ten non-native species and 25 native forest species. The most often cited tree species were introduced ones (Table 2). These trees are the

Table 1. Application of the SAS2 method 'Scoring tips' (according to Chevalier et al. 2013; the villagers participating in these studies were for the most part unable to read or write; hence the need for the use of tangible markers such as beans).

	y1	y2	y3
tree species x1	a (x1; y1)	a (x1; y2)	a (x1; y3)
tree species x2	a (x2; y1)	a (x2; y2)	a (x2; y3)
tree species x3	a (x3; y1)	a (x3; y2)	a (x3; y3)
total number of beans used N (yj)	N (y1)	N (y2)	N (y3)
weight of the criterion a (yj) using M beans	a (y1)	a (y2)	a (y3)

Table 2. Introduced and native tree species used for timber in four villages.

Trees	Bongabe	Ambodivoarabe	Ambatobe	Morarano
Introduced species				
Acacia mangium Wild.	x	x		x
Albizia lebbeck Benth.		x	x	x
Albizia sp.	x	x	x	x
Artocarpus altilis Fosberg	x			
Artocarpus heterophyllus Lam.	x		x	x
Eucalyptus citriodora Hook.	x	x	x	x
Eucalyptus robusta Sm.	x	x	x	x
Grevillea banksii R. Br.		x	x	
Pinus caribaea Morelet	x	x	x	x
Spathodea campanulata Beauv.	x	x		
Native species				
Anthostema madagascariense Baill.			x	x
Chaetocarpus rabaraba Capuron			x	
Colubrina faraloatra Capuron			x	
Cynometra spp.			x	
Dalbergia chapelieri Baill.			x	
Diospyros spp.			x	x
Dombeya oblongifolia Cay.				x
Faucherea sp. Lecomte		x	x	
Harungana madagascariensis Lam.		x		x
Homalium spp. Jacq.			x	
Intsia bijuga Colebr. (Kuntze)		x	x	x
Mauloutchia spp. Warb.				x
Ocotea spp. Aubl.				x
Oncostemum spp. A. Juss.				x
Phyllarthron madagascariense K. Schum	x	x	x	
Plectronia micranta Baker			x	
Pseudopteris sp. Baill.		x		
Rhopalocarpus spp. Bojer				x
Schizolaena spp. Thouars	x			
Stephanostegia capuronii Markgr.			x	
Streblus obovata Lour.			x	
Symphonia tanelensis L. f.			x	
Terminalia catappa L.				x
Uapaca louvelii Baill.			x	x
Xylopia sp. L.		x		

most abundant in the agricultural landscapes surrounding the villages, and people are used to planting them for income. Among native tree species (Table 2), people cited those with which, for various reasons, they have maintained relationships of use or belief. The most well-known native tree species, cited by three of the four groups, were: *Intsia bijuga* (Colebr.) Kuntze (Fabaceae) and *Phyllarthron madagascariense* K. Schum. (Bignoniaceae).

The 35 trees appreciated for timber are ranked together with their relative level of appreciation, regarding each criterion. Figure 1 shows the species that local people prefer to use for timber, depending on what they are willing to use them for. Introduced species cited ranked first with regards to growth rate, whereas native ones were the most valued species for intrinsic wood qualities such as rot resistance and timber hardness. However, *Pinus caribaea* Morelet (Pinaceae) was particularly appreciated for its upright growth form, regardless of the species type. Among introduced species, *Eucalyptus robusta* was said to present the best rot resistance, along with the hardest wood.

Whereas all groups interviewed use approximately the same introduced tree species for timber for construction and other uses (seven or eight in total for each group), we observed differences in terms of the number of native tree species used from one single group to another: 2 for A, 6 for B, 15 for C, and 11 for D. This can be linked to the size of the main forest fragment still occurring on the village's land. The more forest is left on their land, the more people use and know forest tree species (Table 3).

The most important qualities in dictating preferences for planting a tree species, from the perspective of using it for timber, are listed in Figure 2. We can observe that people value certain criteria more than others. Surprisingly considering their short-term needs in timber, the growth rate criterion was considered to be less important than the durability of the wood. Timber's intrinsic qualities such as rot resistance or hardness were cited as more important than the growth rate in three of the four villages. Fast growth was considered the most important criterion by informants of group C.

DISCUSSION

We acknowledge that our results are insufficient to allow detailed statistical analyses, since only four groups of people were surveyed. However, the people interviewed are all potential participants in cooperative forest management at Analalava. We can therefore assume that their responses are the ones that matter the most in this context.

MISCELLANEOUS NEEDS TO BE MET. Our results show that people in the villages where we undertook surveys are interested in and knowledgeable about diverse species of forest trees with value as timber. Among the introduced species, some are naturalized and abundant in agricultural landscapes surrounding the villages, particularly in *savoka* (fallows): *Eucalyptus robusta*, *Albizia* spp., and *Grevillea banksii* R.Br (Proteaceae). Others, fruit trees which do not propagate so easily, were planted in the fields: *Artocarpus altilis* Fosberg and *A. heterophyllus* Lam. (Moraceae). Certain native cited species regenerate readily in the *savoka*, such as *Harungana madagascariensis* and *Dombeya oblongifolia* Arenes (Malvaceae). The others are found only in the small secondary forest fragments, 0.1 to 1 hectare in size, and located between two and five kilometers away from the nearest village. Therefore, people use a large range of tree species: not only species that are abundant in the agricultural landscapes around the village but also native forest species that can only be found in little remaining forest fragments, located far from the village. Use and local access rules are drawn up regarding these forest fragments to prevent charcoal production from native species and to restrict the timber harvesting right to one or several lineages. However these rules are rarely enforced, which de facto leads to free access. Consequently, forest fragments are progressively disappearing.

