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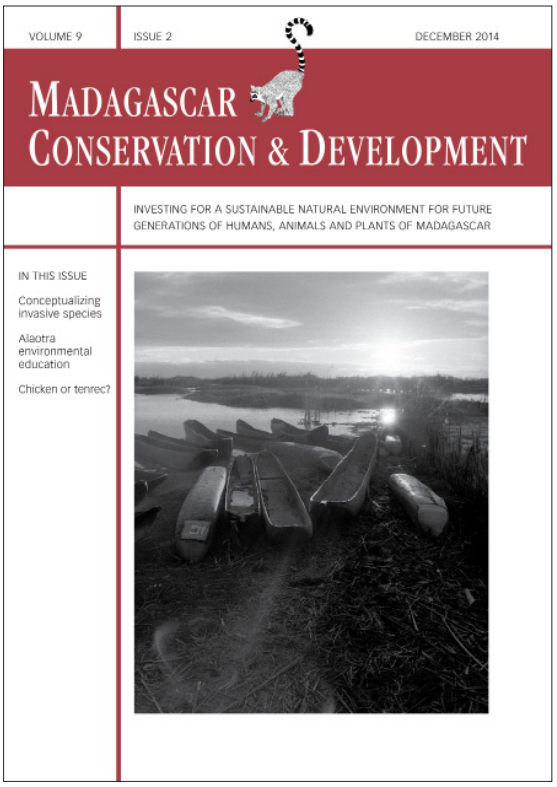
MADAGASCAR CONSERVATION & DEVELOPMENT

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

IN THIS ISSUE



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Tinker, tailor, wise man, madman, taxman – please!

1.6, 2.5, 6, 7.2, 9, 11… These numbers represent the human population in billions during the course of the last century during the years 1900, 1950 and 2000. The latter three are the current estimate and projections for the years 2030 and 2100, respectively. Though estimates differ according to model assumptions and scenarios used (cf. Gerland et al. 2014, or Samir and Lutz 2015), these are remarkable, if not alarming numbers. Consider how much of the planet's resources are been used currently (some 1.5 Earths, cf. Global Footprint Network 2013), and how these dwindling resources will need to serve ever more people in the future. Technological advancement and innovations may, with luck, increase the degree of efficiency, or slow down the resource consumption rate (cf. Randers' (2012) book '2052: A Global Forecast for the Next Forty Years' in which social and environmental scenarios are outlined concerning how future resource consumption may take place). According to Davidson and Andrews (2013), resources exploitation can lead to increased ecological impact despite overall consumption levels remaining constant since accessibility will become more difficult (law of diminishing returns). In terms of resource users, the human population will eventually reach a plateau. For this, the current global fertility rate of women needs to start decreasing faster than it is currently doing: just at a glance, India with 2.5 children per woman ranks at 81st place out of 224 countries, Madagascar is on 33rd with 4.28, and Niger ranks top with the globally highest fertility rate at 6.81 children per woman.

An estimated 2.2 billion people live currently on less than US$ 2 per day; access to education, healthcare, electricity, potable water and other critical services remains problematic for many people living in developing economies (World Bank 2014). In the year 2000, 189 countries met at the UN and in their United Nations Millennium Declaration (Resolution 55/2 of 8 September 2000) they shared a vision and responsibility to ensure worldwide economic and social development, human dignity and equity. The declaration lists eight goals to be achieved by the year 2015; these Millennium Development Goals (MDGs) are rooted in the concept of sustainable development: 1. eradicate extreme poverty and hunger; 2. achieve universal primary education; 3.promote gender equality and empower women; 4. reduce child mortality; 5. improve maternal health; 6. combat HIV/aids, malaria and other diseases; 7. ensure environmental sustainability; 8. develop a global partnership for development (United Nations 2014a).

These are, admittedly, highly ambitious goals and formulating this collective responsibility across the globe within the time frame of 15 years will not be an easy task. Nonetheless, enormous progress has been made towards achieving the MDGs by the end of 2015. Global poverty continues to decline, with an estimated 700 million people being lifted out of extreme poverty (e.g., Indonesia's extreme poverty rate has been reduced by 70 %). More children than ever are attending primary school (from 102 million in 2000 to 58 million out of school children of primary school age in 2012). Child deaths (under-five mortality rate) have dropped dramatically (it has been almost halved since 1990, which means that more than six million fewer children died in 2013 than in 1990). But despite substantial progress, about 1 in 5 people still live on less than US$ 1.25 per day in many developing regions (United Nations 2014a). Bangladesh, for example, has reduced the proportion of underweight children from 62 % in 1990 to 37 % in 2011. However, globally, still 1 in 8 or 842 million children under age five suffer from chronic malnutrition. Efforts to build on the MDGs and to achieve a world of prosperity, equity, freedom, dignity and peace will have to continue unabated (with the post-2015 development agenda talks being in full swing now). The UN further states that "(…) MDGs are making a real difference in people's lives and, with 'strong leadership' and 'accountability' [emphasize added], this progress can be expanded in most of the world's countries by the target date of 2015" (United Nations 2014b).

Madagascar has been through five years under the regime of a transitional administration (the High Authority of Transition), a period of economic disorder and international isolation (e.g., Ploch and Cook 2012, Randrianja 2012). Presidential and legislative elections took place in Madagascar in December 2013. Hery Rajaonarimampianina was elected president and assumed his role on 25 January 2014. Immediately, the African Union and Southern African Development Community lifted their suspensions, and the European Union's development program, as well as the World Bank and International Monetary Fund started reinstating development funds. Since last June, Madagascar was again eligible for the AGOA (African Growth and Opportunities Act) (IRIN 2014). This is a vital step for Madagascar's economy and development as according to Fukunishi (2013) the political turmoil led to a reduction of over 64 % in US-trade only, affecting mainly unskilled workers. In 2010, over 228,000 jobs have been lost as a direct consequence of the aid decline and blocked trade agreements (Chatham House 2013).

The high uncertainty linked to the period of political instability and the consequent lack of investment had severe economic and social consequences for Madagascar. According to the 1,200 Malagasy participants of the Afrobarometer (2013), an independent research consortium assessing social, political and economic atmosphere in sub-Saharan Africa, development of the country deteriorated during the past five years. The United Nations Development Programme (UNDP 2014) ranks Madagascar 151 out of 186 countries in its Human Development Index (a measure similar to the better known Gross Domestic Product GDP), down from 143 in 2008 (prior the crisis). This translates to 93 % of Malagasy living below the $US 2 per day poverty line, which is a 4-point increase from 89 % in 2001; 43 % live below the $US 1.25 per day extreme poverty line, a steep increase from 26.5 % in 2005 (World Bank 2014).

Madagascar managed to stay on track during the period 2002–2006 in terms of achieving its Millennium Development Goals (MDG Monitor 2007). Improvements mainly in the health and education sectors were responsible for a drop in poverty. The increased and continuous spending on health during the 2002–2008 period, from 113–245 billion Ariary showed demon-

strable results. Immunization coverage increased significantly for measles and DPT3 (diphtheria, pertussis and tuberculosis). The under-five mortality rate dropped from 161 ‰ in 1990 to 86 ‰ in 2004 (UNICEF et al. 2011). In 2005, the Malagasy government committed to achieve the objectives of the Education for All act by 2015. Public expenditure for education increased from 243–585 billion Ariary from 2002–2008 (BTI 2014). Consequently, the net primary school enrollment increased steadily to over 87 % (MDG Monitor 2007). With the onset of the political crisis these expenditures came to an abrupt halt. During the crisis period, the number of out-of-school children increased by more than 600,000 (World Bank 2013). The lack of governmental funding forced many parents to shoulder the costs of schooling. Many teachers, as for example in the case of the Alaotra no longer received regular training (Reibelt et al. 2014). The quality of learning continuously decreased, e.g., primary completion rate is now at 68.8 % versus the 100 % as stated goal (MDG Monitor 2014). Many healthcare centers have been closed down. According to these trends, it seems unlikely that Madagascar can achieve the UN MDGs by 2015, something affirmed by Madagascar's new president.

The challenges for Madagascar are manifold. According to a recent report by the International Crisis Group (2014), an independent non-partisan institution sees Madagascar on a fragile path since "the election was a cosmetic shift of power, not a fundamental transformation of a system that needs more than just a makeover". The new government is currently facing several issues that require immediate addressing. A locust plague has spread across Madagascar putting several million people at risk of experiencing famine (FAO 2014). As a legacy of the transition period, where there has been a severe lack of law enforcement, gangs of well-armed cattle thieves have taken massive advantage. The new government started to take action by creating more presence in previously neglected regions, and according to Hery Rajaonarimampianina's speech on 25 September 2014 in front of the UN General Assembly, his government has also opened a greater number of health care centers in the past few months. These are promising signs and necessary actions showing that the new government is already looking beyond the Millennium Development Goals: "Our primary goal is to bring our people out of their precarious situation" (…) "the aim is not only to improve livelihoods at home, but to transform Madagascar into a 'food hub' in the region" referring to increased investments into agriculture. We can hope that this will not risk turning into facilitating land grabbing of larger proportions bringing scrupulous companies back into Madagascar (e.g., Franchi et al. 2013, Neimark 2013).

Strong leadership and particularly accountability are two salient ingredients of governance that have been sorely lacking during the transition period. We only can hope that the current government is strong and willing enough to fully commit to upscale its efforts towards the post-2015 development agenda, for the uplifting of the most vulnerable of its citizens. The good news in Madagascar is, that due to its large-scale agricultural dependence (over 83 % of the people live in rural areas and 64 % of these households earn their livelihood from agricultural activities), the country seems to be more resilient than the figures might suggest, thereby preventing the country as a whole from sliding into a larger scale catastrophe.

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SPOTLIGHTS

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Approaching invasive species in Madagascar

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ABSTRACT

While a number of plants, animals, and insects in Madagascar have been called 'invasive', the topic of invasive species has until recently received less attention here than in other island contexts. Some species, often alien to Madagascar and introduced by humans, have expanded their range rapidly and have had both negative and positive effects on landscapes, on native biodiversity, and on livelihoods. Examples include the prickly pear (*raketa*), the silver wattle (*mimosa*), and, recently, the Asian common toad (*radaka boka*). Building on a conceptual approach to 'invasive species', this paper emphasizes the importance of inclusive and deliberative site- and population-specific management of invasive species. It analyses three separate concepts commonly used in definitions of invasion: the origin, behaviour, and effects of particular species. It places these concepts in their broader social and ecological context, with particular attention to local perspectives on invasive species. We illustrate these concepts with Malagasy examples and data. The examples demonstrate that while invasions can have dramatic consequences, there can be multiple, often competing, interests as well as site-specific biophysical, environmental, and cultural considerations that need to be taken into account when designing policy and management interventions. We conclude with a number of lessons learned.

RÉSUMÉ

Contrairement à la plupart des autres îles, et en dépit du qualificatif 'invasif' rattaché depuis longtemps à certaines espèces qui s'y sont naturalisées, les réflexions autour de l'approche des espèces invasives à Madagascar demeurent récentes. L'opuntia (*Opuntia* spp.) figure certes parmi les plus anciens exemples d'espèces traités dans la littérature sur les invasions biologiques. Mais ce n'est vraiment qu'avec le retentissement médiatique autour de la détection en 2011 de la présence du crapaud masqué (*Duttaphrynus melanostictus*) et la recherche d'une parade appropriée que s'est affirmée la nécessité de traiter cette question des espèces invasives en tant que telle.

Une posture nativiste et uniforme qui ignorerait la spécificité des contextes biophysiques et socio-économiques locaux, mais aussi la pluralité des formes d'invasion biologique et des définitions qui s'y rattachent, ne saurait être privilégiée. L'article montre qu'il s'agit de situer les réflexions dans un contexte insulaire socio-économique dans lequel les espèces allogènes tiennent depuis longtemps une large place. Il défend en outre la nécessité d'envisager les espèces invasives non pas selon une forme de perception unique et autoritariste, mais selon une diversité de points de vue, conforme aux conflits d'intérêts qui se manifestent parfois, et mettant plutôt en avant le caractère exogène des espèces invasives, leurs effets (négatifs, mais aussi positifs) sur le milieu, ou leur mode de fonctionnement (dispersion, dominance) dans des contextes spécifiques et locaux.

Il convient en particulier d'observer qu'aux coûts générés par les invasions biologiques peuvent s'ajouter des bénéfices économiques, et que les impacts écologiques néfastes peuvent se combiner avec des incidences heureuses, y compris auprès d'espèces indigènes en situation critique. En outre, le point de vue des populations humaines, leur connaissance d'espèces invasives quotidiennement rencontrées, leur réticence à scinder le vivant en espèces indigènes et allogène, mais aussi leur vision pragmatique, ne sauraient être mésestimés, et moins encore oubliés. Enfin, l'article invite à prendre du recul face aux effets rhétoriques liés aux discours conventionnels sur les invasions biologiques, à éviter les amalgames et les généralisations excessives, à tenir compte des contraintes environnementales mais aussi des aspirations socio-économiques des populations locales, et à prendre en compte la diversité des spécificités locales, qu'elles soient biophysiques ou sociales.

En conclusion, il est sans doute heureux que Madagascar n'ait rejoint que très récemment la mouvance internationale des réflexions sur les espèces invasives : cela lui permet en effet d'être en mesure de disposer d'une position équilibrée, déjouant certains discours catastrophistes, et préférant une approche résolument contextualisée, à l'échelle nationale comme aux échelles régionales.

INTRODUCTION

In 2011, the Asian common toad, *Duttaphrynus melanostictus* arrived in the port of the city of Toamasina and began to make

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its home in Malagasy soil. By early 2014, this species – which releases a toxin from its paratoid gland when stressed – had been spotted up to six kilometres from the port. Alarm bells were rung about the threat to biodiversity, amphibian diseases, water supplies, and domestic animal health from these "invasive venomous toads" (Kolby 2014, R. 2014). The spectre was raised of Australia's infamous experience with another bufonid, the cane toad[1] from the Americas, which has colonised much of northern Australia, affecting native biodiversity and becoming a nuisance for people (Seton and Bradley 2004). Yet calls in the high-profile journal Nature for rapid efforts to eradicate the Asian common toad in Madagascar led to a debate over the possible collateral damage of rapid eradication efforts, including the potential killing of native toads or the unforeseen consequence – or possible futility – of draining potential breeding ponds (Andreone 2014, Mecke 2014).

Such debates are hardly new: nearly one hundred years ago, the control of an invasive variety of *Opuntia* (prickly pear cactus, raketa) in the south of Madagascar through the release of a scale insect[2] met with vehement protest, given the plant's utility as a famine food (Middleton 1999, Kaufmann 2001, Binggeli 2003a). Yet, such debates over invasive species are relatively rare in Madagascar. The topic has received "scant attention in recent decades" and "little is known about the distribution or impact of any introduced species" (Binggeli 2003b: 257). In comparison with elsewhere, conservation decision-makers and actors in Madagascar have tended not to focus on invasive species, not seeing them as a major issue (Carrière et al. 2008). Invasions were not addressed, for instance, at the 2006 Conservation International biodiversity symposium held in Madagascar (ibid.). The first event to focus on invasive species on the island was only held at the University of Antananarivo on 9–10 October 2013.

The above context, together with the recognition that there are indeed a fair number of invasive species on the island (Binggeli 2003b; Kull et al. 2012), suggests that it is important to consider how one should approach the question of invasive species in Madagascar. With the continuously growing volume and speed of human movements and trade in recent years, chances increase for further introductions of non-native plants and animals. It can be tempting to adopt a hardline nativist posture that rallies resources to fight invasions perceived at first glance to be uniform threats to the economy or to biodiversity. However, as the debates over the cane toad and prickly pear hint, there are multiple, often competing, interests as well as site-specific biophysical, environmental, and cultural considerations to take into account. Even the terminology and definitions of 'invasion' can be confusing. In order to highlight and address these complexities, this paper approaches the issue of invasive species in Madagascar from a conceptual point of view. It dissects the concept of invasion, illustrates it with Malagasy examples and data, and provides some recommendations for policy and practice. Our analysis suggests that it is important to avoid categorical approaches, and emphasizes instead the importance of a deliberative site- and population-specific approach.

BACKGROUND: A MELTING POT ISLAND

Madagascar, a large island of highly endemic flora and fauna and relatively recent human settlement, nonetheless hosts numerous life forms familiar around the tropics and subtropics. For instance, to choose one landscape, a visitor from southern India, Mozambique, or Fiji would not feel too out of place in eastern Madagascar. There, the mix of cultivated and spontaneous plants and animals is a Malagasy version of the typical cosmopolitan humid tropical smallholder landscape. The fallow hillsides and field and path edges are made of a number of species, both native and introduced, some of which are rapid colonizers of open terrain. Common species include *Rubus alceifolius* (Moluccan bramble), *Clidemia hirta* (Koster's curse), *Ravenala madagascariensis* (traveller's palm), Pteridophytes (ferns), *Aframomum angustifolium* (wild ginger), *Bambusa* spp. (bamboo), *Eucalyptus*, *Pinus* spp. (pines), *Psiadia altissima* (dingadingana), *Lantana camara*, *Psidium cattleianum* (strawberry guava), *Albizia* spp., *Grevillea* spp., and nevermind domestic and commensal animals like *Bos indicus* (cattle), *Canis lupus* (dogs), and *Rattus rattus* (rats). Like elsewhere around the world, humans have introduced a wide variety of plants and animals over the past millennia for diverse reasons: food, economic aspirations, aesthetics, or accidentally.

The study of non-native species and weeds on the island arguably began with the indefatigable Perrier de la Bâthie's publication of *Les pestes végétales à Madagascar* (1928) and *Les plantes introduites à Madagascar* (1931–32) and the management issues regarding prickly pears and lantana in which he became embroiled (Middleton 1999, Kaufmann 2001, Binggeli 2003a, c). Aside from agronomic and forestry work on introducing new cultivars and on fighting common nuisance plants, little attention was given to 'invasives' as a category until Pierre Binggeli's contributions to the tome Natural History of Madagascar. Binggeli's (2003b) main chapter provides a landmark overview of the island's invasive plant species, but laments that the "dearth of quantitative data and information prevents the production of a comprehensive review" (Binggeli 2003b: 257). He lists 38 species of flowering plants as invasive in Madagascar, or at least present on the island and known to be invasive elsewhere. He highlights the historical stories and ecosystem effects of nine species in detail, six in the main chapter (*Clidemia hirta*, *Cissus quadrangularis*, *Psidium cattleianum*, *Rubus alceifolius*, *Rubus rosifolius*, and *Solanum auriculatum*) three others in separate chapters (Binggeli 2003a, c, d): *Opuntia*, *Lantana camara*, and *Eichhornia crassipes* (water hyacinth). More recently, a biological conservation textbook adapted for a Malagasy audience devotes five pages to invasive species (Primack and Ratsirarson 2005), and in 2012 we built on the work of Perrier de la Bâthie and Binggeli to establish an extensive inventory of plant species introduced to the island. In this inventory we noted whether species had displayed invasive behaviour (Kull et al. 2012).

WHAT ARE 'INVASIVE' SPECIES?

In discussing invasive species, it quickly becomes apparent that the concept is open to interpretation. First of all, while the term is applied to species, it is of course never a species that is invasive, but particular populations of some species in particular habitats or ecological conditions (Colautti and MacIsaac 2004). Conversely, species that are invaders in one place may in turn be threatened in their native habitat. Second, it has been amply shown that the language of invasion and its reliance on military or nationalistic metaphors predisposes

people to think in certain ways about those life forms labelled invasive (Tassin and Kull 2012). Third, and most importantly for this paper, even the scientific definitions of 'invasive species' differ strongly in their emphases (Colautti and MacIsaac 2004, Tassin 2014). In this section we review the concept of invasion at a general theoretical level; in the sections that follow we apply each of the key themes raised here (origin, behaviour, effects, and local perspectives) to invasive species in Madagascar.

There are three main axes in definitions of invasive species that get emphasized, suppressed, or elided depending on the point of view and goals of the person using the term (Larson 2007). These are the 'effects' (and our judgement of those effects), the 'origin' (where a species is thought to come from), and the 'behaviour' (the act of rapid spread and domination) of the particular population of 'invasive' species. These correspond with the terms often used in such cases, like alien, invasive, weed (or pest for animals and insects). Particular definitions emphasize one or the other axis, or two, or uncritically mix bits of all three.

The focus on 'effects' is probably the oldest axis in the concept of invasive species, for the concepts of weeds and pests existed long before the science of invasion biology. Research of a more applied perspective tends to favour definitions of invasive species that emphasize this aspect – a negative impact such as threats to indigenous biodiversity, or quantifiable economic costs (McNeely 2001, Simberloff et al. 2013). People will of course always judge plants and animals and the consequences of their introduction or proliferation; opinions, thinking, and judgement are part of being human. These judgements will of course vary with peoples' interests, prevalent ideas, and the current economic situation. For instance, the judgement of impact may be coloured by the native or non-native status of a species, with effects judged negatively just because a species is 'alien' (or, conversely, romanticized because it is 'exotic'). Moreover, consensus can be misleading, because it reflects a dominant, sometimes hegemonic, way of thinking.