Indeed, those native species have irreplaceable qualities. Traditional Betsimisaraka houses are raised on stilts and built from wood, especially the native *Ravenala madagascariensis* whose stem, leaves and trunk are used to construct walls, roofing and floor materials; twenty beams and thirty pillars are also required. The introduced species *Pinus caribaea* is used for the roof and wall thanks to its upright growth form, whereas *Eucalyptus ro-*

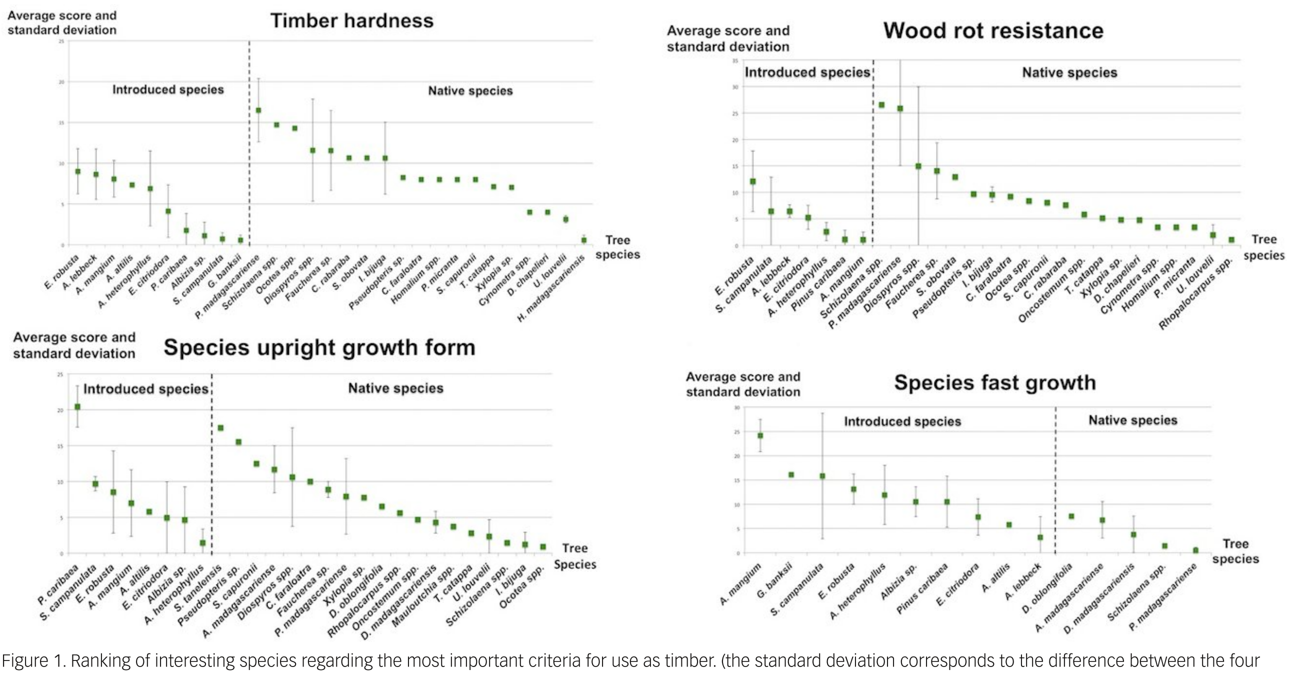

Figure 1. Ranking of interesting species regarding the most important criteria for use as timber. (the standard deviation corresponds to the difference between the four responses).

Table 3. The different villages characteristics, based on interviews and personal observations of several co-authors. (the relative wealth was estimated by criteria such as: number of families having a concrete house).

Village	Distance to Foulpointe (km)	Size of main secondary forest fragment	Relative wealth	Important land dispute
Bongabe	5	0	x	
Ambodivoarabe	10	< 0,5 ha	x	
Ambatobe	6	> 1ha		x
Morarano	12	> 0,5 ha		x

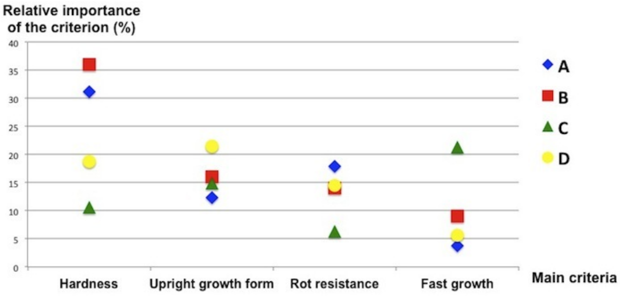

Figure 1. Ranking of interesting species regarding the most important criteria for use as timber. (the standard deviation corresponds to the difference between the four responses).

busta, harder and more resistant, is preferred for stilts. However, along the east coast of Madagascar, where cyclones are frequent, and heavy rainfall is a constant, the wood used to build houses must be resistant to rot. As one farmer put it: "Here we need solid wood for construction. With wood taken from native forests, the house lasts for more than 40 years. Using *Eucalyptus*, it has to be rebuilt every seven years and the pillars have to be changed every four years." Their exceptional timber hardness and rot resistance, but also their acceptable upright growth form, make species such as *Phyllarthron madagascariense*, *Faucherea* sp. (Sapotaceae), and *Diospyros* spp. (Ebenaceae) the most highly valued species for house stilts and pillars (Mahefa 2010). Rot resistant wood of *Albizia lebbeck* makes it desirable for pirogue building. To produce tools such as farm tool handles, or cooking tools, wood hardness is also an essential quality, and the hard wood of *Faucherea* sp. is also particularly appreciated for pestle and mortar fabrication (Mahefa 2010). Introduced species serve for common, everyday needs, but native species are used for specific needs, for example to change roof beams in one's house, or for funerals: exceptional rot resistance of *Diospyros* spp. makes them desirable for fabrication of coffin lids (Mahefa 2010). In sum, increasing the spectrum of usable species is also part of a risk management strategy, offering several alternatives to local people seeking to respond to varying situations. For all these reasons, native and introduced tree species are complementary for timber supply.

ECOSYSTEM SERVICES AND EXISTING TRADE-OFFS. Besides timber production, trees also provide other kinds of ecosystem services. Considering introduced species: for example, *Acacia mangium* Willd. (Fabaceae) fixes atmospheric nitrogen, in symbiosis with rhizobacteria, and thereby its building of soil fertility is known by the local population. The bark of *Albizia lebbeck* is used to treat conjunctivitis; *Pinus caribaea* is used as a living fence (Mahefa 2010).

Considering the native species: the multipurpose leguminous tree *Intsia bijuga* is used as a source of green manure, and is also valued for its highly durable wood (Mahefa 2010). The same is true of *Faucherea* sp., which is in the third category of quality wood classification (Gueneau 1971, Louvel 1922) and suits for cabinetwork. Other species have cultural importance: the sacred tree *Phyllarthron madagascariense* is used for ceremonies; *Terminalia catappa* L. (Combretaceae) symbolizes the location of the cemeteries; *Pseudopteris decipiens* Baill. (Sapindaceae) is planted in the villages for its aesthetic qualities, and also as a local traditional symbol of Malagasy culture; *Harungana madagascariensis* is used as an indicator of soil fertility, sap, leaves, etc. are used in traditional pharmacopoeia, and the wood is preferred for tool handles (Mahefa 2010). According to de Groot et al. (2010), the integration of ecosystem services is a tool for achieving better land use management. Before the protected area was established at Analalava, the forest fragment supplied provisioning ecosystem services to local people, in the form of firewood, timber, honey, bushmeat, fruits and mushrooms, medicinal plants, basketry material, and more. According to the conservation strategy used in the protected area of Analalava, trade-offs do exist between the above-cited provisioning services and economic development. Accordingly, alternative resources and services must be developed to compensate for the setting aside of the protected area and the resulting loss of services provided by the forest in the past. In this context, consider the case of timber taken from the forest, which is considered by local people to be the most valuable ecosystem service furnished in the past by the Analalava forest. For this provisioning service in particular, direct and indirect compensation offered to local people seems not to be sufficient, since they continue to harvest wood in the little forest fragments left in proximity to their villages. Furthermore, strong attachment remains to certain native species among local people, for the large range of services they provide, especially provisioning (medicine, timber), cultural (traditional spirituality, symbol, aesthetic value) and supporting to agriculture (soil fertility).

TAKING LOCAL KNOWLEDGE INTO ACCOUNT IN CONSERVATION AND SUSTAINABLE DEVELOPMENT. Ecological qualities of native trees used for ecological restoration, such as *Uapaca louvelii* Baill. (Euphorbiaceae) and *Intsia bijuga*, both of which are able to survive in abandoned fields, should be combined with the stakeholders' appreciation of the species. For example, experiments could be conducted on how some farmers would plant and use native tree species seedlings if they had access to them. This could be made possible if, in addition to distributing seedlings of non-native timber species, seedlings of sought-after native timber species were offered as well. Also, comparisons with on-going similar experiments within other community based conservation projects on the east coast of Madagascar, such as the one led by the Adefa association in Manompana (Adefa Association 2008), would be useful.

A major barrier to such plantation activities would be the unclear status of land tenure. It is obvious that this kind of activity cannot be pursued if the local population is afraid of possible land grabs. Turk (2005) considered the conditions under which native species planting could be implemented in Madagascar. One was that local managers and local population should agree on a common objective such as forest restoration or connectivity re-establishment. However, given the shortage of farming land in our study area, no lands are available for forest restoration outside the protected area. On the contrary, an approach that promotes diversity and heterogeneity should be encouraged (Rives et al. 2013) and a mix of introduced and native species should be promoted for people to cultivate them on their own lands as part of a 'melting pot of biodiversity' (Kull et al. 2013). This would increase ecological resilience of the forest ecosystem and the semi-cultural landscape.

The relatively slow growth rate of native tree species could also stand in the way of their plantation. However, each individual has its own reasons to plant as Rialland (1999) puts it. It depends on the farmer's availability, objectives, knowledge, and mental representation of the trees. Some farmers will be likely to plant certain native species because of the services provided, including heritage values and soil fertility. Other farmers, especially those in precarious situations, with short-term needs, will more likely require other incentives to plant native tree species, such as direct or indirect payments via ecocertification of agricultural produce. One example of certification is the sustainable agriculture network implemented by Rain Forest Alliance within several communities in Northern Madagascar (Rain Forest Alliance 2011). A decrease in the possible choices of tree species would result in a loss of local traditional knowledge, or cultural biodiversity. Conversely, supporting knowledge about how people perceive and use their environment, and natural resources, may help in local management, both in and outside of protected areas.