Other definitions of invasive species specifically break with the question of impact. Richardson et al. (2000: 93) suggest "that the term 'invasive' should be used without any inference to environmental or economic impact", noting that terms like 'pests' and 'weeds' are suitable labels for those cases. Richardson et al. go on to define invasive species as, essentially, those that are alien (those which owe their presence in a given area to purposeful or accidental human introduction), naturalized (those which reproduce consistently without human intervention), and in addition those that have the potential to spread over a considerable area and at a high speed. The underlying narrative could be said to be that when humans take species beyond their natural ranges and they reproduce abundantly, the rules of the game are broken. This is a dual focus on origins and behaviour, but with the additional layer of human agency. The work of Richardson and colleagues strongly emphasizes biogeographic themes like native distributions and dispersal barriers (mountains, climate bands, or oceans). Their focus on human agency in moving species across such barriers is on the one hand practically quite relevant (humans move many species, quite frequently, and in great numbers; our actions can in principle be managed through policy) but also conceptually problematic as it reifies a divide between nature and culture (Frawley and McCalman 2014).

A strict focus on origins, where non-native status is linked to the concept of invasive species, has several issues (Warren 2007, Davis et al. 2011). For one, the concept of 'nativeness' is spatially and temporally relative, in the sense that species ranges are not fixed but 'naturally' shift over space and time (Webber and Scott 2012). Second, nativeness is also scale sensitive: a species can be native to Madagascar, but only to certain regions of the island, and can also have been introduced from one region to another one. We do not know the current range, the pre-human range, nor the range at last glacial maximum (for instance) for most Malagasy species, which complicates such discussion. For convenience, in online databases, floras, and species lists, native status is often reported using administrative or geopolitical entities, which can lead to awkward policy conundrums, as when a garden shop sells a 'native plant' that is actually only native to a distant corner of the same country (Head and Muir 2004). In Madagascar, for instance, the native species *Delonix regia* (flamboyant) and *Terminalia mantaly* are originally restricted to the south, but have been planted as ornamentals around the island (and across the tropics in general). Third, sometimes there are problematic associations made between species origins and national identity, both in terms of nationalism about natives and fear of the alien (Comaroff and Comaroff 2001, Tassin and Kull 2012, Mastnak et al. 2014). Finally, invasive behaviour is not limited to non-native species (Valéry et al. 2009). We turn to this theme now.

'Behaviour', or the act of rapid spread and dominance in particular ecological contexts, is probably the part of the invasive species concept most closely related to the dictionary meaning of the word 'invasive' in the sense of "intruding on the domain of another". Davis (2009) has promoted an approach to invasion biology re-centred on 'species redistribution' and the means by which some species expand or contract in different ecological contexts. Along these lines, Valéry et al. (2008: 1349) define invasion to be when a species acquires "a competitive advantage following the disappearance of natural obstacles to its proliferation, which allows it to spread rapidly and to conquer novel areas within recipient ecosystems in which it becomes a dominant population". One must of course be careful not to separate this behaviour from the human driving actions (land use, pollution, climate change, as well as transport) that lie hidden and unexplored behind these processes (Tassin 2014).

The above concepts, in varying combinations, have been used to produce official and scientific knowledge about a category – 'invasive species' – that was invented some fifty years ago (Richardson 2010). It is important to realize, however, that these formal representations, which carry the power of science and result in categories, lists, and policies used by government agencies, jostle up against different forms of knowledge and understanding, including practical everyday tactile and emotional experiences and indigenous or alternative local perspectives (Kull and Rangan In press). Different people have different approaches to the plants and animals they encounter in their fields, gardens, yards, and streets, sometimes reflecting dominant scientific ideas, and sometimes running counter to them. Paying attention to these 'local perspectives' both helps to critically reflect on 'official' categories and to find more pragmatic, contextual, and just management approaches (Bentley et al. 2005, Trigger 2008).

In the next four sections, we apply each of these ways of defining invasive species – origin, behaviour, effects, and local perspectives – to the case of Madagascar.

ORIGIN: NATIVE OR NOT NATIVE TO MADAGASCAR?

The Indian Ocean forms a clear biogeographical barrier around Madagascar, at least for terrestrial species. Species have periodically crossed this barrier, including lemurs and chameleons (Dewar and Richard 2012, Tolley et al. 2013). Human travel and trade over the last two, perhaps four, millennia undoubtedly increased the frequency and magnitude of introductions. While the exact nature and timing of prehistoric migrations and trade links between Madagascar, nearby coastal Africa, the Indian Ocean rim, and the distant homeland of Austronesian settlers remains contested (Beaujard 2011, Dewar 2014), ample opportunities existed for transfers, and these transfers enabled society to flourish on the island but also introduced certain 'alien' weeds and pests. European and colonial contacts, and modern agronomic and forestry interventions, and global trade increased the possibilities for new species to arrive (Kull et al. 2012).

Madagascar hosts 50 or 60 introduced animal species and around 1,200 introduced vascular plant species. We documented elsewhere (Kull et al. 2012) that the absolute number of introduced plant species is small when compared to other island groups (the other islands are typically wealthier places with more trade in ornamentals). The relative number of introduced species (ca. 1,200) compared to the native flora (at least 11,220: Callmander et al. 2011) is also small, more typical of continents, in part due to the large number of native species. However, the percentage of introduced plant species that has been labelled 'invasive' (following any definition) is relatively high, at 8.9 per cent. This likely reflects the fact that while the introduced flora is relatively small, it includes many common weedy plants but fewer specialized ornamentals.

While being an island should make it relatively easy to distinguish native from alien, the antiquity and ubiquity of human and non-human dispersal of species means that many species are cryptogenic. We found 174 plant species on Madagascar with uncertain status (Kull et al. 2012). Furthermore, within the island's borders, researchers have identified biogeographic barriers or distinct native distribution zones that could be used to label plants or animals as non-native in other parts of the island (Wilmé et al. 2012, Ganzhorn et al. 2014). These distinctions can be difficult to identify (surveys are not always comprehensive) and to use as a basis for management (if a species is found near, but outside its supposed native range, what should one do, particularly in a context of climate change?). Finally, species native to Madagascar have also shown invasive tendencies on the island, for instance *Cynanchum* vines in Beza Mahafaly Special Reserve (Sussman and Rakotozafy 1994, Ratsirarson 2005).

In sum, on the one hand, a singular focus on origins in approaching invasives is problematic. While many of the prominent invasive species in Madagascar discussed below in terms of behaviour or impact are alien, some are not alien, some are cryptogenic, and some arrived by themselves. Non-native species can be invaders, but they can also form fundamental pillars of the country's economy and culture, as do rice, vanilla, cloves, eucalyptus and zebu. On the other hand, given that many (though not all) problematic species are those that are introduced from far away, a focus on origins suggests a key intervention strategy for mitigating future invasions: phytosanitary control. The borders of an island nation like Madagascar are the one place where it is practically and institutionally possible, though difficult, to screen the entry of new alien species. Such care may have avoided the introductions of species widely considered problematic elsewhere, such as *Acridotheres tristis* (the common myna), a cosmopolitan commensal bird.[3] It has now spread across many of the anthropogenic landscapes of the island, arriving in Antananarivo a decade ago (Primack and Ratsirarson 2005).

BEHAVIOUR: SPREADING AND DOMINANCE IN DISTURBED HABITAT

Plants and animals that spread rapidly and gain dominance – often in environments made 'invasible' through human interventions like ploughing, deforestation, fertilization, irrigation, fire control, or other modifications to existing soil or vegetation, or indeed through natural forest blowdowns from cyclones (Alpert et al. 2000) – are numerous on the island (Perrier de la Bâthie 1928, 1931–1932; Binggeli 2003b). Such invasive behaviour occurs at several scales. At the spatial and temporal scale of an annual cropfield, examples include diverse herbaceous adventive plants, both native and introduced, such as *Bidens pilosa, Heteropogon contortus*, and *Leersia hexandra* (Husson et al. 2010); in a slash-and-burn plot the dominant species are initially grasses and then other pioneers like *Harungana madagascariensis* (Randriamalala et al. 2014). At the scale of a small protected area and a particular management intervention (the exclusion of cattle grazing from a 100 ha parcel), one might mention the rapid spread of *Cynanchum* vines into the forest canopy at Beza Mahafaly Special Reserve (Sussman and Rakotozafy 1994, Ratsirarson 2005). At a regional and decadal scale, examples of invasive behaviour include the spread of *Lantana camara* to cover 100,000 ha in the Mangoro valley a century ago (Binggeli 2003c), the ubiquity of silver wattle in parts of highlands (Kull et al. 2007), the development of monotypic stands of *Ziziphus jujuba* (jujube) in the 1970s near Ankarafantsika in the northwest, the recent explosion of *Grevillea banksii* in many sections of the eastern lowlands, the spread of *Acridotheres tristis* across the island, and – potentially – the spread of *Duttaphrynus melanostictus,* the toad mentioned in the introduction.

The above examples hint at an important point: often there is a temporal aspect to invasive behaviour. Invasive plants are often heliophilous pioneers, some of which have relatively short life spans and which, without further disturbance, are complemented or replaced by other species. For instance, the spread of non-native 'invaders' like *Cecropia*, *Musanga* and *Clidemia hirta* in disturbed tropical rainforest is akin to the behaviour of early successional species and they are likely to be replaced by more shade tolerant native forest trees over time (Holland and Olson 1989, Whitmore 1990, Rakotonirina et al. 2007). In other cases, the impact of logging and subsequent invasion appears to last much longer, even centuries (Brown and Gurevitch 2004). For both plants and animals, their evolutionary and competitive advantages eventually decline as local predators and pathogens adapt to the new opportunity. For instance, *Lantana*

invasions in several tropical islands – such as New Caledonia (Tassin 2014), Timor (McWilliam 2000) – at first spread quickly and then subsided, which may be the case in Madagascar, given the alarm with which Perrier de la Bâthie viewed 100,000 ha invaded eighty years ago (Binggeli 2003c) and its widespread but not particularly invasive state today.

Environmental managers sometimes rely on the capacity for certain species to spread rapidly and become dominant to achieve certain goals, most commonly for protection or restoration of degraded lands. Two small trees (*Acacia dealbata* and *Grevillea banksii*) whose seeds were widely dispersed in the Lake Alaotra region for erosion control and 'regreening' because of their colonizing ability were actually widely considered to be failures, for they did not establish themselves nor become dominant (Tassin 1995). This is in sharp contrast to their spread in other more suitable regions, as we note elsewhere.

Interestingly, Perrier de la Bâthie's (1931–1932) seminal review of the island's introduced plants classified species based on their behaviour and the kinds of disturbed areas they were found in. His categories included cultivated plants (i.e., no invasive behaviour), and three groupings of pioneer and light-demanding species: *plantes adventices* (essentially, weeds), *rudérales* (growing around houses and waste heaps), and *messicoles* (growing in fields, along paths, road verges). Perrier de la Bâthie also listed 72 native or endemic plants that have become ruderal or messicole, emphasizing the incompatibility of the category 'behaviour' with that of 'origins'. More recently, a team of agronomists has prepared a guide to the fallow field plants and crop weeds (*adventices des cultures*) of Madagascar (Husson et al. 2010), using plant behaviour (colonization) in particular habitats (crop fields and fallows) as the overall criteria for inclusion.

EFFECTS: NEGATIVE AND POSITIVE OUTCOMES

When speaking about the effects of invasive species, the focus tends to be on economic burdens (such as reduced agricultural harvests or increased management budgets) or impacts on biodiversity (such as threatening native species or transforming habitats). It is important, however, to remember that effects can be both positive and negative, and that the determination of whether effects are good or bad always incorporates an element of human judgement (Tassin and Kull 2015). Here we provide examples of a number of different types of effects on Madagascar.

ECONOMIC COSTS. Crop field weeds, both native and introduced, reduce agricultural productivity by competing with crops and by necessitating costly labour or chemical treatments (which in turn may lead to pollution or toxic health effects). Husson et al. (2010) review the principle weed plants from an agronomic perspective, and catalogue the types of manual or herbicide control found to be most effective. The *Eichhornia crassipes* (water hyacinth) clogs many lakes and waterways including the Pangalanes Canal and Lake Alaotra, as well as rice fields. The city of Antananarivo expends considerable effort in removing it annually from Lake Anosy (Binggeli 2003d). As far as animals go, we might highlight the impact of *Rattus rattus* (black rats), which arrived with early humans and spread in disturbed habitats around the island associated with human settlements, and which have serious consequences in terms of spreading diseases, threatening food stocks, and even eating rice in the rice fields (Lehtonen et al. 2001, Tollenaere et al. 2010). Likewise, the recent spread of *Procambarus* 'Marmorkrebs' (marbled crayfish) in rivers close to Antananarivo is thought to threaten rice production (Jones et al. 2009, Kawai et al. 2009).

ECONOMIC BENEFITS. Villagers take advantage of a diverse number of invasive plants for their livelihoods, making the most of what they find in their landscapes. Lehavana (2012) lists *Opuntia, Grevillea, Psidium cattleianum, Oreochromis niloticus,* and *Rubus alceifolius* as species appreciated as food, wood, or otherwise; one could also add to this list *Pinus* for construction wood, *Ziziphus jujuba* for charcoal and fruits, and so on. The use of invasive *Opuntia* species in the south as cattle fodder and as hedges has been widely documented (Binggeli 2003a, Kaufmann 2004, Kaufmann and Tsirahamba 2006, Middleton 2012). The spread of *Acacia dealbata* (silver wattle or *mimosa*) across the highlands contributes fuelwood, charcoal, minor construction wood, and soil fertility and is broadly appreciated (Kull et al. 2007, Tassin et al. 2012). Even *Eichhornia crassipes*, the water hyacinth, has found some use as pig food and in artisanal basket weaving (Rakotomalala 2014).

It is not just villagers who benefit economically from some invasive species. The trade in charcoal and other wood products from invasive wattles, grevillea, and pines, in different regions of the island, feed important commodity chains into the main cities. On a different note, in Ranomafana National Park, key tourist sites are invaded by the *Psidium cattleianum* and according to park managers these sites help ensure a 100 percent success rate in finding lemurs to show to tourists, ensuring the economic success of the park (Carrière et al. 2008). Of course, this fruit bearing species is also highly appreciated by villagers for diverse uses and marketable products – food, jam, alcohol. Villagers also practice slash-and-burn farming in land rendered more fertile by diverse invaders, including *Psidium* (Carrière et al. 2008).

ECOLOGICAL COSTS. Diverse negative ecological impacts have been noted. As in other contexts, the presence of feral or invasive predatory animals appears to have more stark consequences than that of plants. The introduced fish known locally as *fibata* (snakehead, *Channa maculata*), brought to the island through President Ratsiraka's enthusiasm for aquaculture, is now found in most lakes around the island (Masuda et al. 1984, Sparks and Stiassny 2003). At Lake Alaotra, collection of this fish is one of the reasons villagers burn marshlands that are crucial habitat of the gentle lemur (*Hapalemur alaotrensis*) (Copsey et al. 2009). It has been widely suggested that the fish may be responsible for the local extinction of the fish genus *Paratilapia* and the total loss of the Alaotra grebe (*Tachybaptus rufolavatus*), but causality has not been scientifically proven. A landmark early assessment of Madagascar's freshwater fishes paints a stark picture of the likely impact of diverse introduced fish on native species. It found almost no native fish species in some inland lakes and waterways stocked with introduced fish (Reinthal and Stiassny 1991, see also Lévêque 1997, Sparks and Stiassny 2003 and Irwin et al. 2010). On the mammal front, feral cats have been shown to predate on sifaka (*Propithecus verreauxi*) at Beza Mahafaly Special Reserve (Brockman et al. 2008), while feral dogs have reduced fosa (*Cryptoprocta ferox*) populations in Ankarafantsika National Park (Barcala 2009). While rats are widely known

the world over to have devastating impacts on native fauna, and such impacts are imputed for Madagascar (Hingston et al. 2005), Ganzhorn (2003) demonstrates for one case study in the Menabe that there is no indication of negative interactions between rats and native small mammals. As far as insects, Irwin et al. (2010) remind readers that at Tampolo forest in the east, the presence of white-footed ant (*Technomyrmex albipes*) in disturbed, fragmented forest is associated with reduced native ant populations.

As far as plants, some examples suffice. Thick carpets of *Eichhornia crassipes* are detrimental to a native duck species (*Thalassornis leuconotus*) at Alaotra (Binggeli 2003d). Pines (*Pinus*) spreading into tapia (*Uapaca bojeri*) woodlands or montane park areas like Andringitra or Ibity may have allelopathic effects on the soil (Bosshard and Mermod 1996). The large African vine *Cissus quadrangularis* smothers trees and apparently prevents regeneration in degraded gallery forests of the far south, such as Berenty (Binggeli 2003b). The invasion of logged forests by plants such as *Psidium cattleianum*, *Eucalyptus robusta*, and *Syzygium jambos* is suggested to prevent regeneration of native forest species and result in lower species richness (Brown and Gurevitch 2004).

Species like *Leucaena leucocephala* have been labelled in the literature as "transformer species", because they "change the character, condition, form or nature of ecosystems over a substantial area" (Richardson et al. 2000: 98). This particular species from the Americas is known to form monotypic stands in diverse places where it has been introduced (e.g., Australia, New Caledonia, Fiji). In Madagascar, it has been studied in detail at Orangea forest (near Antsiranana), where it was labelled a conflict of interest due to its transformation of local vegetation communities at the same time as its beneficial uses by local people and livestock (Raharinaivo 2013). At the other end of the island, *Leucaena* is known to have caused 'bald lemur syndrome' in groups of *Lemur catta* that fed on it (Jolly 2009).

ECOLOGICAL BENEFITS. Invasive species may have positive impacts on ecological processes as diverse as soil erosion, habitat provision, or forest regeneration. Foresters have encouraged the invasions of *Pinus*, *Grevillea*, and other species into *lavaka* erosion gullies and other degraded land in order to stabilize the soils (Tassin 1995, Carrière and Randriambanona 2007). *Acacia dealbata* in the highlands, and *Grevillea banksii* in the eastern coastal region, have been considered positively by many policy makers and foresters for 're-greening' and adding tree cover to a landscape perceived to be degraded (Kull et al. 2007). Indeed, both were considered for aerial distribution of seeds by foresters.[4]

Some native species are opportunistic and feed on invasive species or use them as habitat. In some cases, this may positively affect the native species (Tassin and Kull 2015), though further research is warranted. For instance, lantana flowers are a favourite food of an endemic butterfly (*Hypolimnas dexithea*) at Montagne d'Ambre (Binggeli 2003c). Native lemurs, bats, and birds feed on a number of introduced species (Gérard et al. In lit.). As one example, white collared brown lemurs (*Eulemur cinereiceps*) in Manombo forest were shown to rely on introduced plants often considered invasive (*Cecropia peltata*, *Aframomum angustifolium*) as 'fallback' food opportunities in habitat disturbed by a cyclone (Ralainasolo et al. 2008). Finally, afforested zones of *Eucalyptus*, *Pinus*, and *Acacia* – the latter two sometimes invasive – in the eastern highlands play a role in attracting seed dispersers and helping to regenerate native forest vegetation in former pastures (Randriambanona 2008).

LOCAL PERSPECTIVES

What does the Malagasy public think about 'invasive species', and what can their perspective contribute to science and policy? Like anywhere, peoples' views will vary based on the nature of their daily lives, location, and occupations, and their exposure and familiarity with local, foreign, and scientific ideas about the environment and terms such as 'invasives' and 'weeds'. Based on some preliminary fieldwork in a few rural areas[5], we can suggest a number of important observations.

1. Awareness: Farmers, as well as conservation agents, are (unsurprisingly) quite aware of new and/or rapidly-spreading plants or animals in their crop fields or broader environs. When asked, they could quickly point to something new that they had not seen before, or mention a plant or animal that was problematic for their farming activities. We were shown four new plants in cropfields in four different sites; all had only been observed for a season or two in the memory of the farmers who showed them to us. Likewise, people in the eastern lowlands were quite aware of the rapid expansion of *Grevillea*.