CONCLUSION

Clearly, in our study area, introduced species are indispensable for timber production and have been part of people's lives for several decades. Yet, their wood cannot replace all the uses once served by wood originating from native tree species. Since a restricted range of species cannot perform all the functions nor be used for all the purposes for which local people need wood, it seems that species-level biodiversity has a social importance in the study area. The diverse uses of timber must be taken into account by conservation and development workers, including the spiritual and cultural importance of some tree species and their medicinal use. Fast-growing introduced tree species certainly have their place in Madagascar's agricultural landscapes; slower-growing native tree species have their place as well. The interest of local people in a certain range of species could be used to improve conservation and restoration strategies. This approach could help reduce the pressure on forest fragments and enhance landscape connectivity, thereby benefiting conservation, sustainable development and restoration goals.

Futhermore, conserving and reintroducing native species within a protected area is essential but may not be enough for their long-term conservation, nor a way to sustain local people's livelihoods. Promoting the active protection and reintroduction of certain native species when possible in the working landscapes where people live can contribute to both these goals. In this way, a more participative management of the Analalava protected area and surrounding landscapes, based on local ecological knowledge, could be implemented with beneficial outcomes for both, conservation objectives and human livelihoods.

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

S1. Characteristics of the introduced and native tree species used for timber in four villages.

ARTICLE

http://dx.doi.org/10.4314/mcd.v10i3s.7

Habitat corridor utilization by the gray mouse lemur, *Microcebus murinus*, in the littoral forest fragments of southeastern Madagascar

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ABSTRACT

Habitat fragmentation has reached a dramatic level in Madagascar. As the size of many remaining forest fragments is unlikely to maintain viable animal populations in the long-term, connecting isolated subpopulations by creating corridors is important to support gene flow and the persistence of the endemic fauna, including lemurs. Since restoration with endemic trees is slow, exotic trees may represent a faster alternative to initiate habitats that can be used by animals. Here, we studied whether or not grey mouse lemurs, *Microcebus murinus*, use corridors composed of exotic and native trees of different age and composition to move between littoral forest fragments. For this, we trapped *M. murinus* in four forest fragments and mixed tree plantations between the fragments. One of the corridors was composed of a mixture of endemic and mature exotic *Eucalyptus robusta* trees. The second corridor consisted mainly of an old stand of exotic *Melaleuca quinquenervia*. The third corridor was composed of exotic *Acacia mangium* trees planted in 2009. During four years of study, only one male *M.murinus* used the *Melaleuca* corridor, while several *M. murinus* were caught in the *Eucalyptus* and the *Acacia* corridor in 2013. The density of the corridor under-story appeared to influence the number of individuals captured; the corridor with highest understory density was used most. The captures within the corridors illustrate that exotic trees allow movements of mouse lemurs within less than 5 years after plantation.

RÉSUMÉ

La perte et la fragmentation de l'habitat ont atteint une dimension dramatique à Madagascar. Même si les menaces résiduelles pourraient être atténuées, il est improbable que la taille actuelle de plusieurs fragments de forêts soit suffisante pour maintenir des populations animales viables à long terme. Connecter des sous-populations isolées en créant des corridors biologiques est une stratégie pour restaurer le flux génétique et appuyer le maintien des faunes endémiques, y compris les lémuriens. Étant donné que la restauration des habitats avec des plantes endémiques est lente, des espèces de plantes allogènes peuvent constituer une alternative rapide et peu onéreuse pour démarrer une restauration ainsi que pour créer des habitats utilisables par les animaux. Dans cette étude, nous examinons l'utilisation de corridors biologiques composés de différentes plantes allogènes par *Microcebus murinus* pour circuler entre divers fragments forestiers dans le Sud-Est de Madagascar. Notre but est de déterminer l'âge et la composition floristique des forêts restaurées qui permettraient la dispersion de *M. murinus* entre différents fragments. Pour cela, nous avons effectué une méthode de capture de *M. murinus* dans quatre fragments forestiers et dans des plantations d'arbres mixtes entre les fragments. Un des corridors biologiques était composé d'un mélange de plantes endémiques et allogènes dont *Eucalyptus robusta*. Le deuxième était principalement un vieux peuplement de *Melaleuca quinquinerva*. Le troisième corridor n'était composé que d'arbres allogènes, principalement des *Acacia mangium*, qui avaient été plantés en 2009. Les résultats montrent que *M. murinus* est abondant dans tous les sites de forêt. Pendant les quatre années d'étude, seul un mâle est passé d'un fragment à l'autre en utilisant le corridor de *Melaleuca*, et seul un mâle *M. murinus* a été capturé dans le corridor d'*Acacia* en 2012. En 2013, 29 individus de *M. murinus* ont été capturés dans deux des corridors suivis dans cette étude, incluant celui composé seulement de plantes allogènes, mais aucun animal n'a été capturé dans le corridor composé seulement de *Melaleuca*. La densité de la strate arbustive du corridor semble influencer le nombre d'individus capturés, le corridor ayant une densité élevée d'arbuste étant le plus utilisé. Ceci montre que les études de capture-recapture avec des *Microcebus*, qui sont des animaux ayant une courte durée de vie, ne sont pas efficaces pour documenter la dispersion de cette espèce dans les forêts littorales et la fonctionnalité des corridors.

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Par contre, les captures dans les corridors et dans les zones avoisinantes en 2013 suggèrent que la probabilité de flux génétique entre les fragments était élevée, et indiquent nettement que les plantes allogènes peuvent encourager les mouvements de *M. murinus*, même dans les peuplements jeunes de moins de cinq ans.