2. An engagement with particular plant species, more than with categories like 'invasive' or 'exotic': At a local scale, broad categories like 'invasive species' or 'exotic species' are much less useful in discussions than names or examples of specific plants or animals. Indeed, terms like invasive species do not exist in the Malagasy language. There is a Malagasy word that translates closer to the French *mauvaises herbes* than the English 'weed': *ahidratsy* or literally 'bad grass'. Farmers appear to have a rather specific, narrow use of this word – restricted to plants in cropfields that reduce the harvest, compete with the crop; it does not include fallow plants. This is confirmed and even narrowed further by a dictionary definition as "a grass growing with rice that requires weeding" (Rajemisa-Raolison 2003). Our discussions with farmers went much further when we spoke about the character, advantages, and disadvantages of particular species in specific contexts, rather than when we used abstract generalities.

3. Withholding judgment and searching for utility: The term *ahidratsy*, as mentioned above, contains the judgment *ratsy* (bad) within it. Farmers were generally quite hesitant to label new, unknown plants *ahidratsy*. This is not due to ignorance. Instead, farmers told us "no, this plant is not an *ahidratsy*" for various reasons – for the plant was useful, for it was not a weed of crop fields, or because the farmer did not know yet whether the plant was damaging or useful. For instance, in two villages east of Lake Alaotra, people mentioned the arrival of a new plant that they did not know. They showed the plant to us – it had a spiny thistle-like shape, producing thousands of seeds. It grew prolifically across several fields of market vegetable crops (tomato, cucumber, Chinese cabbage), with both mature plants and numerous seedlings. Despite its obvious weedy aspects, the farmers refused to call it *ahidratsy*, as they did not yet know what it was nor its potential uses. The plant in question in this case was *Argemone mexicana* (Mexican poppy), which is a common alien weed in southwestern Madagascar and was already sold as a medicinal plant in the outdoor market in Antananarivo over twenty years ago (Boiteau and Allorge-Boiteau 1993, Husson et

al. 2010).[6] In general, curious farmers rapidly adopt new plants for their diverse utilities. For instance, *Senna occidentalis* was introduced to the Alaotra area in the 1950s, and soon became part of the local pharmacopeia of medicinal plants.

4. Origin unimportant: Villagers were largely either unaware of or unconcerned with a plant's origins, as is the case in many parts of the world. While experiences might be different in other places, or with well-known species, in our experience on this set of field visits the topic of whether a plant was native or alien never came up as a topic with villagers unless we specifically asked about it. In no case was origin linked to impact or behaviour. Indeed, people generally looked perplexed when we asked whether a species was "*gasy na vahiny?*" (Malagasy or visitors?). When asked this question directly regarding introduced plants like *Lantana* or *Grevillea*, most people responded without hesitation that they were *gasy*.[7] A few conversations were more nuanced, with one farmer suggesting that if a plant had a name in the Malagasy language, it was probably from Madagascar, and if it did not, that it was brought more recently. He compared *Lantana* (*radriaka*) which he presumes (erroneously) was Malagasy with *Albizia* (*albiza*) which he correctly identified as introduced. It should, however, be noted that the Malagasy language does label a number of plant varieties with epithets (like *vazaha*) that may indicate origin, like *angivy* (*Solanum erythracanthum*, a native nightshade family plant) versus *angivimbazaha* (cultivated eggplant), or *dingadingana* (native *Psiadia altissima*) versus *dingadingambazaha* (non-native *Justicia gendarussa*).[8]

LESSONS FOR APPROACHING INVASIVE SPECIES IN MADAGASCAR

Despite being considered in the recent past by many conservation actors and policy makers to not be much of an issue (Carrière et al. 2008), recent reviews cite invasive species as major threats to Madagascar's biodiversity (Irwin et al. 2010, Rakotomanana et al. 2013). The latter article, for instance, mentions the possible arrival in Madagascar of the chytrid fungus *Batrachochytrium dendrobatidis*, which has had terrible impacts on its amphibian hosts in many regions throughout the world. So, given these concerns, what should we do about invasive species in Madagascar? Our review – based on the insights from dividing the issue into several conceptual categories (origins, behaviour, and effects, as well as local perspectives) – suggests a number of lessons that may guide research, policy, and management.

1. 'Invasive' is often an imprecise term used for rhetorical effect: The term is used by different people, following different definitions that group different processes (such as crossing biogeographic boundaries with anthropogenic help, or spreading quickly on its own) and different judgments (about origins, or about impact). The term often sticks to a species, when it is more appropriately applied to particular populations of a species in particular contexts. The term can also distract attention from the human uses of the environment that render certain sites invasible, focusing the blame on species rather than the human context. So care is advised in using the term; we should strive to be more specific in describing the phenomena we observe.

2. To be more specific, we should be clear about origins, behaviour, and effects, and distinguish between rather different categories like plants, predators, and pathogens. We might follow the lead of the local people, whose discussions are very site- and species-specific: Madagascar hosts over a thousand alien species, but only a subset have spread quickly or become problematic. Some populations of particular species, whether alien or native, spread quickly and become dominant when given the opportunity. This behaviour occurs at different spatial and temporal scales. Different species populations have different effects, both positive and negative, and some can be qualified as noxious weeds or pests. Being more specific helps us know what we are talking about. For instance, when Amsellem et al. (2000) state that the non-native bramble *Rubus alceifolius* is not especially invasive on Madagascar, compared to elsewhere, it is unclear whether 'invasive' refers to spreading behaviour or negative impact, or both. Being specific also brings to the forefront what aspects are important for management: is it about border control of new alien pathogen arrivals, is it about managing land better to make it less invasible by a transformer species, or is it about seeking to mitigate negative impacts on crop production of a particular pest?

3. Many plants and animal populations labeled 'invasive' have positive as well as negative aspects: This is shown by local peoples' resourcefulness in making use of *Argemone mexicana*, *Acacia*, *Grevillea*, *Melaleuca*, and *Potamochoerus larvatus*, just to name a few, or by the opportunistic use by some native fauna of *Psidium*, *Eucalyptus, Lantana* and other introduced and sometimes invasive plants as food or habitat.

4. The mix of positive and negative impacts, and the location of invasions in lands and waters of livelihood and cultural importance to local people, means that social justice and economic development should be considered alongside ecological conservation: The process of decision-making and management should be as inclusive as possible. To paraphrase Forsyth and Sikor's (2013: 120) discussion of justice in the management of forests, the management of invasives "is a process that never becomes perfect (…). The process of discussion, where social inclusion itself is critically sought and predefined norms are not imposed, might lead to a more just outcome because it acknowledges that the definition of benefits is influenced by social inclusion and that facts and norms influence each other." Such deliberative management is necessary, for "human desires for preserving certain social values in landscapes in contradiction to actual transformations is often at the heart of definitions of and conflicts over weeds or invasives" (Kull and Rangan In press).

5. Different management strategies and approaches for invasives are applicable to different sites and social contexts: First of all, there is the option, in some cases, of direct interventions on populations of weeds, pests, and other 'invasives' that farmers, environmental managers, or others decide to eradicate (if feasible) or at least to control. This usually requires serious investments. Labour for cutting, catching, or killing is frequently arduous or expensive. Chemical control is possible – see for instance the work of Miandrimanana et al. (2014) on invasive *Melaleuca quinquenervia* (*niaouli* or paperbark) in Analalava – but it can have deleterious toxic effects on ecosystems and people. Biocontrol research to identify appropriate biocontrol agents, to test them for host specificity, and to release them is expensive and prone to unexpected effects, as shown by the spread of crop-thieving *Acridotheres tristis* introduced to

control locusts,[9] or the colonial era debates over the release of scale insects to control *Opuntia* mentioned earlier.

A second set of strategies focuses not on the invaders themselves, but on the environments which they invade. As our earlier discussions suggest, in many cases invasive behaviour is shaped by the environmental context. Human changes to the environment – ploughing, fertilization, irrigation, deforestation, removal of predators, changes to fire regimes – can open opportunities that certain plants and animals exploit. There is evidence from Ranomafana National Park, for instance, that protected areas, by stopping habitat fragmentation and anthropogenic disturbance, reduce the presence and opportunity for spread of common invasive species (Brown et al. 2009). Agronomists have long looked at ways to reduce weed growth that involve not just herbicides, but also different ploughing and fertilizing strategies. So, depending on the context, interventions on invasions may need to focus on land or marine management rather than the invaders themselves.

A third kind of intervention arises from the 'origins' concept. As noted earlier, an important lever for controlling future invasions is blocking entry to the island of those non-native species that society deems (in an informed, deliberative process) might carry risks above a certain threshold. Several other governments take a precautionary approach at their borders, seeking to screen new arrivals of species for potential problems. For instance, Australia has established a strong biosecurity quarantine service at sea- and airports, and uses decision tools that weigh benefits and risks of potential new pests and pathogens based on experience elsewhere (Kumschick and Richardson 2013). One might add that given the importance of propagule pressure in leading to invasions, internal policies might be used to discourage the anthropogenic diffusion of problematic plants and animals already present on the island.

Fourth, another strategy worth exploring in many cases is compromise or even "living with" invasive species (Head et al. In lit.). The financial and human resources to cope with biological invasions that are already widespread are limited. Pragmatic approaches should be locally relevant, socially appropriate, and result from prioritization exercises. In many cases, this might mean doing nothing, or managing particular important sites (for farmers, for local cultural reasons, for biodiversity), rather than waging blanket wars against particular species. In some ways, it is fortunate that Madagascar has come to focus on biological invasions rather late compared to other regions, for it allows researchers and managers to apply a more mature, balanced approach, than the categorical, catastrophist alarm that is sometimes raised. In many cases, plants and animal seen as invasive are – in practical, non-idealistic terms – important opportunities for rural economic, social, and ecological sustainability. They give people subsistence and livelihood alternatives, particularly when access to native forests is restricted by conservation policies (Carrière et al. 2008), and they can serve as important components in resilient smallholder farming landscapes (Kull et al. 2013).

In conclusion, our review has shown the importance of a deliberative approach specific to particular sites, species, and categories of invasion. The capacity for certain populations of plants and animals to spread rapidly, transform landscapes, and become a nuisance to humans or wildlife is certainly worthy of concern and action. However, each case will have its social and ecological particularities, and a blanket approach is not feasible, not realistic, nor likely to be fair to the people living their daily lives in these landscapes. Researchers can contribute carefully-acquired knowledge about different invasions and their contexts; managers and policymakers must use the information available to them, and in inclusive deliberations with local people and other interested groups decided on the most appropriate plans for action. On this note, to return to our opening example of the common Asian toad in Toamasina, we send our best wishes to the teams working with local communities to assess the risks and identify feasible and appropriate management options at this early stage in the invasion.

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NOTES

[1] The cane toad is *Rhinella marina* (previously *Bufo marinus*).

[2] The scale insect was *Dactylopius*, of the same genus as the carmine-producing cochineal.

[3] Newton (1863: 349) saw the bird at Fenerive and Foulepoint in the 19th century.

[4] Gabrielle Rajoelison, ESSA-Forêts, pers. comm., July 10, 2014.

[5] Based on scoping field trip by CK with Herizo Tantely Razafimampanana in July 2014 consisting of discussions and terrain walks with villagers in two sites in the central highlands, two sites near Lake Alaotra, one site near Beforona, and three sites near Vatomandry.

[6] *Argemona mexicana* is probably not all that new to the region; one of us (JT) suspects having seen it in the Alaotra area in the early 1990s.

[7] SC (pers. observ.) had different experiences in earlier interviews about eucalypts, where younger generations considered the plants to be 'gasy' but old people recognized them as introduced.

[8] For a more detailed discussion of plants labeled 'gasy', 'vazaha', and 'manga', see Kull et al. (In press). Several of the numerous plants and seeds available from the Silo National des Graines Forestières (<http://www.sngf-madagascar.mg/> accessed 8 November 2014) have vazaha in their name.

[9] The impacts of *Acridotheres tristis* are not documented in Madagascar, as far as we know, though farmers interviewed stated it was a crop field pest (though not the worst). Elsewhere, the bird is known to compete with other bird species for food and nest sites, and to cause damage to crops, particularly fruits (Global Invasive Species Database, <http://www.issg.org/database/species/impact_info.asp?si=108&fr=1&sts=tss&lang=EN> accessed 20 November 2014).

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

FIGURE S1. Overlapping definitions of 'invasive species' in their broader, often social, context (by C. Kull).

TABLE S1. Summary of native, introduced, and invasive introduced species in Madagascar.

ARTICLE

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Environmental education in its infancy at Lake Alaotra, Madagascar

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ABSTRACT

Madagascar is renowned for its unique biodiversity but also for the continuous degradation of its natural environment and its high poverty rate. In order to achieve sustainable development, environmental education has been assigned a key role. In the lake Alaotra region, Madagascar's most important rice and inland fish production area, primary schools are the sole formal education for the majority of the population. In order to gain an overview on the education of 'tomorrow's' resource users, this study assessed the general state of the school system and of environmental education in particular. The focus was on understanding local definitions of environmental education, its application and local perceptions of environmental problems. Over 50 in-depth interviews were conducted using the Funnel approach with teachers from 18 public primary schools. The interviews were supplemented with focus groups and a participatory problem analysis workshop. Teachers in the Alaotra region provided a different definition of environmental education than the United Nations. Their focus is on social aspects rather than the actual problems of the natural environment, which represents a different point of view than non-governmental organizations (NGOs) from abroad, who are the main promoters of environmental education in the area. This indicates that education for sustainable development might be more suitable in the region than the currently promoted environmental education. When developing educational programs, it is important to include the teachers in the development processes to ensure inclusion of local views and needs. This will increase the probability that such programs are locally meaningful and useful.

RÉSUMÉ

Si Madagascar est réputée pour sa biodiversité unique, elle l'est aussi pour la dégradation de son environnement naturel et son taux de pauvreté élevé. L'éducation à l'environnement est un élément important dans l'accès au développement durable. Dans la région Alaotra qui est le principal producteur de riz et de poissons d'eau douce de Madagascar, l'éducation est dispensée presqu'exclusivement par les écoles primaires pour la majorité de la population limitrophe du lac Alaotra. Pour comprendre globalement l'éducation des futurs utilisateurs des ressources, l'étude a évalué la situation qui prévaut dans le système scolaire en général et celui de l'éducation environnementale en particulier. Les travaux se sont concentrés sur les définitions locales de l'éducation environnementale, sa mise en œuvre et les perceptions locales des problèmes environnementaux. Plus de 50 interviews détaillées ont été réalisées avec des enseignants de 18 écoles primaires sous méthode Funnel. Les interviews ont été complétées par des groupes de discussion et un atelier participatif portant sur l'analyse du problème. Les enseignants de la région de l'Alaotra ont énoncé une définition différente de l'éducation environnementale que celle proposée par les Nations Unies. Leur priorité porte davantage sur les aspects sociaux que sur les problèmes de l'environnement naturel lui-même, divergeant ainsi du point de vue des organisations non gouvernementales (ONG) étrangères, qui sont actuellement les principaux promoteurs de l'éducation environnementale dans la région. Il apparait ainsi que l'éducation portant sur le développement durable pourrait être plus appropriée que l'éducation environnementale. Lors de l'élaboration des programmes éducatifs, il est donc important d'inclure des enseignants pour veiller à ce que les visions et besoins locaux soient considérés, ce qui donnera plus de chances aux dits programmes de prendre du sens et de servir leur dessein.

INTRODUCTION

ENVIRONMENTAL EDUCATION. Environmental education became globally recognized some 40 years ago (Palmer 2003) and today comprises all efforts that help individuals or societies to develop the necessary skills to enable informed decisions and actions to improve the environment. The objectives of environmental education were defined and refined during the international environmental workshop in Belgrade, Yugoslavia (Belgrade Charter 1975, UNESCO 1976) and the first international inter-governmental conference on environmental

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education in Tbilisi, Georgia (Tbilisi Declaration 1977, UNESCO 1978). The objectives of environmental education are to help groups and individuals to develop (i) 'awareness' towards the environment and environmental problems, (ii) 'knowledge' and a basic understanding of the environment, its ecosystem functions and services, and linked problems, (iii) positive 'attitudes' and concern for the environment and the motivation for active participation of individuals and societies in environmental improvement and protection, (iv) 'skills' for identifying and solving environmental problems, and (v) 'participation', i.e., being actively involved in solving environmental problems (UNESCO 1976, UNESCO 1978).

Agenda 21 (the global action plan towards sustainable development adopted at the UN Conference on Environment and Development held in Rio de Janeiro, Brazil, in 1992) points out the crucial role of education for reaching sustainable development, declaring it to be "critical for achieving environmental and ethical awareness, values and attitudes, skills and behavior" (UNCED 1992: 320). People educated in this way will be capable to understand environmental and development issues and to act accordingly, thus allowing public participation in decision-making and ensuring sustainable development in the long-run (ibid). The UNESCO states that "educators are one of the most important levers to realize educational change and to facilitate learning for sustainable development" (UNESCO 2013: 2).

ENVIRONMENTAL EDUCATION AND SUSTAINABLE DEVELOPMENT. The concept of sustainable development was first recognized in the World Conservation Strategy (IUCN 1980), and reached fame with the Brundtland Report "Our common future" seven years later where sustainable development was defined as "meeting the needs of the present without compromising the ability of future generations to meet their needs" (WCED 1987: 43). The Report applied a global view on the links between environmental and socio-economic issues, as well as future well-being for humanity, considering an economic, social and political perspective. It expressed human's dependency on the environment as well as local, regional, national and global linkage and interdependency of ecology and economy (WCED 1987: 5). Education has been assigned a key role in achieving the global aim of sustainable development (IUCN 1980). The fourth international conference on environmental education, Tbilisiplus30 dealt with the arising question how to bridge the gap between environmental education and education for sustainable development and set a global agenda for the 'UN Decade of Education for Sustainable Development' for the period 2005 to 2014 (Combes 2005, Liimatainen 2013) in order to establish an essential contribution to human development.

While environmental education focusses on the amelioration of the environment with no close link to development, education for sustainable development is concerned about the human beings, linking environmental and developmental issues (Pavlova 2011). According to Agenda 21, "Education, including formal education, public awareness and training should be recognized as a process by which human beings and societies can reach their fullest potential. Education is critical for promoting sustainable development and improving the capacity of the people to address environment and development issues" (UNCED 1992: 320). There is, however, a discrepancy in the interpretation of the two paradigms of environmental education and education for sustainable development (McKeown and Hopkins 2003); some countries use these concepts interchangeably, while others see the first as part of the second, or vice versa (Pavlova 2011).

The UNESCO proposal for the Global Action Programme (follow-up for the 'UN Decade of Education for Sustainable Development' after 2014) applies the term 'education for sustainable development' for all activities that will promote such evolution, "(…) irrespective of whether they themselves use the term ESD or – depending on their history, cultural context or specific priority areas – environmental education, sustainability education, global education, development education, or other" (UNESCO 2013: 2).

THE MADAGASCAR CONTEXT. A growing challenge in many developing countries is the reconciliation of a continuously increasing demand for agricultural products while conserving biodiversity, maintaining ecological functions and providing critical ecosystem services to sustain local livelihoods (Harvey et al. 2008, Brussaard et al. 2010). Madagascar, despite having received considerable international conservation and development attention in the past decades (Horning 2008), is still one of the poorest countries (UNDP 2013) while facing continuous degradation of its natural environment and an ongoing loss of its unique biodiversity.

The Human Development Index (HDI), calculated by the United Nations Development Programme (UNDP), is an alternative measure to the better known Gross Domestic Product (GDP) to assess a country's development state, which is measured by achievements in the dimensions of life expectancy, education, and available resources for living. Education is especially important as a stepping stone towards improved health; according to the UNDP, "a mother's education is more important to her child's survival than is household income or wealth" (UNDP 2013: 89). Madagascar with a HDI of 0.483 ranks 151 out of 187, figuring in the 'low human development group' together with many other African countries (UNDP 2013). It has globally one of the highest population growths rates (3 %) and one of the lowest median ages of 18.2. This is paralleled by an extremely high primary school dropout rate of 65.4 % (in comparison, total sub-Saharan Africa is at 37.8 %, countries from the 'very high human development' group oscillate around 3.8 %) leaving the majority of Madagascar's population without any secondary or tertiary education. Mean years of schooling in Madagascar are at 5.2, opposed to 11.5 in countries with high HDI, but still better than in Sub-Saharan Africa with 4.7 (ibid).

Madagascar is at great risk of increasing vulnerability and degradation due to overexploitation and climate change (Hannah et al. 2008, Shepherd et al. 2013); the 2030s-projections of vulnerability to climatic extremes and disasters even put Madagascar into the globally highest risk group due to its increasing poverty (Shepherd et al. 2013). Education is crucial to acquire further competences needed to deal with threats in the future (Muttarak and Lutz 2014). This begs the question whether the current school system is capable to shoulder this responsibility?