INTRODUCTION

Deforestation and habitat fragmentation, caused by logging and agricultural practices, are the leading causes of biodiversity decline worldwide (e.g., Fischer and Lindenmayer 2007, Habel and Zachos 2012). Fragmentation can result in a series of small subpopulations in the residual habitat, each with a high risk of going locally extinct or suffering from genetic drift (Templeton et al. 1990). This can reduce the ability of the subpopulations to adapt to environmental changes, with lowered fertility and reduced resistance to pathogens and parasites (Schad et al. 2005, Habel and Schmitt 2012).

Madagascar's forests are highly fragmented (Harper et al. 2007). In particular, the littoral forests of Madagascar are a top conservation priority, with the few remaining fragments being mostly smaller than 1,000 ha (Ganzhorn et al. 2001). These habitats are of great biological importance due to their floral diversity. They contain 13% of Madagascar's plant diversity, with at least 40 plant species endemic to Fort Dauphin's littoral forests alongside various endemic and threatened fauna species (Consiglio et al. 2006, Rabenantoandro et al. 2007, Lowry et al. 2008, Wesener 2009). These forest fragments are thought to be too small for the survival of viable populations of most forest-dependent vertebrate species (Ganzhorn et al. 2000, Watson et al. 2004).

Habitat corridors could link isolated populations, and thus mitigate isolation effects (e.g., Hilty et al. 2012). For the implementation of conservation actions, the question remains to understand what vegetation characteristics will allow the movements of animals and thus act as a corridor (Saunders et al. 1991, Hobbs 1992, Fischer and Lindenmayer 2007, Irwin et al. 2010). In Madagascar, natural or facilitated regeneration of natural forests from deforested areas is too slow to counteract forest loss. Non-native plantations can be established faster. This is particularly important in the littoral forests that grow on nutrient-poor sandy soil (Rarivoson et al. 2007, Ducousso et al. 2008). Therefore, it is essential to determine the effectiveness of corridors consisting of non-native plant species that would facilitate the movements of species between patches of fragmented habitats (Ganzhorn 1987, Irwin et al. 2010).

For the present paper, we first investigated whether or not, and at what state, corridors with varying exotic tree composition and vegetation structure represent suitable habitat for mouse lemurs (*Microcebus murinus*), a small nocturnal lemur species that is known to use a large variety of forest habitats (Mittermeier et al. 2010). This species was chosen as study species because it can respond rapidly to environmental changes due to its short generation times and high population densities (Ganzhorn and Schmid 1998). In addition, this small-sized species is likely to be vulnerable to predation when passing through areas with inadequate foliage protection (Goodman et al. 1993). Therefore, they are more constraint to forest habitats than larger lemurs, which can occasionally cross open space over larger distances, such as the sympatric *Eulemur collaris* (Donati et al. 2007). In *M. murinus*, males are the dispersing sex (Radespiel et al. 2001, Fredsted et al. 2004). Therefore, we expect more males than females moving through the corridors. Second, we compared the effectiveness of two different methods to monitor movements of mouse lemurs between forest fragments across an unsuitable matrix consisting of bare sand or heath vegetation.

METHODS

STUDY SITE. This study was conducted in the littoral forest fragments of Mandena, southeastern Madagascar, located at 24° 95'S, 46° 99'E (Figure 1). The study area consists of the forest fragments, M15 and M16 (the Mandena Conservation Zone), the forest fragments M13, M20, and TOK (Antokonlala), and the habitat corridors which link them (abbreviated as CM15-M13, CM16-M20, CM15-TOK; "M" stands for "Mandena" and the number indicates the number of the forest fragment at Mandena; "C" stands for "corridor" linking the fragments; Figure 2, Table 1). "TOK" consists of an old plantation of *Eucalyptus robusta*, planted prior to 1975

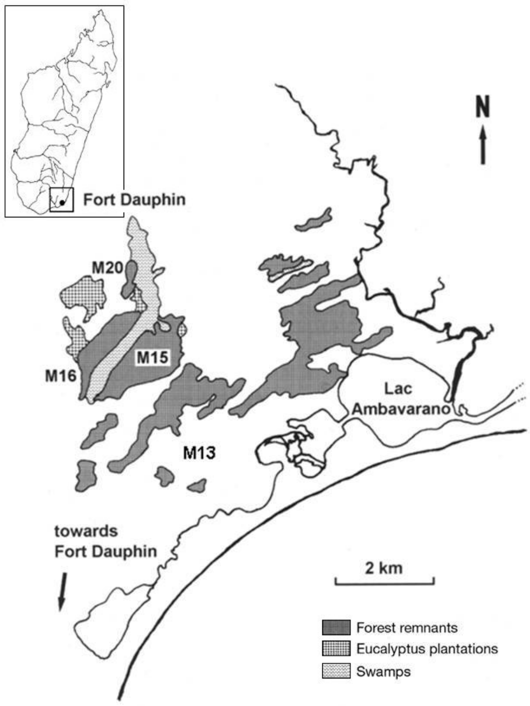

Figure 1. The Fort Dauphin region of south-east Madagascar, with the littoral forest fragments depicted in black (as of 2006) and the area of Mandena highlighted in red (modified from Bollen and Donati 2006).

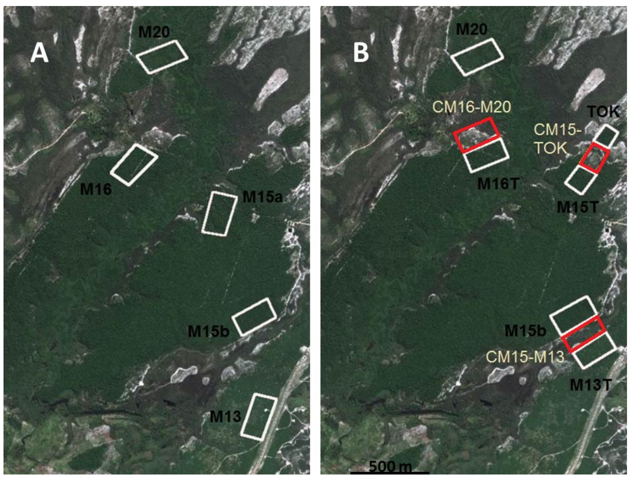

Figure 2. Trapping grid locations in the forest fragments (white) and the corridors (red). A: Trapping grid locations for captures between 2009 and 2012. B: Trapping grid locations for the study in 2013; note that the large distance between the M20 and CM16-M20 trapping grids is due to the presence of a large swamp, which separates them (modified from Google Earth).

Table 1. Vegetation characteristics of the study sites in Mandena. Fragment size (in hectares) as of 2005; canopy cover from Vincelette et al. (2007b); density of trees in forest fragments; *based on "Point-centred-quarters" (Ganzhorn et al. (2007b), and **based on "Whittaker plots" (additional sites established in 2013 and corridors, Blanthorn 2013).

Site	Size (ha)	% Canopy cover	Density of trees per ha			Number of tree species			% Exotic species		
			≥ 10 cm	5.0 – 9.9 cm	< 5 cm	≥ 10 cm	5.0 – 9.9 cm	< 5 cm	≥ 10 cm	5.0 – 9.9 cm	< 5 cm
Forest fragments											
M13*	109	≤ 20	81	210					0	0	0
M13T**			230	800	19000	19	4	18	0	0	0
M15a*	95	51 – 70	356	693					0	0	0
M15b											
M15T**			320	1200	19000	21	5	16	0	0	0
TOK	2										
M16*	53	51 – 70	356	693					0	0	0
M16T**			300	4200	22000	21	3	19	0	0	0
M20*	6	≤ 20	156	730					0	0	0
M20**			170	400	22000	13	2	25	0	0	0
Corridors											
CM15-M13**		0	155	600	5000	2	2	2	100	100	100
CM15-TOK**		0	230	400	7000	4	2	12	98	100	35
CM16-M20**		0	280	200	4500	1	1	7	100	100	29

with a rich undergrowth of native trees. It is unclear whether *E. robusta* had been planted within degraded native forest or whether the native forest regenerated after the plantation of *E. robusta*.

The Mandena Conservation Zone is part of Quebec Iron and Titanium (QIT) Madagascar Minerals' (QMM) environmental program that seeks to minimise the impacts of ilmenite mining on the regional biodiversity (Temple et al. 2012). The company is required to restore the mined area after mining. In order to achieve this goal, various long-term studies have been carried out to understand the present biodiversity patterns and ecosystem processes (e.g., Ganzhorn et al. 2007a, Lowry et al. 2008, Temple et al. 2012). As part of its environmental activities, the company has established tree plantations around the conservation zone with much emphasis on the eventual connection of the fragmented littoral forests of Mandena through habitat corridors (Vincelette et al. 2007b). These corridors consist of a mixture of native and introduced plant species (mainly *Eucalyptus, Acacia* and *Casuarina*), that will aid in the restoration of the impoverished soil as well as provide a fast-growing matrix for the movement of animals. This will eventually facilitate the dispersal of seeds of native tree species by animal frugivores (Bollen and Donati 2006). Several corridors have been established between fragments M15 and M16 and the surrounding fragments, three of which were included in this study (CM16-M20, CM15-M13, CM15-TOK; Table 1; Figure 3). The two fragments M16 and M20 are connected (CM16-M20) via a swamp with exotic *Melaleuca quinquenervia* that had established itself at least 20 years ago prior to the onset of the restoration activities. The fragments M13 and M15 were connected by *Acacia mangium*, planted in 2009 to create the corridor CM15-M13. Up to the time of study in 2013, this corridor contained next to no undergrowth of native tree species. Fragment M15 and "TOK" are linked by *E. robusta* and some regenerating native tree species (CM15-TOK).

LONG-TERM STUDY ON LARGE-SCALE DISPERSAL. First, the question of whether or not corridors between forest fragments would be effective was studied using long-term study plots established in the littoral forest fragments M13, M15a, M16, and M20 between 1998 and 2000 (Ramanamanjato and Ganzhorn 2001, Ganzhorn et al. 2007b, Figure 2A). M20 is located about 450 m north of M16. M16 and M15a are about 550 m apart and connected via littoral forest and native swamp vegetation. M15b is a newly established trapping grid some 550 m south of M15a; both are located within the continuous littoral forest of M15. M15b served as control to estimate whether or not dispersing individuals can be found in two trapping grids, spaced at the same distance within a fragment as the distance between trapping grids in different fragments. M15b was separated from M13 by open sand, with forest restoration activities starting between these two fragments in 2009.

We set up Sherman Traps baited with banana in these five permanent trapping grids (in M13, M15a, M15b, M16, and M20) for four nights every three months from February 2009 to August 2012. Each trapping grid consisted of 40 trapping stations with one trap on the ground and one trap in trees or bushes. Trapping stations were spaced 25 m apart in parallel transects, which were also 25 m apart (Ramanamanjato and Ganzhorn 2001). While designed originally to study population dynamics of small mammals, data collected during this period were also used to assess how far the mouse lemurs dispersed in the area and whether or not standardized trapping can be used to monitor movements between fragments.