EDUCATION IN MADAGASCAR. Madagascar had one of the first Sub-Saharan African school systems during the Merina Kings and Queens period with formal schools mainly in the central highlands around Antananarivo, targeting the noble classes (*andraina*) only (Antal and Ndrianjafy 2013). With the French colonialists the formal school system started to reach

	Acronym	Meaning
Organisation school system	CISCO	*Circonscription Scolaire*; regional school authorities, responsible for amelioration of results and delivery of the school curriculum
	DREN	*Direction Régionale de l'Education Nationale*; Regional authority for education that governs several CISCOs, i.e. representing the link between ministry and CISCOs
	ENF	*Enseignants FRAM*; community recruited teachers that are paid by the FRAM. *ENF subventionnées* obtain additional salary by the ministry in contrast to *ENF non-subventionnées*
	EP	*Ecole privée*; Primary private schools
	EPP	*Ecole primaire publique*; Primary public schools
	FRAM	In Malagasy *Fikambanan'ny Ray Amandrenin'ny Mpantra*. Association of pupils' parents; the FRAM pay e.g. (part of) the salaries of the ENF, but also necessary school material and reparations
	T1 to T7	First to seventh grade (in Malagasy T= *taona*; year)
	ZAP	*Zone administrative et pédagogique*; local administrative districts. The Chefs ZAP are the links between CISCO and schools and in charge of teacher trainings
School subjects and methodology	SVT	*Science de la Vie et de la Terre;* school subject 'Earth and life science'
	FFMOM	In Malagasy *Fanabeazana sy Famolavolana Maha-Olomendrika*; *Education civique*; School subject 'Social studies'
	APS	*Approche par la situation*; teaching approach
	APC	*Approche par la compétence* ; teaching approach
	MITAFA	In Malagasy *Miaramamolavola ny Tanana ho Fahalalana*. A hands-on teaching approach to obtain knowledge; introduced by the NGO DEFI to transmit scientific topics via experiments
International context	GDP	Gross Domestic Product
	HDI	Human Development Index
	UN	United Nations
	UNCED	United Nations Conference on Environment and Development (Rio de Janeiro, 1992)
	UNDP	United Nations Development Programme
	UNEP	United Nations Environment Programme
	UNESCO	United Nations Educational, Scientific and Cultural Organization
	WCED	World Commission on Environment and Development
Other	ARDI	Participative problem analysis approach. In a workshop, all actors, resources, dynamics, and interactions linked with a defined problem are identified
	ENS	*Ecole Normale Supérieure*. Teacher training school in Antananarivo
	INSTAT	*Institut National de la Statistique*; governmental entity for production and collection of official information and statistics on Madagascar
	MWC	NGO 'Madagascar Wildlife Conservation'
	NGO	Non-governmental organization

more remote areas in Madagascar. The education system in Madagascar was modeled based on the French system: *maternelle*, *collège*, and *lycée* with the *baccalauréat* exam at the end, and option to continue at university level (Sharp 2002). The Malagasy school system continued to mimic the French one also after Madagascar's independence (1960) and lasted until 1972, marking the end of the First Republic under President Philibert Tsiranana (Randrianja and Ellis 2009).

The period of 'rebelling' began in 1972 when a nationalist movement demanded the end of 'neo-colonialism', leading to the fall of the Tsiranana regime and the creation of a transitional government responsible for the introduction of the *malgachisation* of teaching (ibid). A socialist revolution led to the Second Republic under President Didier Ratsiraka, who adopted and furthered the *malgachisation* beyond the education system (Johnson 2006). Ratsiraka introduced the official Malagasy language, which was based on the Merina dialect from the central highlands. As a consequence, many non-Merina teachers speaking different dialects, and who had received all of their previous education and training in French, struggled to suddenly use exclusively the new official language (Sharp 2002). The promotion and propagation of new schools by the socialist regime led to a lack of well trained teachers, but also a lack of financial resources impeded the new government to target the country's 11,000 *fokontany*, especially in more rural areas. Parents often had to collect money to contribute or pay the salaries of the teachers or to provide teaching equipment such as textbooks or furniture (Johnson 2006). The lack of Malagasy teaching textbooks forced many teachers to translate the French textbooks into Malagasy. Consequently, little Malagasy culture was actually taught in schools (Sharp 2002).

With the installment of the Third Republic in 1992 under President Albert Zafy, many policies were reversed again, and French was reinstalled to assure quality in teaching and education. According to Johnson (2006), however, the problem was now a lack of teachers being able to speak and teach in French, since many teachers serving under the First Republic had in the meantime been retired. Another recurring problem was the lack of French written textbooks. The Forth Republic of President Marc Ravalomanana was a period of 'policy borrowing' (cf. Johnson 2006) to improve the school system by looking at other countries' systems. English as third official language was also introduced as third school language in primary schools. Ravalomanana invested in the building of thousands of new primary schools, and delivering also free basic material to students. During the years 1997–2007, the number of school inscriptions at primary level went up from 82 % to 100 %; while during 2000–2006, the number of repeaters went down from 30 % to 18 % (MENRS 2008). According to Randrianja (2012), these improvements were due to efforts of parents associations or FRAM supporting teachers' salaries, therefore contributing significantly to the increase of number of teachers (especially ENFs). The political crisis (2009–2013) resulted in many parents struggling to survive and not being able to support the ENFs (ibid). To date, Madagascar, as many developing countries, has a "dual-track system, with the well-off attending good schools and universities, mostly privately funded, and the poor attending inadequate, mostly publicly funded facilities" (UNDP 2013: 31, cf. Glick and Sahn 2006).

THE ALAOTRA CONTEXT. The primary economic driver in the Alaotra region is based on fisheries and rice production (Andrianandrasana et al. 2005, Monographie Régionale 2012). The human population of Amparafaravola and Ambatondrazaka, the two lake districts of the Alaotra-Mangoro region, has increased from some 110,000 people in the 1960s to over 550,000 in 2011 (INSTAT 2012). A majority of people are rice cultivators, fishermen, vegetable farmers or cattle breeders, or occupy different professions at the same time to support their livelihoods (Rakotoarisoa et al. In press).

High population growth and changes in the ecological state of Lake Alaotra are linked with declining ecosystem services (Pidgeon 1996, Lammers et al. In press). The remaining wetland system is exposed to increasing pressures, and overexploitation causes decreasing productivity (e.g., Raharijaona and Randrianarison 1999) potentially leading to a lose-lose scenario, i.e., a downward spiral of poverty and environmental degradation as described by Sunderlin et al. (2005). To counteract this resource dependency and depletion, non-governmental organizations (NGOs) such as Durrell Wildlife Conservation Trust (Durrell) have been working in the region for more than 20 years. A case study done by Durrell has shown a positive correlation between education and environmental awareness (Andrianandrasana et al. 2005). The Madagascar Wildlife Conservation (MWC) found increased knowledge for environmental issues in school children after participation in the environmental education program (Dolins et al. 2010, Rendigs et al. In press). MWC has been running this program since 2006 and developed culturally and regionally adapted posters and comic books for the region to be used in public primary schools by trained teachers (Maminirina et al. 2006).

The goal of this study is to assess the state of environmental education in the Alaotra primary public schools. It is assumed that significant numbers of future resource users can be reached if environmental education is implemented on primary school level. Environmental education can strengthen conservation efforts such as maintaining ecosystem functions and biodiversity by contributing to improved awareness of and appreciation for the natural environment. Assessing the current situation is the first step in developing suitable and regionally adapted environmental education programs. Such education is hypothesized to advance sustainable development. This paper has two main objectives: (i) to understand the perceptions of 'environment' and 'environmental education' at primary schools at the teacher level, and (ii) to describe the school structure in terms of readiness for environmental education.

METHODOLOGY

A total of 18 primary schools around Lake Alaotra were selected based on the following criteria: (i) Public primary school; (ii) adjacency to the lake and remaining marshes; and (iii) accessibility, i.e., vicinity to Routes Nationales 3 and 44 (east and west coast of the lake, respectively).

Structured one-on-one interviews with 54 teachers (including 18 school directors) were conducted. Half of the interviewees were selected based on participant lists of former MWC trainings and the other half were randomly sampled teachers without such training. A standardized interview guide according to the Funnel approach (cf. Wittkowski 1994) has been developed in order to avoid a social desirability bias (Paulhus 1991). Interviewers using the Funnel approach start with broader

subjects and gradually narrow down their topics of interest, thereby masking the motivations of the interviewers from the interviewees. The Funnel approach is intended to reduce the tendency of interviewees to answer questions in a way they believe the researcher welcomes, instead of offering their own opinions (ibid). All interviews were audiotaped, transcribed and translated from Malagasy into French. Average interviews were 60 to 90 minutes. Prior informed consent was obtained regarding audiotaping ensuring the teachers' anonymity. It was emphasized that there were no right or wrong answers but a range of different personal opinions. A pilot interview guide was tested with the interviewer, a Malagasy anthropologist, to ensure methodological adequacy and cultural sensitivity, profiting from his experience during former surveys in the region. The interview guide addressed four major topics with multiple sub-questions (cf. Supplementary Material for details): (i) general situation in the village, e.g., social environment; (ii) school environment; (iii) natural environment; (iv) teacher trainings. Major topics included structural conditions of the schools such as availability of material and trainings, environmental situation and problems in the region, as well as environmental education and possibilities of its implementation. After each interview, participants completed a short questionnaire, indicating biographic information and details on their personal education and career.

To allow for triangulation of results, the structured interviews were complemented by further applying a participatory problem analysis workshop, ARDI (Actors, Resources, Dynamics, Interactions; Etienne et al. 2011), focus groups, participant observations and archival research. ARDI is a methodology deployed to collectively analyze a problem. During this two-day workshop, 12 teachers (randomly selected from the 54 interviewees) addressed the problem that there is not enough material for (environmental) education, and determined involved actors, existing and needed resources, dynamics in the system, as well as interactions between its components. Additionally, 6 focus groups totaling 50 participants were conducted. The majority of the teachers were the same as for the interviews (with few replacements). These meetings followed a similar structure as the interviews, but permitted further discussion in greater detail of teaching approaches and other issues. The interviews had revealed some gaps that could be filled with the results from the workshop and meetings. Additional data to complement and verify the interviews was obtained from the group approaches.

Data analysis was supported by the commercially available software program MaxQDA 11 which uses data management techniques such as multiple levels of coding, memo creation and code segment search. Coding is the method by which text is classified, analyzed, and grouped into categories. These were developed, tested and adapted while considering objective, research questions, methodological approaches and resources.

RESULTS

PRIMARY SCHOOL SYSTEM. The two Alaotra CISCOs (*Circonscription Scolaires*) with 43 *Chef* ZAP (*Zone Administrative et Pédagogique*, the administrative districts) currently oversee a total of 702 primary schools; 540 EPPs (*Ecole Primaire Publique*, public schools) and 162 EPs (*Ecole Privée*, private schools). Over 3,300 teachers are responsible for the education of nearly 116,000 pupils between 7 and 15 years old (Maminirina et al. 2006, CISCO 2013). The CISCO Ambatondrazaka teaches students from first to fifth grade while pupils under the authority of CISCO Amparafaravola are supposed to attend primary school until seventh grade (T7). However, T6 (6th grade) and T7 are realized in 61 out of 343 schools only (57 public and 4 private schools) resulting in 17.8 % of the schools implementing this new model of having seven grades in primary school since 2009.

There are three employment types at EPPs: i) *Fonctionnaires*: 930 (37 %) of the present teachers were recruited and are paid directly by the Ministry of National Education; ii) ENFs: 969 (38 %) are community recruited teachers; the *ENF subventionnés* (*ENseignant* FRAM) are paid half by the Ministry of National Education, and by the pupils' parents, respectively; iii) *ENF non-subventionnés*: 643 (25 %) have to be financed by the parents alone.

The 18 sampled schools have an average class size of 49 pupils with a minimum of 18 and a maximum of 92 children per class. School sizes ranged from 5 to 23 classes with 4 to 24 teachers, respectively. Of the 54 interviewees, 74 % were women and 26 % men, reflecting the fact that the majority of the Alaotra EPPs' teachers are women. The retirement age for teachers is at 60 years. The sample size shows that more than half of the teachers are close to retirement (53 %). Almost all teachers have attended secondary school, but only 9 % hold a university degree. Out of the 54 teachers, 65 % are *Fonctionnaires*, 17 % are *ENF subventionnés*, and 18 % are *ENF non-subventionnés*.

The CISCO's responsibility is to implement the school program that the Ministry of National Education delivers via the DREN (*Direction Régionale de l'Éducation Nationale*, regional authority for education). The main objective is a continual amelioration of results, i.e., the increase of successful exams passed by the school children. The *Chefs* ZAP assist the CISCO in the delivery of the school curriculum's content by organizing training sessions to transmit instructions and methodological modifications to the directors and teachers of the EPPs.

According to the teachers, teaching subjects are received in irregular intervals (e.g., the CISCO organized trainings every trimester or every three months). Each month there is a *Journée Pédagogique* (one day teacher training) and once a week a *Conseil de Maîtres* (teacher's meeting) during which the teachers have the opportunity to exchange with their school directors and amongst peers. The *Chef* ZAP as instructor can be supported by the CISCO's *Equipe Pédagogique* as there are the *Adjoint Pédagogique*, the *Conseillers Pédagogiques* and the *Chef* CISCO. The CISCO is also responsible for the follow-up and monitoring of the teachers. These *suivis* are mainly conducted by the *Chefs* ZAP and serve as control measures to ensure the curriculum-relevant topics have been transmitted properly during the CISCO trainings, but also to assess the teachers' ability to implement the provided subject contents.

SCHOOL CURRICULUM AND TEACHING METHODS. One school year in Madagascar lasts nine months, i.e., from October to July. Generally, there is one teacher for each class, teaching all school subjects in the respective level (T1–T5/T7). A lesson takes 30 minutes while the teaching approach consists of consecutive stages which must be completed in order. The revision of the previous lesson is followed by an introduction and *préacquis*, i.e., children will recall what they know already about a certain topic. The next steps are giving the title of the

lesson, teacher presentation of the new lesson, application and group work, and finally ending with an evaluation (report and identification of results as well as rectification).

To execute their lessons, several approaches are available as teachers stated in the ARDI workshop: banking education (sensu Freire 1970, Dewey 2004) where the teacher presents the content to the pupils without discussion or any other interaction; the active and participatory method that are the most efficient ones for teaching, allowing pupils for example to manipulate material during experiments; different strategies such as group work and individual work, encouraging the pupils to play games or using little songs and rhymes to transmit the lesson's content. These methods and strategies are supplemented by approaches (*démarches*) and procedures (*procédés*) from the Ministry of National Education and NGOs. According to the teachers interviewed, the teaching methodologies are changing frequently with the mandatory application of new approaches promoted by the CISCO: APC (*Approche Par la Compétence*), APS (*Approche Par la Situation*), MITAFA (*MIara-mamolavola ny TAnana ho FAhalalàna*, doing experiments with the pupils to understand science; introduced by DEFI, a French NGO). There is a trend to move away from the banking education towards more group and participatory work which is for example encouraged in the APC context. In order to comply with the new directives despite a shortage of material, the teachers oftentimes are forced to develop teaching material on their own. However, since teachers are required to follow the school program, there is often insufficient time available for implementation of these non-traditional methods (e.g., going to the market to introduce mathematical problems in an interesting way).

The main school subjects are mathematics, Malagasy, earth and life science (SVT: *Science de la Vie et de la Terre*), geography, French, social studies (TSM which includes FFMOM/ *éducation civique* and history); complemented by music, art, sports, recitation (i.e., repeating something aloud from memory, e.g., recitation of traditional poems) and reading. The teacher's ranking of these school subjects revealed no common agreement on their practical importance for students later in life. There is, however, a trend showing reading to be the most important skill for adult life, followed by Malagasy, writing and mathematics; the non-school subject household is ranked on second place while environmental education figures comparatively low (Figure 1).

TEACHER'S UNDERSTANDING OF ENVIRONMENTAL EDUCATION. Teachers' understanding of education in general is described mainly as "transmission of knowledge". Several teachers added that education is "learning on the intellectual, physical, and spiritual level" while others described it as learning how to act as a "good citizen", i.e. showing a "good behavior in society". To better understand what exactly environmental education means to the local teachers, we asked this question in the face-to-face interviews, as well as in the ARDI workshop and focus groups. During these group meetings, the following definition of environmental education has been compiled: it is the "transmission of knowledge about the environment", thus "learning about everything that belongs to the environment, about existing environmental problems and their possible solutions", and about the "protection of the environment". The teachers stated that it is important to know who the actors are (who have destructive impact on the environment) to be able to "become a responsible citizen". While teaching environmental education, knowledge on "everything that surrounds us", "the whole that is visible and invisible" is been transmitted. According to them, both, natural environment (e.g., water, forest, including humans) and anthropogenic environment (e.g., houses, roads) are addressed.

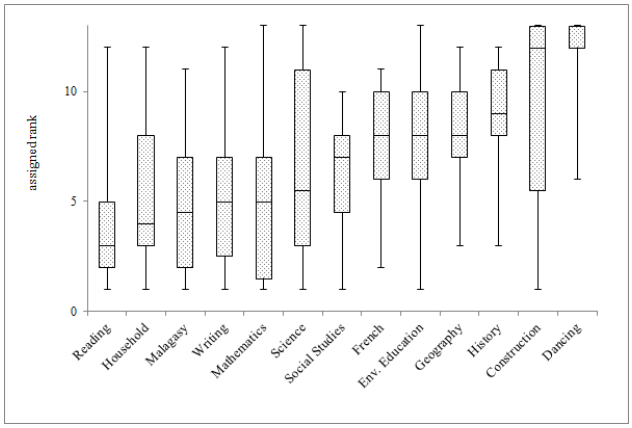

FIGURE 1. Ranking school subjects. Teachers (n=51) ranked 13 cards with school subjects (e.g., Malagasy, geography, history) and non-school subjects (e.g., housekeeping, dancing, environmental education) according to importance for after school life. The box-whisker plots show median, upper and lower quartiles, and minimum and maximum rank of the respective school subjects.

During the one-on-one interviews, simpler definitions of environmental education were listed compared to the group meetings, mainly encompassing what the environment entails and defining environmental education as "transmission of knowledge about these components". Some teachers however also included the conservation aspect: environmental education is "teaching the pupils about the components of the environment and its importance. How can it be conserved? Who is responsible for its destruction? What are the consequences of this destruction?" Another interviewee stated that "environmental education is teaching people what the environment constitutes, its state or condition and finally its conservation".

Teachers state that environmental education is already taught in the current school system even if no specific school subject exists for this. In their opinion, best suitable for the integration of the environmental topics are the school subjects SVT (*Science de la Vie et de la Terre*), FFMOM and geography, but also Malagasy, French, history and even mathematics offer such possibility to some degree.

Building on this background, teachers' opinions on the importance of environmental education compared to school and other non-school subjects varied: though environmental education ranked amongst the least important topics on average (Figure 1), personal opinions were quite diverse. Sixteen percent declared environmental education to be the most important topic, 12 % ranked it on 2nd, 18 % on 3rd and 4 % on 4th and 12 % on 5th rank. The remaining 40 % were distributed on ranks 6 to 11. None of the interviewees ranked it the least important topic for a primary school. In terms of a possible implementation of environmental education, 100 % of the interviewees said that it already is included in the current curriculum, i.e., environmental education appears in many of the topics they are teaching while several book chapters are dealing with the environment. Geography deals with environmental destruction by addressing bush fires and *tavy* (slash and burn agriculture). FFMOM (*Fanabeazana sy Famolavolana Maha-Olomendrika*, i.e., education

with the aim to make the children become an adult person with good manners) also deals with 'the environment' where they introduce environmental education by addressing "all questions concerning the health as for example personal hygiene". When they present possible consequences of using river water, "the environment is already introduced". This example suggests that some teachers believe environmental education is sufficiently taught as soon as the natural or social environment is barely mentioned. Teachers state that other book chapters are explaining 'What is the environment?' or treat the topic 'How to avoid erosion' or 'The protection of the environment', herein focusing on the protection of plants and animals.

The teachers are aware of many kinds of environmental problems in and around their villages. These can be grouped into the three categories 'ecosystem', 'humans', and 'agriculture' (Figure 2). The ecosystem perspective entails destructive human practices and their consequences on the natural environment. The social or human perspective mainly focusses on problems in the village that are related to the low development state, and the agricultural perspective comprises causes of management strategies and climate conditions that have negative impacts on the agricultural output. When describing problems of the natural environment, the teachers oftentimes just briefly mention the environmental issue and then focus on the social impact resulting from it.

When answering the question about regional environmental problems, one third of the interviewees mentioned poverty as a cause for environmental destruction and one fifth tried to explain people's behavior with their mentality or mindset, in particular referring to people's laziness and jealousy: "They know that they shouldn't burn the marshland, but when they see the advantages and benefits of the persons who protect the environment here, they ask themselves why this benefit is not shared but reserved to and kept by one person. So they quarrel and in periods like now [political instable times with no working executive powers / dry season] they continue to burn the marshland". Speaking about mentality, one third of respondents complained that people do not plant trees or do reforestation but also address the problem that "someone burns them [the planted trees] all the time". Teachers declared fire to be the most

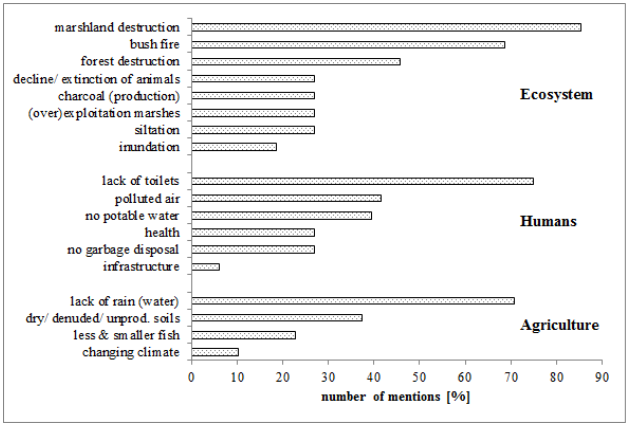

FIGURE 2. Listing regional environmental problems. The teachers specified environmental problems as perceived by them ("Please describe the environmental situation in your community. Are there environmental problems? Which environmental problems do exist?"). The various answers were grouped into the three main categories 'ecosystem', 'humans', and 'agriculture' (problems that affect directly the agricultural production) with the above listed sub-categories. X-axis is the percentage of interviewees (n=48) who mentioned the respective issue listed on y-axis.

threatening problem for an intact environment when showing them ten different photographs with potential environmental problems being present at the lake to date. These photos were chosen according to what had been encountered during the first few weeks on the ground, either by sight or by reports from residents. Almost all interviewees also identified charcoal and erosion to be important environmental pressures (98 and 96 %, respectively), as well as crayfish (92 %). Inundation was judged a potential environmental problem by 77 % of the interviewees, while the invasive fish species snakehead and pesticides were identified by 58 % and 40 %, respectively. Only 25 % declared (marsh-penetrating) zebu to be potentially problematic; 6% listed the invasive plant water hyacinth; rice fields were not listed by any of the teachers (cf. Supplementary Material).

DISCUSSION

LANGUAGE BARRIER. Since many of the Alaotra teachers are not confident with French or speak only little to conduct extensive discussions, all data sampling had to be done in Malagasy. Interestingly, many of these teachers are from the generation of the *malgachisation* and hence did not have the opportunity to learn French. To reduce the risk of missing out on details, i.e., getting lost in translation, different approaches for data sampling were used allowing for triangulation of the results. Additionally, random translations have been cross-checked by the interviewer to ensure quality. Though even with a seemingly small data set (n = 54 out of over 3,300 teachers of public primary schools) we can be confident that the data set is representative, since there were many agreements in terms of responses.

Another language barrier is present in the school system itself. Today, Malagasy primary school classes are bilingual (Malagasy and French). In the first two grades, pupils are taught in Malagasy, the third grade allows theoretically a bilingual transition to 4th and 5th grade where lessons are or at least should, according to the curriculum, be held in French. The question remains, however, to what extent this is or can be realized by the teachers that were educated during the *malgachisation*. Various publications declare the teaching language a key factor for learning (Brock-Utne 2000, Heugh 2000, Benson 2004, Abadzi 2006) and state the importance to teach in the mother tongue. Language as "basic tool for thought, communication, reasoning, and making sense of a rapidly changing world" (Arnold 2004: 3) can even serve for predicting later abilities and school success (Hart and Riseley 1995, Shonkoff and Phillips 2000). In Madagascar, however, exams are held in French from the third grade on which poses a great language barrier to learning and succeeding at school.

LACK OF TRAINED TEACHERS. In the Alaotra region, the primary public schools are facing an uncertain near future due to an increasing lack of professionally trained teachers. A significant body of aging teaching staff is currently close to retirement and teachers are complaining that since 2009 there is no more recruitment of teachers paid by the state (*fonctionnaires*) and thus more ENFs (community-recruited teachers) are hired for less payment. *Fonctionnaires* normally obtain trainings for two years at the École Normale before they are recruited by the Ministry of National Education, whereas the ENFs are selected via application by the CISCO without necessarily having such a considerable education. This could potentially contribute to a deterioration of teachers' educational levels in the region.

Our data sample includes 65 % *fonctionnaires* opposed to 37% in reality. This might result in a slightly different picture regarding teacher's educational levels as well as knowledge and understanding on certain topics. If few well-trained teachers are recruited, this inevitably will leave a void and the overall educational quality level in the first grades will decrease. It is well-known, however that quality teaching is especially crucial in the first grades (Bruns et al. 2003, Abadzi 2006) and that attitude and behavior are mainly developed based on experiences in childhood (e.g., Kidd and Kidd 1989, McDuff and Jacobson 2000, Jacobsen et al. 2006). Sobel (1997) admonishes not to impose ecological problems on children before a certain age to avoid the feelings of fear and disempowerment ('ecophobia'). He suggests age-appropriate environmental education contents for developing the necessary emotional connectedness that will later allow them to deal with the complex ecological issues. Such age-appropriate education, however, requires accordingly trained teachers.

Ongoing political changes and irregular trainings pose on the one hand insecurity and require (methodological) adaptation by the teachers, but also give them the impression that their "expertise is questioned". On the other hand, the principle *formation de formateurs* (cascade training: the *Chefs* ZAP will train directors and teachers on the ground after having received trainings themselves) can offer an effective approach for introducing new methods and the changing requests by the Ministry of National Education keep the educators flexible and open for new teaching approaches. Since 2012 (start of the AMBio research project, Alaotra Marshland Biodiversity), the *Chef* CISCO in Amparafaravola and lately the *Chef* DREN in Ambatondrazaka have been replaced, and further changes are likely to follow. Such instability might be one reason amongst others why plans by the government to restructure and improve the school system, and even to include Malagasy biodiversity into teaching, have been on hold (Dolins et al. 2010). Even if the Malagasy curriculum addresses some environmental topics (cf. Ormsby 2008) there is a lack of site-specific content.

In the past decades, NGOs have been filling these gaps by providing educational material and proposing new teaching approaches (e.g., Waeber 2006, Maminirina et al. 2006, Dolins et al. 2010). However, the provision of material alone might not be sufficient when teachers do not know how to use the material (cf. Dolins et al. 2010) or if they lack understanding of the topic or the motivation to teach it. Developing locally adapted tools and training teachers in how to use them might increase the chance of meaningful use of such educational material in the classroom. The integration of new material should be endorsed by the CISCOs, an approach generally taken by promoters of environmental education in Madagascar (e.g., Masoala curriculum development, Ormsby 2008; MFG's Saturday School at Park Ivoloina, Nirina L. Rakotomalala, pers. comm.; MWC's educational posters and comic books). Teachers in the Alaotra region state that they are regularly using the material provided by MWC. Research by this NGO and ENS (École Normale Supérieure) has shown that the material can be integrated in school subjects such as mathematics, Malagasy, French, geography and SVT (Rafidimanana Rajosera 2013).

A MATTER OF PERSPECTIVE. Many of the NGOs acting in Madagascar are from foreign, mostly western countries and their values and perspectives may differ from those of the Malagasy communities. Concerns about biodiversity loss and threatened lemur species are motivating various NGOs to be active and to bring in environmental education to promote conservation. This situation can possibly cause a 'clash of values'. On the one side are the NGOs with an implicit view on education and the emphasis on environmental education, on the other side the regional traditional value systems with locally meaningful and long-time corroborated perspectives.

A value, as defined by Tilbury (1995: 201) is "a certain belief, attitude or conviction that is consistently reflected in one's behavior. Values determine decisions and actions and are thus of great consequence to environmental education". Breidlid (2009) addresses the drawback of such western-based educational systems in Africa. He criticizes the exclusion of alternative, i.e., African knowledge and value systems from the curricula of the post-colonialized countries. He further states that ignoring traditional values and leaving out the spiritual sphere (traditional beliefs, ancestors) could cause a collapse of the social and moral world and existing solidarity amongst the population might get lost.

Interestingly, in the Alaotra region none of the interviewed teachers did refer, for example, to ancestors as part of the environment despite their important role in tradition and beliefs of the Malagasy population (cf. Jarosz 1994, Keller 2009, Evers and Seagle 2012). A plausible reason for this could be that the current school curriculum is still based on the colonial French school system with many subjects addressing little or no Malagasy context. This assumption is illustrated by the following example. Many teachers mentioned 'polluted air' as environmental problem. French textbooks that are still in use (pers. observ.) are dealing for example with the negative impacts of factories on air quality and consequences for human health. There is no such air pollution in the Alaotra region, but teachers adopt this textbook content on their regional reality: "the environment is also affected because there are no toilets; people defecate everywhere and the air is thus polluted". Polluted air is also oftentimes mentioned in the context of waste dispersal and the lack of garbage disposals.

When the teachers ranked the different 'environmental problems' during the interviews, a congruency of western and regional perceptions appeared, for example regarding fire and charcoal of being main threats in the region. On the other hand, there was often hesitation or confusion whether, for example, the invasive fish species *Channa maculata* is representing an environmental problem (as assumed by a western perspective because it feeds on endemic fish and bird species (Andrianandrasana et al. 2005) or not. This species was chosen as representative for introduced fish species at Lake Alaotra (cf. Pidgeon 1996) that are still common today and consumed regularly. Many teachers mentioned that the *fibata* (vernacular name for *C. maculata*) eats little fish or even stated that it is the enemy of the fish stock in general. But in an environment where malnutrition and lack of protein are wide-spread, some teachers still decided not to put *C. maculata* as environmental problem despite knowing its ecological impacts. This fish thus represents a good example for a trade-off situation between negative environmental impacts versus an improved social situation. The question arises how committed and supportive the teachers can or will practice environmental education if their own 'Lebenswelt' (this translates as 'human-life world',

cf. De Laguna 1960) is not reflected in the teaching material and content? Local realities need to be taken into account to increase probability of acceptance and success of environmental education programs.

Following the UN, teachers are seen as crucial in delivering the sustainability message. At first glance, the teachers' understanding on environmental education seems to be congruent with the international definitions (cf. UNESCO 1976). The teachers define it as the "transmission of all knowledge that is related to the environment (…)" with examples for environment such as forests, the air, stones, roads, and houses. In contrast, the UN concept of environmental education incorporates much more than the local perspective which represents only the first step, the knowledge transfer, of the international definition. Though knowledge is crucial in achieving higher cognitive levels such as understanding, awareness and sensitivity, attitudes and motivation, and skills for participation and action, pure knowledge transfer is clearly not sufficient as teaching objective.

According to the teachers, environmental education already appears in many of the topics they are currently teaching, and several text book chapters are dealing with the environment. However, as some of the following examples show there is a disparity of what the authors understand of environmental education and what the teachers think in this regard. For example, one teacher stated that she included environmental education by giving an arithmetic problem where the children had to calculate the benefit of 20 planted shoots of manioc. Another teacher claimed teaching about health centers to be environmental education, while another stated that discussing the benefits of trees on the hill slopes around Lake Alaotra constitutes environmental education.

During the interviews, when the Alaotra teachers listed environmental problems, the focus revolved mainly around social and health related topics ('humans'). The teachers revealed detailed descriptions and understanding of problems when they talked about social and economic misfits using oftentimes compelling examples. Fewer details were touched on when talking about the natural environment, by barely naming a problem or briefly listing a sequence of several ecosystem-related issues, to end in many cases again with a social-centric environmental problem: "the bush fire causes soil loss and hence the canals here get clogged by the accumulation of mud which are brought by the waters and the streets get flooded", or, "even the well (…) is not very sanitary because it is not covered and when the rain is arriving, the drain water pours into the well, together with the waste from the surroundings". This emphasis on social impacts, even when ostensibly speaking about natural environments, matters locally and needs to be addressed when drafting environmental education programs. During some of the interviews, the impression occurred that the teachers were citing facts without deeper understanding of interrelationships or reasons. Many of the Alaotra teachers are from the generation of the *malgachisation* and have been indoctrinated with recitation teaching by the socialist regime. This causes unpredictable consequences for the next generations as these educators did not learn how to think critically but to learn by heart and to repeat slogans only.

As long as the Alaotra population suffers from deficient hygiene and health issues there will be little sympathy for ecosystem problems, and relationships between deteriorating ecosystem services and health or development might remain misunderstood. A central question remains how the different value systems of external western providers of environmental education (such as NGOs, cf. Rendigs et al. In press) and local teaching staff and communities can be married to achieve development in all environmental aspects in combination with conservation success. This is where environmental education can act as leverage, emphasizing the linkages between a healthy environment and its services, but also by serving the local needs by introducing for example concepts such as PHE (People, Health, and Environment; cf. Robson and Rakotozafy In press) for a successful model in Madagascar).

FROM TEACHER-CENTERED LEARNING TO LEARNER-CENTERED APPROACH. As Kollmus and Agyeman (2002) state, there is no apparent, direct correlation between knowledge and pro-environmental behavior. Having in mind that action competence may be the one main goal of environmental education, Jensen (2002) adds that a clear distinction should be drawn between behavioral change and action. Behavioral change is oftentimes directed by others, while action "should be directed at solving a problem and it should be decided upon by those preparing to carry out the action" (Jensen 2002: 326), direct or indirect, individually or collectively.

How these obvious gaps between environmental knowledge and attitude change towards positive environmental actions may be bridged is still open to debate. It is well known that knowledge about and positive attitudes towards the environment are necessary prerequisites but in themselves are not strong enough to lead to action (Schultz 2011, Heberlein 2012). An environmental education program aimed at changing people's behavior should therefore steer away from teacher-centered learning (banking education). It needs a learner-centered approach that is connected to the scholar's every-day life and has a real issues orientation, and is in its nature participatory and allows the learning process to be driven by the learners. It should integrate new teaching methods like outdoor activities, participative inquiry, group activities and discussions or action learning on real-life problems. This approach targets a broad set of scholars' competencies, thereby facilitating systemic and critical thinking, reflection and future orientated thinking. This strengthens the competencies of learners for shaping their future in a positive way (consider Palmer 2003, Tilbury 2007, Cotton and Winter 2010, de Haan 2010, for an in-depth discussion on appropriate teaching methods). Furthermore, a culture-specific approach to environmental education taking into account local values and belief systems is also needed to address and ensure environmental behavior via education (Boeve-de Pauw and Van Petegem 2011).

The concept of the *Gestaltungskompetenz* (cf. de Haan 2006, and references therein) promotes a learning to invoke change (in for example ecological, economic or social behavior) through a combination of skills acquisition and competencies (i.e., to build on children's every-day experiences) that goes beyond the pure accumulation of 'inert-knowledge' (sensu Renkl et al., 1996). Such knowledge-based or banking education is one of the main challenges in Madagascar's school system. Not surprisingly, teachers judge the school subjects reading, Malagasy, writing, and mathematics as likely most important to be successful in after school life, being congruent with the set

of principles the Ministry of National Education stated for their school children. When leaving the primary schools in Madagascar they are expected to master (i) academic achievements such as skills in reading and writing, arithmetic, and problem solving (e.g., Bloom's taxonomy: comprehension, application, analysis, synthesis and evaluation), (ii) social skills (attitudinal modernity, interpersonal effectiveness, community involvement), and (iii) economic success (earnings and productivity) (Heneveld and Craig 1996). The non-school subject household being ranked on second place by the Alaotra teachers correspondingly represents the social perspective.

The social environment is in teachers' perceptions higher prioritized than the natural environment. Teachers are exposed on a daily basis to social problems which are consequences of the urban environment and carried by the children into the class rooms. For example, many students come from impoverished households, are malnourished, and have poor hygiene. It has been shown that socioeconomic status globally plays a crucial role in children's development (Brooks-Gunn and Duncan 1997, Bradley and Corwyn 2002), and that such low status negatively affects behavioral and cognitive development in children (Grantham-McGregor et al. 2007). This results in poor performance which is reflected in the higher numbers of repeaters, or an increase in the drop-out rate (Arnold et al. 2007). Apart from this, it is well known that the experiences in early childhood shape the later learning processes; physical, cognitive, and emotional development of children are best supported by (various and rich) natural settings, i.e., children have to experience nature themselves to achieve a holistic learning (cf. Rivkin 1995). Following a more proactive and interactive school approach by visiting, for example, the market or the marshes could already act as a stimulant in this direction. Although being envisioned by the school authorities, the realization of the approach remains a challenge due to lack of resources, time and motivation.

Even if the structure of the school system provides opportunities to address environmental education or education for sustainable development, environmental education as defined by the United Nations (UN) is to date implemented in the Alaotra region only on a basic level. Potential drivers and barriers of such implementation remain to be identified. Further research in the next two years thus will focus on barriers that are opposed to the implementation of environmental education into the school curriculum and drivers that will facilitate such implementation in the Alaotra region. Addressing the questions on what potential drivers represent, and how they could be used to tackle potential barriers will help to develop material that is adapted to the regional circumstances and learning environment. Including sustainability issues into the curriculum can be a challenge and should aim for addressing locally relevant terms and appropriate solutions rather than frightening the audience (children as teachers alike) with global problems, which are not understandable, likely irrelevant, let alone solvable on local scale and conditions (Tilbury et al. 2002).

CONCLUSIONS

The school system in Madagascar has a hierarchic structure, and changes are commonly dictated from the Ministry of National Education or DREN and CISCO. It is thus crucial to involve the higher levels of the school system when introducing environmental education, not only the schools themselves. The DREN and CISCOs are the official government entities for the realization of teacher trainings, and are crucial partners in the delivery and implementation of such new tools.

As the primary schools are the sole formal education for a majority of rural children, teachers could act as promoter of education that will allow pupil's to face their future by furthering critical thinking. Teachers are shouldered with this responsibility. It is therefore important to overcome the banking education and to proceed towards a more participative and interactive learning, with teachers needing to be trained by the respective school authorities accordingly. Overcoming the impacts of *malgachisation* however, might still require some time and effort. The regional educators cannot be used only as instruments for implementation, but must be involved during the creation and development of educational tools or programs. It is assumed that this will increase teacher's creativity, motivation and initiative in their teaching process. Including teachers in the tool development process will provide them with new techniques, new approaches, and especially increase confidence to address new topics or to try out new ways themselves.

When drafting environmental education programs, the population's needs, concerns, and local value systems need to be taken into account. Consequently, a participatory approach needs to be chosen when drafting such programs. Given the anthropogenic view and emphasis on social values revealed by the interviews, the Alaotra schools and teachers might be better served with education for sustainable development rather than environmental education only. Following the principles of mutual respect, empathy and understanding will result in educational and development programs which can meet the expectations of all involved parties and are more likely to be continued even if projects or other external input such as funding are coming to an end.

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

FIGURE S1. Ranking environmental problems. Out of ten pictures, the interviewees were asked to choose and rank those that display potential environmental problems.

FIGURE S2. Interview guide for the structured in-depth interviews (in French).

ARTICLE

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Socio-ecological analysis of natural resource use in Betampona Strict Natural Reserve

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ABSTRACT

Without an adequate understanding of the socio-political context in which a natural environment is embedded, it is impossible to prevent, mitigate and adapt to future unwanted changes in the socio-ecological system. It is advantageous for environmental managers to see the social aspects of the socio-ecological system so that they can understand not only the effects but also the motivations of natural resource use. In Madagascar, lemurs and other mammalian wildlife are hotly contested resources because they are threatened and endemic biodiversity and yet are hunted for food throughout the island. Using semi-structured interviews in nearly 300 households in 19 communities surrounding the Betampona Strict Natural Reserve, our team found that more than 60 % of households had consumed wildlife within the past year, with approximately a quarter of wildlife harvest being illegal and nearly 95 % of wildlife harvest being directed to subsistence consumption and not for sale. Although rates of wildlife consumption were quite low throughout the region, we found a strong effect of the presence of the Madagascar Fauna and Flora Group research station. We found that the rates of wildlife consumption increased by 1.3 times for each kilometer distance from the station. Due to the low rates of wildlife consumption, we did not find a significant impact on human health and anemia (as measured through hemoglobin levels), and very low prevalence of anemia generally compared to other regions of Madagascar. Wildlife consumption does not appear to play a tremendous economic or health role in the communities surrounding this particular protected area, and thus increased enforcement of seasonal infractions of legal species and of all illegal species would be warranted. To improve current levels of nutrition, targeted interventions could focus on domesticated livestock diseases that plague the region.