SHORT-TERM CORRIDOR-CENTRED CAPTURES. As we never caught the same individual *Microcebus murinus* in both of the two trapping grids within M15 (M15a and M15b), we questioned whether or not the original design was suitable to assess the effectiveness of corridors. We therefore started trapping directly in the corridors. First, traps were set in the corridor plantation adjacent to M15b towards M13 in August 2012 (= CM15-M13). Subsequently, we set up a study designed explicitly to assess whether or not the corridors were used by *M. murinus* (Blanthorn 2013). For this, new trapping grids were created in May 2013 in three habitat corridors (CM16-M20, CM15-TOK and CM15-M13) (Figure 2B) and right next to the corridors in the forest fragments they link (M16T, M15T, TOK, M13T; M20 and M15b were the same trapping grids as used in the long-term study) with the aim to see whether the mouse lemurs were using the habitat corridors to move. The new trapping grids in the forest fragments were positioned contiguous to the habitat corridors to enhance the chance of recapturing marked animals.

Between May and July 2013, four days were spent trapping at each site. In the corridors, traps were set for another four days

Figure 3. The three types of corridors included in this study. Left: CM15-TOK. Centre: CM16-M20. Right: CM15-M13.

(i.e., eight days in total). Captured animals were marked with Trovan transponders (2.1 x 11.5 mm; Trovan ID 100). An animal's movement across the trapping grids was noted when it was recaptured in a different fragment to where it had initially been captured. The distance moved by an individual was measured as the distance between trapping points of capture and recapture.

VEGETATION DESCRIPTIONS. We established botanical plots in the forest fragments and connecting corridors to quantify the vegetation characteristics (species richness, canopy height and tree density) at each site. These variables have been found to be related to habitat utilization of lemurs in previous studies (e.g., Ganzhorn et al. 1997, Lahann 2008, Sehen et al. 2010). The vegetation of each plot used for the long-term study had been described between 1998 and 2004 based on the point-centred quarters method (Ganzhorn et al. 2011), centred on the 40 trapping stations (Ganzhorn et al. 2007b). For the study sites used for the corridor study in 2013 (Blanthorn 2013), the horizontal and vertical vegetation structures were measured using a modification of the Whittaker plot (Shmida 1984). Our modification involved creating a 50 m by 20 m plot for trees larger than 10 cm dbh (diameter at breast height), with two smaller plots at the centre, one measuring 10 m x 5 m for trees with 5–9.9 cm dbh, and one measuring 5 m x 2 m for trees under 5 cm dbh (Supplementary Material). This was done to incorporate a measurement of the understory plants as *Microcebus* are small primates and likely to utilise such habitats (Lahann 2008). A total of 13 vegetation descriptions were carried out: two in each corridor, one in each fragment (except for TOK) and one in each swamp. The height estimation, dbh and local name were recorded for each plant in the plot. Plants were identified to their vernacular name and the majority to their scientific names, following nomenclature in Randriatafika and Rabenantoandro (2007) and the knowledge of the QMM fauna team.

RESULTS

VEGETATION DESCRIPTIONS. CM15-TOK had the lowest proportion of exotic plant species, and the highest diversity and density of understory trees (Table 1). The corridor between M15 and M13 (CM15-M13) had the highest proportion of exotic trees (100% for all plant dbhs) and the lowest species diversity (two species for each tree size category; Table 1).

LONG-TERM STUDY ON LARGE-SCALE DISPERSAL OF *MICROCEBUS MURINUS*. According to the long-term mark-recapture study carried out from 2009 to 2012, mouse lemurs are abundant in all forest fragments (Figure 4). Only one animal was caught in more than one trapping grid. This male had moved from M20 to M16 between February and August 2010. No individual was recorded to have moved between the three trapping grids (M15a, M15b, M16) located within the continuously forested fragments M15 and M16.

SHORT-TERM CORRIDOR-CENTRED CAPTURES OF *MICROCEBUS MURINUS*. We captured 2–17 *M. murinus* individuals in the forest fragments within a single capture session lasting for four nights. No *M. murinus* were caught in the corridor CM16-M20 that consists mainly of *Melaleuca* with sparse undergrowth due to the swampy nature of the ground and the inhibiting effect of *Melaleuca* on the regeneration of other plant species. In corridor CM15-M13, 2 and 8 *M. murinus* were caught per trapping ses

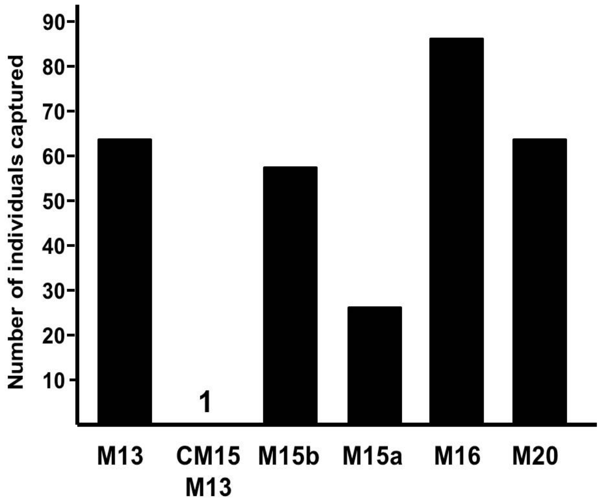

Figure 4. Number of individuals captured in the different permanent trapping plots between 2009 and 2012. In the corridor (CM15-M13) traps were set only in 2012.

sion in 2013. In 2012 only one M. murinus had been caught in this corridor. Seven and 12 different individual M. murinus were caught in corridor CM15-TOK in 2013. This corridor had the highest density of regenerating trees and shrubs.