RÉSUMÉ

Lorsque des changements inopinés surviennent dans un système socio-écologique, il est impossible de prévenir, d'atténuer et d'adapter si le contexte socio-politique dans lequel un environnement naturel évolue n'est pas bien compris. Les gestionnaires de l'environnement ont tout intérêt à considérer les aspects sociaux du système socio-écologique de manière à comprendre non seulement les effets de l'utilisation des ressources naturelles mais aussi ce qui motive cette utilisation. A Madagascar, les lémuriens et d'autres mammifères sont des ressources vivement contestées car ces espèces sont menacées et tout en représentant la biodiversité endémique, elles sont cependant chassées pour leur viande sur l'ensemble de l'île. En utilisant des entretiens semi-structurés auprès de 300 ménages dans 19 communautés villageoises de la périphérie de la Réserve Naturelle Intégrale de Betampona, la présente étude a montré que plus de 60 % des ménages avaient consommé du gibier au cours de l'année écoulée dont environ un quart de manière illégale et près de 95 % pour répondre à des besoins de subsistance mais pas pour la vente. Bien que les taux de consommation de gibier étaient plutôt faibles sur l'ensemble de la région, un fort effet de la présence de la station de recherche de Madagascar Fauna and Flora Group a été noté avec des taux de consommation de gibier multipliés par un facteur de 1,3 pour chaque km distant de la station de recherche. En raison des faibles taux de consommation de gibier, aucun impact significatif sur la santé humaine et l'anémie n'a été observé (tel que mesuré par le taux d'hémoglobine) et une prévalence extrêmement faible de l'anémie générale par rapport à d'autres régions de Madagascar. La consommation de gibier ne semble pas jouer un rôle économique ou sanitaire majeur pour les communautés de la périphérie de cette aire protégée en particulier, de sorte qu'il serait justifié d'appliquer plus strictement les lois portant sur le calendrier de chasse du gibier autorisé et l'interdiction de chasser d'autres espèces. Pour améliorer les niveaux actuels de la nutrition, des interventions ciblées pourraient se concentrer sur les maladies des animaux domestiques qui sévissent dans la région.

INTRODUCTION

Natural resources often play a critical role in human health and livelihoods and many suggest that conservation should attempt to meet all basic human needs (i.e., Kaimowitz and Sheil 2007). In Madagascar, more than 92 % of people live on less than $US 2/day (World Bank 2013) and thus natural resources

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play an instrumental role in providing what their limited financial resources cannot. Throughout Madagascar, several types of natural resources have been shown to play a major role in human livelihoods, through local use of honey (Kremen et al. 1999), construction materials (Kremen et al. 1999), traditional medicines (Golden et al. 2012a), soils/earth (Golden et al. 2012b), and the environment's role in spiritual and cultural practice (i.e., Keller 2009, Golden 2014). Because of the environment's tremendous value to local people in poverty alleviation (e.g., Gardner et al. 2013), conservation can serve to exacerbate conflict over resources, especially when resources are critical for human livelihoods or survival (West and Brockington 2006). Local people's use of wildlife as food, especially the primate diversity, is hotly contested as lemurs are endemic and often endangered (representing more than 20% of the world's primate species and 30% of family-level diversity, Schwitzer et al. 2014). Yet, local Malagasy hunt lemurs for food throughout the island (e.g., Golden 2009, Jenkins et al. 2011). Furthermore, it has been shown that this hunting is not for pleasure but rather serves a tremendous economic (Golden et al. 2014) and health role (Golden et al. 2011). These types of contested resources and the extent to which humans depend on them are necessary to explore on a site-by-site basis to further effective conservation and development programming in adaptive ways (i.e., Margules and Pressey 2000).

The concept that the practices and support of local people are important to the success of protected areas is largely understood (Keller 2009, Corson 2012), and yet, researching local systems in cost-effective ways that will facilitate adaptive conservation management plans is still lacking here in Madagascar. In order to most effectively conserve the biodiversity within protected areas, environmental managers need to understand many aspects of their respective region's environment, including its ecology, demographics, economics, human health status, and agricultural systems, among others. Here, we present the results of a six-month assessment in communities in Madagascar where we collected data concerning conservation-relevant human behaviors in order to understand current levels of environmental pressure, the socio-economic motivation of these pressures, and whether or not the exploitation had significant human welfare consequences.

This rapid assessment represents the first of seven already funded assessments that the MAHERY (Madagascar Health and Environmental Research) team has ongoing in Madagascar. The MAHERY team is a consortium of Malagasy and American researchers who have the expressed aim of understanding (i) current levels of forest pressure from human populations, (ii) the relevance of this exploitation to human livelihoods and health, and (iii) the role of varying forms of conservation governance in dictating local human behaviors vis à vis their environment.

METHODS

STUDY SITE. This study was conducted in 19 villages surrounding the Betampona Strict Natural Reserve, one of the last remaining low altitude rainforest ecosystems in Madagascar (Figure 1). Betampona, the very first protected area established in Madagascar in 1927, is located between E49°12'00"–49°15'00", S17°15'00"–17°55'00" on the east coast of Madagascar, about 40 kilometers from the principal port city of Toamasina. Despite its relatively small size (2,228 hectares),

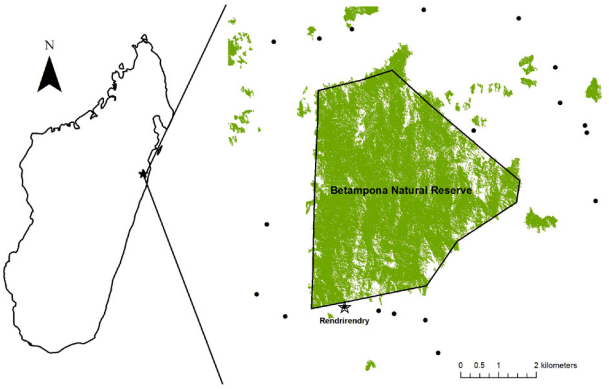

FIGURE 1. Betampona Strict Natural Reserve in eastern Madagascar detailing the protected area limits (black line), forest cover (green) and surveyed communities (black dots).

Betampona is rich in biodiversity, with 11 known lemur species, 88 known bird species and 67 reptile species identified. As a Strict Natural Reserve, access is strictly forbidden to both local people and tourists. Only students and scientists who receive a research permit through Madagascar National Parks (MNP) are allowed entry.

The local population living around the reserve was primarily Betsimisaraka, one of the 18 major ethno-linguistic groups in Madagascar, with members from other groups comprising less than 5% of the population (this study). The principal economic activity was agriculture, of which rice, corn, coffee, cloves, and bananas predominated. Animal husbandry (chickens, ducks and pigs) was conducted mainly for household consumption. Due to its close proximity to Toamasina, many inhabitants have historically left the area for hopes of prosperity in the regional city. The Madagascar Fauna and Flora Group (MFG) manages this protected area in conjunction with MNP; the MFG research station is located in Rendrirendry (Figure 1).

SURVEY PROTOCOLS. Between February and August 2013, two Malagasy researchers (Rabehatonina and Rakotosoa) surveyed 298 households (seven households declined to be interviewed) in 19 communities adjacent to the Betampona Reserve. These researchers were part of the MAHERY (Madagascar Health and Environmental Research) team and had been rigorously trained in survey protocols prior to this research. The communities were not randomly sampled but we attempted to survey all communities adjacent to the protected area. Only three of the 22 communities that surround the protected area were not surveyed due to time constraints. The two enumerators consulted with the local community chiefs and arranged schedules for interviews jointly with local leadership. A village meeting was always held prior to the commencement of surveys. However, the two enumerators were not accompanied by any local guides during the interview process to promote honest answers to sensitive questions. During the community meetings, the research was explained as work trying to understand the ways in which natural resource use and agricultural activities contributed to human food security, health and general wellbeing.

Our survey instrument was designed to gather information regarding natural resource use by administering questions to the male or female head of household. Questions pertained to household demographics, agricultural labor, livestock raising and diseases, income generation, forest resource use, hunt-

ing behavior and taste preferences of animal-source foods. In general, the interviewees were asked to recall events over the past year. Households were selected by one of two methods: i) if a household census existed at the community level, then the local research team selected every third household to participate; ii) if no household census existed at the community level, then the research team selected every third household that they passed in the community. Each head of household provided informed consent to participate in the research survey.

In addition to questions administered solely to the head of household, we also collected health statistics on all available individuals in the surveyed households, totaling 956 individuals within these 298 households. The basic information included sex, birth date, occupation and educational obtainment. The specific health information gathered included anthropometric assessments (height and weight), a history of malaria episodes, a history of deworming medication, and a hemoglobin and blood oxygen level obtained from a portable hemoglobinometer (Rainbow Pulse CO-oximeter from MASIMO). This hemoglobinometer was simple to use and was non-invasive, using photospectrometry rather than a blood sample to assess hemoglobin status. Both enumerators were trained by Golden with supervision from the Madagascar Ministry of Health to carry out these protocols.

VARIABLE CREATION AND ANALYSIS. All data were analyzed in STATA v.13.0. Simple summary statistics were calculated for most forms of environmental resource use and socio-demographic variables. Installable macros packages from the World Health Organization were used to calculate the prevalence of anemia in children and adults. We analyzed the effect of wildlife consumption on hemoglobin levels using an established generalized linear mixed model where all individuals were clustered at the level of the household, hemoglobin was an untransformed continuous outcome variable, wildlife consumption was a log-transformed continuous explanatory variable, and household income and an individual's age were controlled for within the model (Golden et al. 2011). Hemoglobin levels in this population were roughly normally distributed and did not require transformation.

RESULTS

In the 298 surveyed households surrounding Betampona Strict Natural Reserve, there was a mean household size of 3.9 individuals (median 4) with 46.2 % of the population being less than or equal to 16 years of age (Supplementary Material). Eight percent (24 households) reported no cash income in the past year demonstrating high subsistence reliance in these households in particular. Of the households reporting cash income, income was highly positively skewed (median income: $67.50 per household, mean $144.18, SE: $18.19) which demonstrated that although many households were entirely subsistence-driven, some households had entered into cash market economies.

Much like other regions of Madagascar, agricultural labor and much of life centered on rice production. Surrounding the Betampona region, there were two rice crops per year: a swidden rice crop harvested in approximately May and a paddy rice crop (although to a much lesser extent) harvested in approximately November. Local Betsimisaraka in this region participated in the agricultural practice of having a seasonal home, or hamlet, called *lasy* in Malagasy. A minority of the population (25.3%) used *lasy* in the past year, and living in a *lasy* peaked during May at the height of labor demands for swidden agriculture (Supplementary Material). The average *lasy* was a 1.1 hour walk from the center of the community (SE: 0.05 hours) with a maximum distance of 5 hours. This means that the average *lasy* was 4.8 km away if we estimate time-distance relationships and expect normal walking speeds (Ralston 1958), which are likely an overestimate here given the steep and slippery terrain.

Ninety-six percent of the population relied on firewood for cooking and harvested it themselves. Individuals traveled between 0–2 hours for collection, with most frequent collections occurring 15–30 minutes from home. Approximately four-fifths of households had harvested timber (even if just one piece of wood) and 90 % have collected thatch roofing in the past year for personal use showing high dependence on the forest for natural products that can create shelter. High reliance on the forest for healthcare was reported with nearly 82 % of households having harvested traditional medicines from the forest at a rate of approximately once per week. Only 4 % of households had collected honey in the past year. This low rate of collection was not due to preferences but to a devastating bee epidemic that had wiped out hives in the region.

More than 60 % of households had consumed at least one wild animal in the past year but it was very sporadic among households who hunt wildlife. Only 2 of 298 surveyed households possessed a shotgun and the remaining households used predominantly natural products to trap, snare and slingshot animals. All active hunting of tenrec species, as compared to opportunistic hunting, was facilitated by dogs tracking the scent of tenrecs (Table 1).

Of a total of 2,253 animals reported to have been consumed by surveyed households, 23.0 % of animals were illegal to harvest according to the most recent updates to legislation (Rakotoarivelo et al. 2011). Hunting of tenrecs is only authorized from 1 April–31 May (Ordonnance N^{o} 60-126 from Oct. 3, 1960) and this hunting is only legal if also not occurring at night or with dogs or other prohibited equipment. The local MFG staff were not aware of this obscure legislation (and not responsible for educating local people about legislation) and thus, local people were likely ignorant of these policies as well (n.b., we did not survey local people's knowledge of rules). Only 5.3 % of animals consumed were obtained through a sales transaction, and all purchases were made on a household-to-household basis. Only three species were sold: bush pig (*Potamochoerus larvatus*, n=77, mean price $US 2.25/kg), hedgehog tenrec (*Setifer setosus*, n=7, $US 0.60/animal) and the common tenrec (*Tenrec ecaudatus*, n=36, $US 0.45/animal).

When investigating the conservation impact of permanent staff presence and monitoring of infractions by MFG patrols, we found that wildlife harvesting increased by approximately 1.3 (generalized linear mixed model, p=0.035, 95 % CI: 0.1–3.1) times per kilometer distance from the Rendrirendry research station, where the MFG agents and guides are based, even after controlling for the distance to the forest. Therefore, we tended to see an exponential increase of wildlife extraction as distance from the research station increased.

The average household reported eating approximately five wild animals in the past year (Table 1). Almost one in five households had eaten a lemur in the past year, yet at very low levels of consumption. On average, 0.75 lemurs per household were consumed per year. Carnivoran hunting was at even lower

TABLE 1. The volume of mammalian wildlife consumption in communities surrounding the Betampona Strict Natural Reserve, disaggregated by hunting method. The volume of consumption was reported based on the head of household's recall of number of individuals consumed within the past year (NB: wild bird, insect, reptile and amphibian consumption was not surveyed). **P. larvatus* was reported by number of occasions consumed rather than number of individuals as it was frequently purchased as weighed pieces of meat or eaten at friends' homes.

Species	Total consumed	Active hunting [%]	Snaring [%]	Opportunistic hunting [%]	Eaten with friends [%]	Purchased [%]
Tenrec ecaudatus	1,030	53.6	0.3	17.3	10.0	18.6
Microcebus sp.	323	55.1	0.0	43.7	1.2	0.0
Setifer setosus	170	61.8	0.0	20.6	7.6	8.8
*Potamochoerus larvatus**	121	0.0	11.6	8.3	15.0	64.5
Hemicentetes semispinosus	80	53.8	0.0	38.8	3.8	3.8
Microchiroptera sp.	76	93.4	0.0	0.0	6.6	0.0
Viverricula indica	38	0.0	89.5	7.9	2.6	0.0
Galidia elegans	21	9.5	33.3	23.8	33.3	0.0
Hapalemur griseus	7	71.4	0.0	28.6	0.0	0.0
Avahi laniger	7	14.3	0.0	0.0	85.7	0.0
Pteropus rufus	6	0.0	0.0	0.0	100.0	0.0
Salanoia concolor	6	100.0	0.0	0.0	0.0	0.0
Cryptoprocta ferox	4	0.0	0.0	50.0	50.0	0.0
Daubentonia madagascariensis	4	0.0	0.0	0.0	100.0	0.0
Galidictis fasciata	3	66.7	0.0	33.3	0.0	0.0
Lepilemur sp.	2	0.0	0.0	2.0	0.0	0.0
Eulemur albifrons	1	100.0	0.0	0.0	0.0	0.0
Indri indri	1	0.0	0.0	0.0	100.0	0.0
Propithecus diadema	0	.	.	.	.	.
Varecia variegata	0	.	.	.	.	.
Cheirogaleus sp.	0	.	.	.	.	.

levels, with 10% of households participating, and an average 0.16 carnivorans per household consumed per year. Bat hunting was also rare with 2.5% of households consuming bats and on average 0.28 bats per household consumed per year. Tenrec hunting was the most common form of wildlife harvest in the area with more than 50% of household eating them at an average rate of four tenrecs consumed per household per year. More than 20% of households were eating bush pig at an average rate of 250g per year.

We found a very low prevalence of anemia throughout all sub-populations surrounding Betampona. Approximately 13% of children 0–5 years of age, 6% of children 6–12 years of age, 8% of women over 12 and 14% of men over 12 were affected by anemia (World Health Organization 1994). Only 1.2% (12 of 965) of observed subjects would be deemed in the moderate to severe anemia cutoffs (ibid). Unsurprisingly, with very low rates of wildlife harvest locally, we did not find a relationship between wildlife consumption and human nutrition here (generalized linear mixed model, p=0.581) but we did find that women and girls had significantly lower hemoglobin than their male counterparts (T-test, 0.69g/dL, 95% CI: 0.50 – 0.88 g/dL, p<0.001).

Although both the prevalence of anemia and rates of wildlife harvest were low, there was still a tremendous amount of space for dietary improvement. On average, chickens seemed to be the most prevalent type of animal-source food, followed by ducks (Table 2). These poultry also comprised nearly 50% of all individuals number one top taste preference for all animal-source foods, including wildlife (Figure 2).

However, the disease toll on chickens seemed to be the most prevalent of all domesticated meat sources. Locally, there was a disease called *bomona*. According to local descriptions of symptoms and timing, it was very likely to be Newcastle disease. The estimated case-fatality rate was 96% as measured by community perceptions of cause of death. Ducks were also affected by Newcastle disease but also likely affected by Duck plague. The case-fatality rate for ducks across all diseases was approximately 64%. Thirteen percent of households in Betampona had diseased pigs in the past year. Locally, this pig disease was called *pesta* and was characterized by loss of appetite, being unable to stand, foamy mouth, being cold to the touch, vomiting and had an 86% fatality rate. Zebus were affected by *viky* (worms) and *dinta* (flukes). Of six cases where these issues were severe, two led to premature death of the animal.

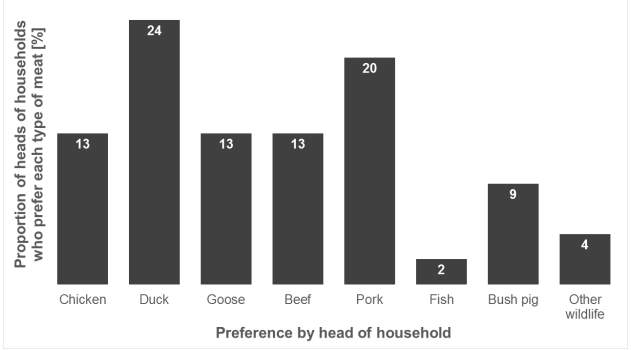

FIGURE 2. Reported number one top taste preferences for all heads of households in the Betampona Strict Natural Reserve. Taste preference rankings could not tie and all individuals surveyed had to rank all meats that they had ever tasted, even if only once.

TABLE 2. The range and mean of household livestock assets in communities surrounding the Betampona Strict Natural Reserve.

Type of livestock	Zebu	Pig	Duck	Chicken	Goose	Cat	Dog
Range (#/household)	0–6	0–9	0–25	0–80	0–40	0–5	0–6
Mean (#/household)	0.17	0.42	1.5	7.5	0.5	0.14	0.26

DISCUSSION

Natural resource use by communities in Madagascar appears to be important to local livelihoods and wellbeing, and may play a role in local poverty alleviation (Gardner et al. 2013). Surrounding the Betampona Strict Natural Reserve, the use of firewood for energy, timber and other forest products for shelter, and honey and wildlife (among many others) for food and nutrition are examples of the interface between environmental integrity and human wellbeing. The availability of these resources may change in the future given current trends in ecosystem transformation. For example, the use of honey is particularly exceptional near Betampona because the rates of collection are so low due to some sort of colony collapse that has affected local bee populations. Local people historicize this rapid decline over the past 5–10 years and this question begs for further study (though see Rasolofoarivao et al. 2013). Honey consumption can be critical to subsistence and hunter-gatherer populations, and may be a unique source of refined sugar and energy in this population (Cordain et al. 2000).

Overall rates of mammalian wildlife harvest appear to be quite low in the communities surrounding Betampona. As a point of comparison, wildlife harvest is substantially lower across all taxa when compared to rates of exploitation in another MAHERY study site, Makira Natural Park, an area over two orders of magnitude larger than Betampona that has allocated 'use' zones (Golden et al. 2014). For instance, 17% of households eat lemurs in Betampona as compared to 49% in Makira, 10% eat carnivorans as compared to 40% in Makira, 20% eat bush pig as compared to 25% in Makira, 51% eat tenrecs as compared to 91% in Makira, and 3% eat bats as compared to 15% in Makira (ibid).

The low rates of terrestrial mammal consumption surrounding Betampona are similar in level to the Alaotra-Mangoro region of eastern Madagascar (Jenkins et al. 2011). We did not focus on other types of wildlife consumed such as birds and reptiles due to lack of adequate time to explore these issues during our interview. This of course limits the reporting on the breadth of resources used which is problematic given our own research experiences in Makira, and based on others research in other parts of Madagascar (i.e., Gardner and Davies 2014).

Future analyses will be required to determine the sustainability of harvest; however, it could be assumed that most species are being sustainably harvested with the exception of species with life history traits that allow almost no levels of sustainable harvest such as the fosa (*Cryptoprocta ferox)*, which was reported to be hunted four times in our study. Assessment of sustainability for protected species is moot but these analyses should be considered for game species such as tenrecs and bats, etc. If the 23% of animals which were illegally hunted were further diminished, it is even more likely that current rates would not be of major conservation concern. Hunting techniques are mainly traditional using trapping and snaring, similar to other hunting studies in Madagascar (Golden 2009, Jenkins et al. 2011, Gardner and Davies 2014, Golden et al. 2014). Hunting with dogs is prevalent throughout the region and is verified by the frequency of dogs observed inside the protected area, as measured by phototrap incidence (Fidisoa Rasambanairivo, pers. comm.). This statistic was important as both dogs and people are prohibited from entering inside the protected area and dogs facilitate hunting of protected species, likely having major impacts on local wildlife.

It is likely that we may be witnessing low harvest rates for one of several reasons: 1) wild animals are less prevalent in this area due to small intact forest size; 2) permanent presence of MFG research staff and monitoring of infractions by local agents; and/or 3) hesitancy to report illegal activity to survey implementers especially in the context of a rapid assessment. Although we concede that the latter reason is certainly possible, we attempted to minimize this bias in several ways. First, the survey implementers were trained in our ongoing longitudinal survey effort in Makira to learn effective methods for gathering information (Golden et al. 2013, 2014). Second, the survey was framed in the context of food security and livelihoods and thus the questions regarding consuming wildlife were not asked from a conservation perspective but rather from one of food security and human health. Lastly, one of our surveyors was born and raised in this region which lends legitimacy to our efforts. Even with these conditions, it is likely that our results were biased and that the levels of wildlife consumption (particularly of protected species) may represent conservative estimates of exploitation.

Assuming that survey bias did not unduly influence our results, it is possible that the permanent presence and monitoring of infractions by the Madagascar Fauna and Flora Group (MFG) do play some role in the low rates of wildlife harvest in the region. To credibly believe our results that permanent research presence and monitoring of infractions affect community levels of wildlife harvest, we must assume that the distance from the MFG research station measure may serve as a proxy for monitoring and enforcement intensity because more direct measures were not collected. Ecological monitoring has been shown to be effective in engaging local people and reducing pressures on the forest in Madagascar (Kremen et al. 1994, Andrianandrasana et al. 2005). From 2009–2010 in Betampona, there were a total of 203 patrols throughout the Betampona region to search for signs of illegal forest activities (MFG, internal report). Patrols were very high during this period (typically only eight patrols per month per year) because research was postponed in Betampona during the Madagascar presidential political transition. Across all forms of infractions, a total of 46% of patrols indicated the presence of illegal forest use. Peaks in illegal activity (as proxied by numbers of patrols indicating infractions on a monthly basis) were parallel to seasons in which local people spent more time in their *lasy* (or seasonal agricultural homes). This is a similar result to our ongoing observations in Makira Natural Park (Golden, unpub. data) and perhaps presents an opportunity for

targeting increased education to particular groups for whom forest policies may not be apparent.

Throughout all age and sex sub-groups disaggregated, we found consistently low rates of anemia. Also, we did not find a significant association between wildlife consumption and anemia in this region. This does not mean that wildlife is not important to the diet as a variety of micronutrients such as fatty acids, zinc, and vitamin B12 may not be consistent with an individual's hemoglobin level (Kraemer and Zimmerman 2007). With that said, the extraordinarily low rates of wildlife harvest in each household appears to not significantly contribute to their health. This presents a fortunate opportunity to increase conservation efforts without fear of negative human health repercussions.

In order to complement local people's reduced access to wildlife as a food source, local populations could improve their health by increasing the productivity of local poultry stocks. And, chicken and ducks comprise 50 % of their top taste preferences, a similar result to Gardner and Davies (2013). Increasing the productivity of these types of livestock will likely lead local people away from wildlife hunting for economic reasons. As a price per kilogram, all species of wildlife are much less expensive than domesticated meat prices. This is consistent with findings from Makira; wildlife is less desirable (as proxied by taste preferences) but also less expensive because it is not market-oriented and the time invested in hunting is not internalized into the price (Golden et al. 2014). If an intervention made domesticated meat more productive and available, the price would drop and local people may naturally wean themselves from wildlife as a food source. Furthermore, because wildlife consumption does not appear to play a tremendous economic or health role in the communities surrounding this particular protected area, increased enforcement of seasonal infractions of legal species and of all illegal species would be warranted.

CONCLUSION

Research on socio-ecological systems is important globally, but particularly essential in Madagascar where local people live in close dependency on the natural resources in their surrounding environments. Understanding the motivations driving natural resource use and the types of benefits received from this resource access may help environmental managers to find parallel goals between environmental conservation and human wellbeing. Until we empirically frame conservation as a benefit to local people, managers will struggle to garner support for community-based natural resource management programs.

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

FIGURE S1. Demographic composition of households surrounding the Betampona Strict Natural Reserve.

FIGURE S2. Proportion of households living in seasonal forest homes (*lasy*).

REVIEW

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Seed dispersal by vertebrates in Madagascar's forests: review and future directions

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ABSTRACT

Madagascar's highly diverse forests are critically threatened because of increasing deforestation, and those that remain are facing declines of vertebrate frugivores that disperse their seeds. Thus, understanding plant-frugivore interactions is of critical importance for the conservation and maintenance of plant diversity in Madagascar. This paper reviews observational and experimental studies of the multifaceted aspects of seed dispersal by vertebrates across Madagascar including the relative importance of different seed vectors, the patterns of seed deposition, and the post-dispersal fate of dispersed seeds. This also aims to lay a foundation for future studies by discussing understudied aspects that are crucial for the understanding of the role of frugivores on plant populations and communities in Malagasy forests. Such perspectives are important given the increasing threats to seed dispersers, the low richness of frugivore assemblages in Malagasy forests and the strong reliance of many plant species on frugivores for their dispersal. Understanding this ecosystem service can provide us insights on plant colonization, community structure, demography and invasion, as well as forest restoration and regeneration.

RÉSUMÉ

Les forêts de Madagascar abritent des communautés de plantes vasculaires exceptionnellement diverses avec un taux d'endémisme s'élevant à 82 %. Malheureusement, hormis les continuelles dégradation et fragmentation menaçant ces forêts, la flore malgache est aussi menacée par l'insuffisance et le déclin des populations d'animaux frugivores qui jouent un rôle fondamental dans la dissémination des graines. La compréhension de ce mécanisme de dissémination des graines par des frugivores est importante pour savoir comment préserver la biodiversité et la régénération forestière ainsi que pour établir des stratégies de conservation des habitats fragmentés. Le présent article constitue une synthèse des publications scientifiques sur les recherches concernant ce mécanisme dans les forêts malgaches. Les informations disponibles sont plutôt limitées mais suggèrent que la majorité des plantes malgaches dépendent des vertébrés frugivores pour la dissémination de leurs graines. Ces études montrent également quelques aspects portant sur des modèles de dispersion des graines et des plantules. Plusieurs éléments relatifs à ce mécanisme sont encore inconnus et nécessitent des recherches approfondies. Les pressions menaçant les différents vecteurs de graines sont discutées, et plus particulièrement celles qui pourraient avoir des effets néfastes sur la démographie des populations de plantes. En outre, des recommandations sont formulées pour permettre l'intégration des interactions frugivore–plante dans la conservation des écosystèmes forestiers malgaches.

INTRODUCTION

Madagascar's forests hold exceptionally diverse vascular plant communities with up to 82 % endemism (Callmander et al. 2011). The increasing threats of habitat destruction and fragmentation facing these forests are well known (Ganzhorn et al. 2001, Harper et al. 2007, Watson et al. 2010, Allnutt et al. 2013); however, another looming threat to Madagascar's flora has recently become apparent: the lack and decline of important seed dispersers such as frugivorous vertebrates. This is critical because Malagasy forests have already depauperate frugivore communities (Langrand 1990, Hawkins and Goodman 2003), which are also currently threatened by the increasing anthropogenic disturbances and climate change (Dunham et al. 2008, Barrett and Ratsimbazafy 2009, Dunham et al. 2011, Dewar and Richard 2012, Ratsimbazafy et al. 2013, Schwitzer et al. 2013). Thus, examining vertebrate-mediated seed dispersal in this system is crucial for understanding the maintenance of plant diversity and for the conservation of the diverse plant communities in Madagascar, which supports one of the world's hottest hotspots of biodiversity (Ganzhorn et al. 2001).

There has been no synthesis about our current knowledge of this ecosystem service in Madagascar. Understanding seed dispersal is important because of the fundamental role of this mechanism in plant colonization, community structure, demography and invasion, and in forest regeneration (Howe and Smallwood 1982, Terborgh et al. 2002, Ibáñez et al. 2006, Schupp et al. 2010, Jordano et al. 2011). Seed dispersal studies have also a central place in conservation, natural restoration of degraded habitats and ecosystem functioning (Farwig and Berens 2012).

In this paper, I synthesize published literature of studies on seed dispersal by frugivorous vertebrates in Malagasy forests to establish a foundation for future studies to understand the importance of frugivores for plant populations. Specifically, I address the following questions in reference to Malagasy forests: i) What is known about seed removal from parent plants? ii) Where are seeds dispersed? and iii) What are the consequences

of dispersal on seed fate? I also review the threats that frugivores are facing, and the potential impacts of the absence of frugivores for Malagasy forests. Further, I discuss research areas that are particularly important for future directions of study that may help us integrate seed dispersal interactions in conservation management in Madagascar's forests.

SYNTHESIS OF SEED DISPERSAL RESEARCH IN MADAGASCAR'S FORESTS

SEED REMOVAL FROM PARENT PLANTS. Fruit traits are important in determining potential dispersal agents, as they are hypothesized to evolve under the selective pressures of seed vectors such that unrelated plant species sharing seed dispersers may have similar traits (Lomáscolo and Schaefer 2010). Such traits include fruit morphology, color, size, presence of edible pulp, presence of wings or any external modifications, husk thickness and weight (Howe and Smallwood 1982). Particularly, in vertebrate-dispersed plant species, traits such as color, size, fruit protection and nutrient reward play an important role in the attraction of seed dispersers (Schaefer et al. 2004, Bollen 2007), and usually match the behavior and physiology of different disperser taxa (Lomáscolo et al. 2010). For example, recent work by Valenta et al. (2013) demonstrates that fruit color and odor predict the selection of fruits in nocturnal mouse lemurs (*Microcebus* spp.), which have dichromatic color vision; fruits dispersed by these species showed greater color contrast from leaves under moonlight conditions than non-dispersed fruits. Overall, a majority of plant species in Malagasy forests have fruit traits that suggest adaptation for seed dispersal by frugivorous vertebrates (Scharfe and Schlund 1996, Birkinshaw 2001, Bollen et al. 2004a, Bollen et al. 2005), especially by primates. In the littoral forest of Sainte Luce, for instance, a majority of tree species, especially large-seeded ones, critically depend on *Eulemur* (*fulvus*) *collaris* for seed dispersal, although specific fruit traits were not tightly correlated with specific groups of frugivores (Bollen et al. 2004a). In addition, morphological and chemical analyses of fruit traits supported a predominance of primate-dispersed species in a Malagasy tree community compared to a similar tree community in South Africa (Voigt et al. 2004).

Large- and small-sized lemurs are often reported as the main frugivores and primary seed dispersers in Madagascar's forests; however, studies of seed dispersal by bats and birds have been limited (Supplementary Material). In addition to the important quantity of ripe fruits in their diet, they are able to defecate intact and viable large- and small-sized seeds, which can enhance seed germination and seedling growth (Dew and Wright 1998, Razafindratsima and Razafimahatratra 2010, Moses and Semple 2011, Razafindratsima and Martinez 2012, Sato 2012). For example, *Varecia variegata* in the southeastern Manombo rainforest passed the seeds of 40 different plant species during a 3-month study period, and the lemur-passed seeds had higher germination success than non-passed seeds (Moses and Semple 2011). It is, however, possible that not all frugivorous lemurs have positive dispersal effects on their feeding plants. For instance, a behavioral comparison among sympatric lemurs suggests that *Propithecus* spp., which spend up to 48 % of their feeding time on fruits (Overdorff and Strait 1998), are mainly seed predators. They consume both ripe and unripe fruits, masticating seeds while feeding or dropping seed pieces under the parent trees, and digesting those that they swallowed (Ralisoamalala 1996, Dew and Wright 1998, Overdorff and Strait 1998, Böhning-Gaese et al. 1999). Also, the effectiveness of dispersal has been observed to vary across lemur species (Overdorff and Strait 1998, Razafindratsima et al. 2014). For example, *Varecia variegata editorum* in the southeastern rainforest of Ranomafana National Park were observed to perform long-distance seed dispersal compared to its sympatric *Eulemur* spp. (Razafindratsima et al. 2014).

Besides primates, birds are also recognized as one of the major groups of seed dispersers in tropical ecosystems (Fleming 1979, Herrera 2002). Madagascar has a relatively low richness of bird species compared to other tropical regions (Kissling et al. 2012); and only about 10 % of bird species in Madagascar are known to consume fruits (del Hoyo et al. 1992). However, the limited number of studies on seed-dispersal by birds in Madagascar demonstrates that some frugivorous birds may act as effective seed dispersers. While their diversity is low relative to other tropical forests, their high abundances may make them important dispersers in the system, and particularly given the current decline of frugivorous lemurs. Six of the known frugivorous bird species were observed to swallow and disperse the seeds of several small-seeded plant species across Madagascar (Supplementary Material), especially understory shrubs (Rakotomanana et al. 2003). For instance, *Philepitta castanea* in the rainforest of Ranomafana are estimated to disperse 85.7 % of ingested seeds away from the parent crowns (ibid). The Madagascar blue pigeon (*Alectroenas madagascariensis*), feeds on many of the same large-seeded fruits as large-bodied diurnal lemurs (pers. observ.), and is distributed across the entire eastern rainforest region. This species may carry out an important ecosystem service, particularly in areas where lemur populations are dwindling, though future studies are warranted. The two parrot species, *Coracopsis nigra* and *C. vasa*, appear to be mainly seed predators because they either peck at fruits and drop them under the parent tree, or destroy the majority of seeds they consume by splitting or digesting the seeds (Scharfe and Schlund 1996, Goodman et al. 1997, Bollen et al. 2004a, b). However, these parrots can also be opportunistic seed dispersers as they were occasionally observed carrying seeds in their beaks away from the parent crowns (Böhning-Gaese et al. 1995, Bleher and Böhning-Gaese 2001).

Some studies also suggest that frugivorous bats can act as important seed dispersers in Madagascar as they are swallowing and defecating the intact seeds of small-seeded plant species (Bollen and Van Elsacker 2002, Long and Racey 2007, Picot et al. 2007, Ratrimomanarivo 2007, Andrianaivoarivelo et al. 2011, Andrianaivoarivelo et al. 2012). Bats may also play important role in ensuring genetic exchange between forest fragments because they are able to travel long-distances from their roost for foraging (Bollen and Van Elsacker 2002, Andrianaivoarivelo et al. 2011). For example, fecal analyses by Picot et al. (2007) showed that seeds of trees located at least five kilometers from the roost were frequently recorded in the diet of the Malagasy fruit bat *Eidolon dupreanum*. Furthermore, the passage of seeds through the digestive tracts of bats appears to facilitate seed germination (Andrianaivoarivelo et al. 2011).

Other frugivorous vertebrate groups such as lizards, fish, tortoises and bush pigs can also be effective dispersers in tropical forests (Valido and Olesen 2007, Anderson et al. 2011, Blake et al. 2012), but studies of the seed-dispersal services by such

groups in Malagasy ecosystems are limited. Three frugivorous reptilian species (*Oplurus cuvieri, Pyxis planicauda* and *Zonosaurus laticaudatus*) are listed as potential seed dispersers in the western dry forest of Kirindy (Ganzhorn et al. 1999). Work exploring the role of reptiles is an important area of research in this area, particularly in the arid habitats of Madagascar. Pedrono et al. (2013) report that the two extinct species of Malagasy giant tortoises (*Aldabrachelys grandidieri* and *A. abrupta*) may have played the role of seed dispersers for large-sized seeds as their close relative *Aldabrachelys gigantea* are effective seed dispersers on Aldabra atoll.

SEED DEPOSITION. Removal of seeds away from parent plants is not enough to assess the quality and effectiveness of different dispersal vectors because the patterns of seed deposition can influence plant recruitment (Schupp et al. 2010, Wang and Smith 2002). Three aspects are often discussed as crucial in determining the consequences of seed dispersal on plant reproductive success: the distances of dispersed seeds from parent and conspecific adult trees, the microsites (i.e., local environment) where seeds land, and the aggregation patterns of seed dispersion (Muller-Landau and Hardesty 2005).

The distance of a seed from its parent tree can strongly influence its recruitment because it allows the seeds to escape density-dependent mortality resulting from species-specific natural enemies, and reduces sibling competition near parent and conspecific adult-trees (Janzen 1970, Connell 1971, Hubbell 1979). Although limited, studies of seed-dispersal distances in Madagascar have provided useful information regarding the patterns of seed dispersal in Malagasy forests, and the effectiveness of some dispersal groups. Using data on gut-passage times, movement patterns and home ranges, which can often be used to predict dispersal distance in vertebrate-dispersed plants (Muller-Landau and Hardesty 2005), studies have reported short average dispersal distance (83–180 m) for tree species that are dispersed by large-bodied lemur species (Moses and Semple 2011, Martinez and Razafindratsima 2014, Razafindratsima et al. 2014), which may be due to their relatively small home-range sizes and day-range lengths (Razafindratsima et al. 2014). Bleher and Böhning-Gaese (2000, 2001) also reported that a bird-dispersed tree, *Commiphora guillauminii*, in the western dry forest of Kirindy had shorter dispersal distances than its congener in South Africa, affecting seedling establishment (i.e., independent growth of emerging seedlings) and spatial distribution. This short-dispersal pattern of *Commiphora* resulted in high genetic differentiation of trees at a local spatial scale (Voigt et al. 2009). Malagasy fruit bats may be able to perform long-distance seed dispersal (> 500 m) because they can travel relatively far from their roost to feed (Bollen and Van Elsacker 2002, Picot et al. 2007), but empirical studies are lacking. Long seed-dispersal distances were rarely observed for lemur-dispersed trees. However, such long-distance dispersal events, even rare, may be important because they can facilitate the colonization of new habitat and increase gene flow between and within populations (Cain et al. 2000). For instance, a genetic study of the spread of *Beccariophoenix madagascariensis*, which is a palm species with lemur-dispersed fruits in eastern Malagasy forest, suggest that long-distance seed dispersal may have contributed to the significant gene flow observed between populations that are within three kilometers of each other (Shapcott et al. 2007).

The microsites, in which seeds land after removal from their parent plants, can also influence their germination and survivorship, the probability of seedling establishment and survival, and subsequent recruitment success (Howe and Smallwood 1982, Muller-Landau and Hardesty 2005, Beckman and Rogers 2013). Thus, a critical step in understanding the effectiveness of frugivores as seed dispersers is to examine how biotic and abiotic factors associated with the microsites, where frugivores disperse seeds, affect seed fate. Work addressing such question in Madagascar is limited, but would contribute greatly to our understanding of the impacts of frugivores on the demography of plant populations. For example, a recent study by Razafindratsima and Dunham (2014) in Ranomafana National Park demonstrates that seeds of *Cryptocarya crassifolia* dispersed by three frugivorous lemurs into gap habitat (<55 % canopy cover) had higher recruitment probability than those dispersed under more closed canopies.

The degree and scale of seed aggregations are also crucial for plant recruitment success; for example, high clumping of seeds may result in high density-dependent seed mortality because it increases resource competition among siblings and attracts seed-predators (Schupp et al. 2002, Muller-Landau and Hardesty 2005). Clumping can also be beneficial for plants because it can reduce interspecific competition (Muller-Landau and Hardesty 2005), and increase disperser attraction for subsequent dispersal as a result of clumped distribution of trees that share seed dispersers (Clark et al. 2004). In general, low clumping is expected for wind-dispersed species (Muller-Landau and Hardesty 2005), but seed dispersal by animals is likely to result in high clumping (Schupp et al. 2002). These patterns may vary by animal taxa and by dispersal systems (Clark et al. 2004). In Malagasy systems, the seeds of bat-dispersed plant species were often disproportionately deposited near roost trees (Picot et al. 2007), but we do not know whether such microsites are favorable for seedling establishment. There is also a paucity of published research detailing the spatial distribution of seed dispersal in Madagascar forests; the understanding of such aspect could provide us better insights on the role of frugivores in structuring plant communities.