The number of animals captured in the forest fragments per trapping session was significantly higher than the numbers captured in the corridors (data for 2013 from the first capture session: Mann-Whitney-U test: $U = 1.5$, $p < 0.05$). There was no significant difference between the sex-ratio of the animals captured in the forest to those captured in the corridors (Fisher's exact test: $p = 0.16$). Around half of these animals were then recaptured in a different habitat area. A higher number (nine out of 13) of these were males (not significant). The distance they moved between trapping sites ranged from 25 m to 200 m, with females moving on average further (100–200 m; mean 169 m) than males (25–175 m; mean 114 m). The difference was not significant.

DISCUSSION

As large areas of continuous habitats continue to shrink, linking populations in remnant habitats and facilitating the survival of species in anthropogenic habitats has become a prime initiative around the world. Some examples of this include creating a network of connected habitats in Europe through the program "Natura 2000" (Ostermann 1998), connecting forest fragments of the Mata Atlantica in South America (Tabarelli et al. 2005), and facilitating animal migrations in Africa (Bartlam-Brooks et al. 2011) or wildlife in Asia (Wikramanayake et al. 2004, reviewed by Gardner et al. 2010). While restoration with native plants is certainly desirable (Holloway 2003, Birkinshaw et al. 2009), plantations with non-native plants may sometimes provide alternatives as they often are faster growing and may provide benefits for humans, thus becoming more attractive and acceptable for local people (Gérard et al. 2015). In Madagascar, the study of the role of anthropogenic habitats for the native fauna has a long history (e.g., Petter et al. 1977, Ganzhorn 1987, Goodman et al. 1996, Irwin et al. 2010, Martin et al. 2012), but plantations are rarely used as a tool to mitigate fragmentation effects. Thus, our experience and knowledge of the possibilities of plantations for restoration and conservation action in Madagascar is limited.

Within large-scale restoration obligations after a mining operation (Vincelette et al. 2007a, Temple et al. 2012), various corridors were planted to link isolated remnants of littoral forest fragments in southeastern Madagascar (Rarivoson et al. 2007, Vincelette et al. 2007c). These plantations offered the possibility to study the efficiency of restoration activities for native plants and animals. Apart from one mouse lemur that had moved from M20 to the permanent trapping grid of M16, no other individual was found to have moved between any of the permanent trapping grids, neither within the continuous forest block M15/M16, nor through the vegetation between forest fragments. Since the continuous forest of M15/M16 does not provide a physical barrier for *Microcebus murinus*, and these lemurs are known to move over several hundred meters (Radespiel et al. 2003, Schliehe-Diecks et al. 2012), we conclude that this method was not sensitive enough to assess movements over distances of several hundred meters.

In the second approach, trapping grids were installed directly in the corridor and at either side of the corridor in the natural forest fragments. This design revealed that several *Microcebus murinus* used the corridors as well as the bordering natural forest and actually moved repeatedly between these different portions of habitat. Though none of these animals actually used the corridor to cross the matrix and move from one forest fragment to the other, the results show that planted woody vegetation can provide useful habitats at least for *M. murinus* within about four years. This should contribute substantially to the connectivity of the remaining forest fragments. Our preliminary habitat characterization indicates that structural features of the vegetation were more important than plant species diversity, though small sample size prohibited statistical analyses. More data is necessary to investigate this aspect in more detail.

While it is encouraging that plantations with fast growing trees are used by arboreal lemurs, it should be kept in mind that *Microcebus murinus* is not a habitat specialist, but occurs in a wide range of different habitats (Petter et al. 1977, Irwin et al. 2010, Mittermeier et al. 2010). Therefore, this species may be less hesitant to use non-native vegetation than other lemur species. Except for *Avahi meridionalis*, all the other lemur species occurring in Mandena (*Cheirogaleus* spp., *Hapalemur meridionalis* and *Eulemur collaris*) use the *Melaleuca* stands to feed on nectar when trees are flowering and for travel and resting (e.g., Lahann 2008, Eppley et al. In press). *E. collaris* are known to cross bare ground or heath vegetation between forest fragments (Donati et al. 2007) and *H. meridionalis* is feeding intensively on grass on the ground (Eppley and Donati 2009). None of these species has been seen during visual inventories of the corridors (Blanthorn 2013). Therefore, we cannot speculate whether or not these planted corridors provide the habitat characteristics required by these lemur species.

Many non-native plant species, including *Melaleuca quinquenervia* and *Acacia mangium* can be invasive (Gérard et al. 2015). This should be considered when using exotic plants for habitat restoration, buffer zones or corridors (Simberloff et al. 2013). For the time being, *Melaleuca* remains restricted to swamp areas and *Acacia mangium* has not shown any signs to move into the natural littoral forests (J. Rabenantoandro, pers. comm.).

In conclusion, our findings suggest that habitat corridors composed of exotic, or mixtures of exotic and native, plant species can facilitate the movement of gray mouse lemurs. The density of the understory appears to be more important to these small lemurs than the presence of native plants. The presence of individuals in corridors only 3–4 years after they had been planted suggests that the likelihood of genetic flow across the fragments via the corridor is high, and likely to improve as the corridors mature and become more established.

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