These three attributes of seed deposition patterns are expected to increase the odds of recruitment success for individual seeds and may therefore affect plant demography (Howe and Smallwood 1982). For instance, nonrandom seed dispersal by three frugivorous lemurs in Ranomafana rainforest increased per-seed sapling recruitment by four fold compared to no dispersal (i.e., seeds simply falling under parent trees) (Razafindratsima and Dunham 2014). Also, the spatial distribution of *Commiphora guillauminii* seedlings (bird-dispersed tree species) in the western dry forest of Kirindy (Böhning-Gaese et al. 1999), and of a lemur-dispersed tamarind species (*Tamarindus indica*) in southern dry forest of Berenty (Mertl-Millhollen et al. 2011) revealed a significantly higher probability of seedling establishment away from the parent trees than beneath the parent crowns. These dynamics may differ by plant species that experience different environmental conditions, and much research is needed to understand how plant demographic patterns as well as how plant populations might be affected by the absence of dispersers.

POST-DISPERSAL SEED FATE AND PLANT RECRUITMENT SUCCESS. After dispersal, seeds experience a number of factors that influence their germination and recruitment (e.g., predation, disease, and nutrient availability). Frugivore dispersers can influence germination as a result of removal of pulp or husks (which removes germination inhibitors), scarification of seeds, and fertilization with fecal matter (cf. Traveset et al. 2007 for review). There are mixed results from manipulative experiments (in laboratory and nursery) examining the germination of seeds that passed through the guts of Malagasy frugivores compared with non-passed seeds. Seeds passed through the guts of some lemur species had higher germination success than seeds that were manually extracted from fruits (Dew and Wright 1998, Razafindratsima and Razafimahatratra 2010, Moses and Semple 2011, Razafindratsima and Martinez 2012, Sato 2012). The same beneficial effects on the germination of their dispersed seeds are also observed in the fruit bat *Eidolon dupreanum* (Picot et al. 2007). However, seeds passed through the guts of the velvet asity *Philepitta castanea* (Rakotomanana et al. 2003) had less successful germination than non-passed seeds. There was no effect of gut-passage on the germination of seeds for those passed by *Eulemur rufifrons* (cited as *E. fulvus*) at the dry forest of Kirindy (Scharfe and Schlund 1996), and the fruit bat *Pteropus rufus* in the littoral forest of Sainte Luce (Bollen and Van Elsacker 2002). Also, Overdorff and Strait (1998) found that none of the five plant species passed by *Eulemur rufifrons* of the rainforest of Ranomafana in the early dry season germinated, whereas Dew and Wright (1998) reported a high proportion of germination for seeds passed by this species in the late dry season. Passage of seeds through guts can also reduce seed predation. For instance, seeds of the genus *Grewia* defecated by *Eulemur rufifrons* (cited as *E. rufus*) in the dry forest of Kirindy were neither preyed on by predators nor removed by secondary dispersers while non-defecated seeds were destroyed by insects and secondarily dispersed by ants (Spehn and Ganzhorn 2000).

Dispersed seeds may also be susceptible to subsequent movement by secondary seed dispersers (e.g., ants, rodents and dung beetles) or by other means (e.g., runoff). Secondary dispersal often significantly changes the patterns of seed deposition, and thus affects plant recruitment success (Vander Wall et al. 2005). For example, secondarily dispersed seeds buried by dung beetles may have a higher seedling establishment than non-removed seeds (Andresen 2001). Scatter-hoarding rodents can also reduce seed spatial clumping as they remove individual seeds into their caches, which may be far from the seed source (Wang and Smith 2002). There are few studies that quantified the rates and effects of secondary dispersal in Malagasy forests, mainly by ants and rodents. In an ant-foraging experiment in Kirindy forest, Böhning-Gaese et al. (1999) observed that *Aphaenogaster swammerdami* increased seed clumping by depositing secondarily removed seeds in piles at the edge of the colony, while *Pheidole* sp. carried seeds into their colony. Also, secondary dispersal by these ant species increased the establishment success of plants, but at a lower magnitude than the activity of primary dispersers. In addition, Voigt et al. (2002) found higher rates of secondary dispersal by ants of *Commiphora* seeds in a Malagasy site compared to a South African site. As for secondary dispersal by rodents, a predator exclosure experiment by Dausmann et al. (2008) showed that up to 100 % of the seeds were removed within seven days, mainly by native rodents. In addition, work by Goodman and Sterling (1996) showed that native Malagasy rodents cache seeds in their burrows, but the effects of caching on seed viability were not quantified. Studies of secondary dispersal can provide us better insights on the pattern of diversity and persistence of some plant species, especially those adapted for dispersal by extinct large-sized frugivores (Jansen et al. 2012). Much research is needed on this aspect in Malagasy forests.

EXTINCT SEED DISPERSERS AND THREATS TO SEED DISPERSAL. Seed dispersal of Malagasy plants may be restricted due to the low diversity of available and effective dispersers, and may be at risk because of the pressures threatening disperser communities. Madagascar's forests have already lost at least 34 large-sized endemic vertebrates, and the extant communities are vulnerable to anthropogenic and climate pressures (Pedrono et al. 2013). The extinct megafauna could have been effective seed dispersers of many native plant species in Madagascar, especially large-seeded species (Crowley et al. 2011, Pedrono et al. 2013). Reconstruction and inference of diet in extinct lemur species demonstrate that most of them were consuming fruits (Godfrey et al. 1997) and were most likely the main primary seed dispersers of large-seeded native trees (Crowley et al. 2013). Also, the extinct large-bodied flightless bird of the genus *Aepyornis* could have been the main seed dispersers of the spiny fruits of *Uncarina* (Midgley and Illing 2009). This endemic plant species has mature fruits with large grapple hooks not adapted for consumption by extant Malagasy vertebrates, but the hooks may adhere to the bird's feet when mature fruits fall on ground (Midgley and Illing 2009). Extinct giant tortoises may have also been important seed dispersers in Madagascar. The Aldabra giant tortoise, currently found on the Aldabra Atoll (400 km north of Madagascar) is thought to be the same, or a subspecies of a giant tortoise now extinct in Madagascar. Hnatiuk (1978) reported that this species has a long gut-retention time and may have been responsible for the introduction of several Malagasy plant species on Aldabra Atoll as a result of transmarine migration from Madagascar. Thus, they may have been active seed dispersers when they inhabited Madagascar as well. A feeding experiment was recently done by Andriantsaralaza et al. (2014), in which Aldabra giant tortoises at Tsimbazaza zoo in Antananarivo, were fed with the fruits of a Malagasy endemic baobab species, which is thought to have no extant seed dispersers. Results supported that this extinct species could have played important role as seed dispersers of this large-seeded plant species by defecating intact and viable seeds.

The decline or loss of dispersers in a community may alter seed dispersal mechanism and subsequent recruitment dynamics (e.g., Cordeiro and Howe 2003) leading to changes in plant community structure. In Madagascar, studies examining the impacts of the absence of dispersers on plant communities are limited. Work by Ganzhorn et al. (1999) in the dry forest of Kirindy shows that forest fragments without *Eulemur rufifrons* had fewer lemur-dispersed trees regenerating than fragments with lemurs, suggesting that forest regeneration in Kirindy depends on the presence of lemur dispersers. With a low diversity of frugivores and a lack of effective dispersers in certain areas (Bleher and Böhning-Gaese 2000), seed dispersal in Madagascar may be at risk, and Malagasy plant communities may be especially susceptible to failures in recruitment and/or regeneration. Moreover, the disappearance of large frugivores

in Malagasy ecosystems could also mean that plants formerly dispersed by megafauna in Madagascar, including large-seeded and seeds with thick husks, are at risk of dispersal limitation with low recruitment success.

CONCLUDING REMARKS AND FUTURE DIRECTIONS

As seed dispersal is crucial for the maintenance of natural forest ecosystems, conservation approaches should consider prioritizing the protection of both plant and animal species involved in this mechanism, and the management of 'high-quality habitats' that are favorable for seedling establishment at the community-level (Farwig and Berens 2012). Approaches for the restoration of degraded and fragmented forests should also incorporate seed dispersal interactions. For example, the restoration of forest fragments in Masoala National Park by the Wildlife Conservation Society, which aimed in attracting seed dispersers to bring forest seed species into the fragments (Holloway 2000), was successful in that regard as *Varecia rubra* were observed depositing seeds in the regenerating forests (Martinez and Razafindratsima 2014). Increasing connectivity of forest fragments via corridors may also encourage the movement of dispersers between fragments and thus enhance their regeneration.

Previous work on seed dispersal in Madagascar has contributed greatly to our understanding of the roles of frugivores as seed dispersers in Madagascar's forests. However, more research is still needed. An important future direction for understanding the importance of frugivore-mediated seed dispersal is to address questions related to the ability of dispersers to replace each other in Malagasy forests given that ecosystem resilience can be mitigated if the extinction of one species could be offset by other species with equivalent ecological services (Walker 1995). Recent work by Pedrono et al. (2013) suggests that the introduction of frugivorous tortoises that are closely related to the extinct Malagasy giant tortoises could help in the restoration of the dispersal of large-seeded species that currently have no known effective dispersers. A similar introduction project of the Aldabra giant tortoises to replace extinct tortoise species on the Mascarene island of Rodrigues has proven success restoring seed dispersal and removing exotic vegetation on the island (ibid).

Work addressing questions related to the disruption of plant-disperser interactions in Madagascar would also lead to a better understanding of the importance of seed dispersal in maintaining plant diversity in Malagasy forests. The long- and short-term impacts of low diversity of seed dispersers on plant communities have rarely been studied, and the repercussions are still unclear (but cf. Bleher and Böhning-Gaese 2000, 2001); however it has been suggested that the loss of frugivores from the ecosystem may have long-term impacts on future forest composition (cf. review in Farwig and Berens 2012).

Another important focus of future studies is to address questions related to understudied taxonomic and functional groups such as birds, nocturnal species, secondary dispersers and granivores (i.e., seed-eating animals). Granivores, such as rodents, are often considered as seed predators since they forage on and masticate ripe seeds; however they can be effective secondary seed dispersers (Forget and Cuijpers 2008), and could maintain the dispersal of large-seeded plant species as they presumably can fill-in partially the role of extinct megafauna as seed dispersers through scatter-hoarding of seeds (Jansen et al. 2012).

Future studies should also be expanded to other regions of Madagascar because the disperser communities we know so far were restricted to a small portion of the forested areas (Figure 1). In addition, long-term studies need to be established and maintained to examine temporal variations in seed dispersal mechanisms and the dynamics of plant recruitment to better improve our understanding of the effects of dispersers on plant populations. We also need to examine plant recruitment at the habitat-level because we cannot make implicit assumptions of disperser effectiveness based solely on their ability to remove seeds away from parent trees and deposit intact and viable seeds. There are abiotic factors and biotic interactions in the environment that could influence the establishment success of deposited seeds depending on where seeds land.

The future research outlined here would form a more comprehensive framework necessary to understand and conserve the critical ecosystem service of seed dispersal by vertebrates in Madagascar. Based on the few published studies, it is clear that the topic area is ripe for further exploration. There is also an urgent need for inter-disciplinary researchers to form collaborative networks to explore mechanisms underlying the patterns of plant diversity in Madagascar, and predict patterns of plant demography and forest dynamics relative to the loss of dispersers.

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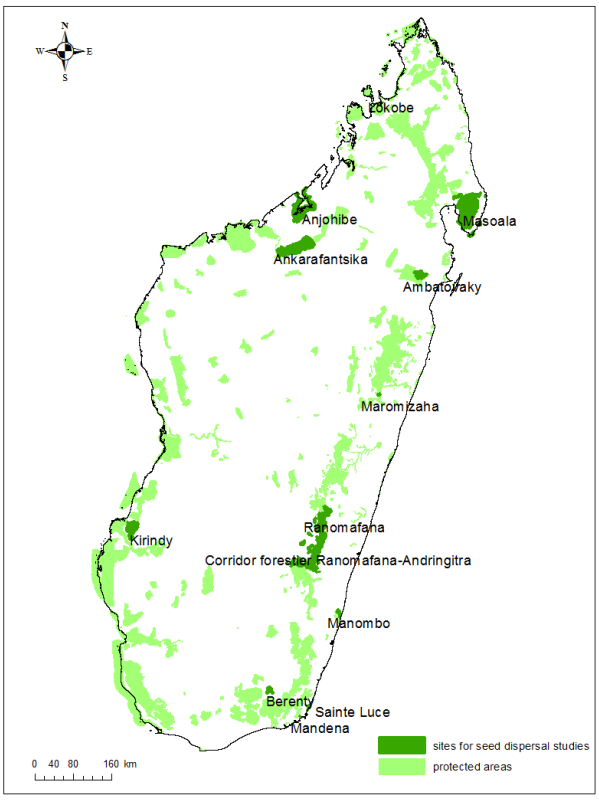

FIGURE 1. Location of sites in Madagascar where seed dispersal studies were conducted (shapefile source: REBIOMA project 2010).

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SUPPLEMENTARY MATERIAL.

AVAILABLE ONLINE ONLY.

TABLE S1. List of known extant vertebrate species in Madagascar with fruits as an important diet item, and their potential roles as primary seed dispersers or predators.

SHORT NOTE

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Extension of gray-brown mouse lemur (*Microcebus griseorufus*) activity period in a disturbed forest in southwestern Madagascar

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ABSTRACT

Habitat disturbances may impact behaviors of animals, including their activity patterns. In southwestern Madagascar, timing of gray-brown mouse lemur activities was investigated in adjacent forests with different levels of human disturbance. Mouse lemurs were encountered more frequently during the second part of the night in the unfenced, more disturbed forest than in the fenced, less-disturbed forest. The extension of mouse lemur activity period in the unfenced forest may be due to differences in forest composition resulting in higher travel costs or a loss of canopy cover which may limit their use of torpor.

RÉSUMÉ

Les perturbations de l'habitat peuvent avoir un impact sur le comportement des animaux, y compris sur leur rythme d'activité. Le déroulement des activités des microcèbes a été étudié dans des forêts adjacentes du Sud-ouest de Madagascar. Une de ces forêts a été protégée du pâturage par une clôture tandis que l'autre ne profitait pas d'un tel dispositif en étant ainsi nettement exploitée par l'Homme et son bétail. Les microcèbes ont été rencontrés plus fréquemment au cours de la deuxième partie de la nuit dans la forêt non clôturée que dans la forêt clôturée. Bien que cette étude n'ait pas permis de détecter des différences dans la disponibilité des insectes ou des fruits, des évaluations plus détaillées de la composition des espèces d'arbres et l'abondance des insectes sont nécessaires pour déterminer l'impact de la qualité nutritionnelle ou de la distribution des ressources sur les rythmes d'activité des microcèbes dans la forêt non clôturée. D'un autre côté, l'allongement de la période d'activité des microcèbes dans la forêt non clôturée peut être lié à une perte de la couverture de la canopée, elle-même à l'origine d'une élévation des températures diurnes dans la forêt non clôturée qui réduirait la durée pendant laquelle les microcèbes pourraient être en torpeur dans cette forêt.

INTRODUCTION

Forest loss, fragmentation, and degradation in Madagascar are threats to its unique biodiversity (Harper et al. 2007). Human activities including hunting of animals, illegal harvesting of plants, and clearing of land for agriculture disturb Malagasy forests (Goodman 2006, Patel 2007, Irwin et al. 2010, Brown et al. 2013). These disturbances degrade forests by altering their structure, affecting resource availability and community composition (Irwin et al. 2010, Brown et al. 2013).

Madagascar's endemic lemurs are tied to forests, yet few studies explore lemur behavioral ecology across disturbance gradients (Irwin et al. 2010). Mouse lemurs (*Microcebus* spp.) are widespread in a variety of forest types including areas of anthropogenic disturbance (Radespiel 2007, Atsalis 2008). Ranging from 30–110 g in body mass (Atsalis et al. 1996, Rasoloarison et al. 2000, Wrogemann et al. 2001), nocturnal mouse lemurs consume an omnivorous diet (Radespiel 2007, Atsalis 2008). In resource-poor seasons, mouse lemurs may enter a daily or extended period of torpor in which they lower their metabolic rate and reduce energy needs (Schmid 2000, Schmid and Speakman 2000, Kobbe and Dausmann 2009).

Mouse lemurs show an array of responses to different habitat disturbances. In western Madagascar, population densities of gray mouse lemurs (*Microcebus murinus*) were lower in a secondary forest than in a primary forest (Ganzhorn and Schmid 1998). Gray mouse lemurs in large forest fragments along the east coast were found to have a higher parasite load if they inhabited a more degraded fragment (Raharivololona and Ganzhorn 2009). Mouse lemurs (*M. rufus* and *M. lehilahytsara*) from eastern rainforest localities had stable isotope values that suggested a shift toward a more faunivorous diet in fragments and degraded habitats (Crowley et al. 2013) and gray-brown mouse lemurs (*M. griseorufus*) in the southeast reduced gum feeding and increased insect feeding in disturbed forests (Rasoazanabary 2011).

Habitat degradation may also impact the activity pattern of mouse lemurs. Resources may be spaced further apart in degraded habitat, causing mouse lemurs to increase their ranges and activity period to obtain sufficient resources. Alternatively, because mouse lemurs can reduce their energy needs through the use of torpor, they may shorten their activity period. During a 1.5 month study during the dry season at the Beza Mahafaly Special Reserve (BMSR) in southeastern Madagascar, I assessed whether the activity period of gray-brown mouse lemurs (*Microcebus griseorufus*) varied in two adjacent deciduous forests with differing disturbance levels.

METHODS

Parcel 1 of BMSR is approximately 80 hectares in size and bordered on one side by the ephemeral Sakamena River (Figure 1).

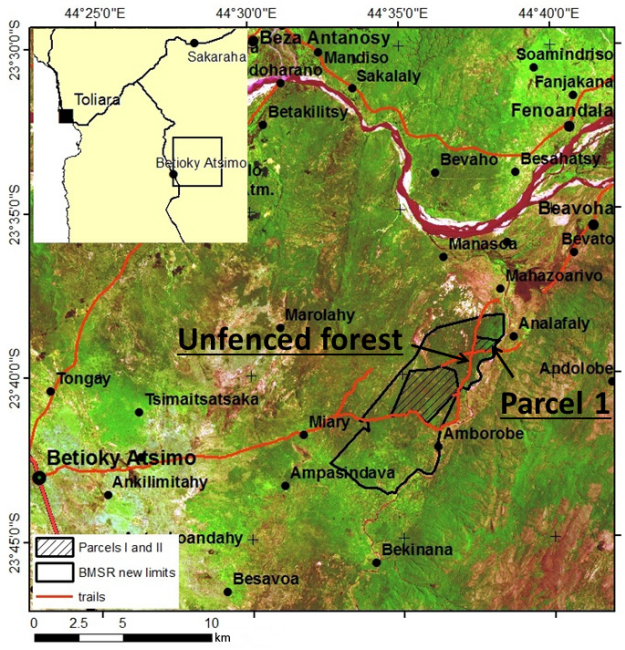

FIGURE 1. Beza Mahafaly Special Reserve with locations of Parcel 1 and the unfenced forests highlighted. Map modified from <http://bezamahafaly.commons.yale.edu/en/maps-and-direction/>

Because of its proximity to the river, soils in the eastern side are moister and support a gallery forest (Sussman and Ratsirarson 2006, Axel and Maurer 2011). Moving west from the river the soils become drier and the forest composition transitions to dry deciduous forest (ibid). This parcel is relatively undisturbed as it is protected from grazing animals by a perimeter fence (Sussman and Ratsirarson 2006). Grazing animals occasionally enter Parcel 1 when fences are down (pers. observ.) or they are hidden in the reserve by local villagers to protect the animals from thieves (Youssouf and Rasoazanabary 2008). Minor disturbances come from a 100 m x 100 m grid of footpaths created for researchers and also used by local villagers for travel. Local villagers also enter the reserve for occasional collection of fruits (Rasoazanabary 2011).

The neighboring forest (approximately 850 hectares) is located between Parcel 1 and Parcel 2 (Axel and Maurer 2011). Separated from Parcel 1 by the intersection of two dirt roads, this dry deciduous forest is similar to the adjacent western edge of Parcel 1 (ibid). The boundaries of BMSR were recently extended to include this forest; however no perimeter fence protects it. Grazing by goats and cattle in this forest is common and trees have been cut down so that browsing animals can feed on their leaves. Numerous oxcart trails, footpaths, and corral clearings are found in this forest. Because the protected Parcel 1 and this unfenced forest are only separated by the road intersection, variables such as local weather conditions and noise disturbances from the roads are similar.

Between 1 June and 10 July 2011, a six-person research team examined forest structure, food availability, and mouse lemur behaviors in Parcel 1 and the unfenced forest. To compare forest structure between the two forests, we established three transects approximately 1 km in length in the unfenced forest. Transects paralleled each other, running due west from the road, with 200 m between each transect. In Parcel 1, I selected three established trails from the existing gridded trail system. As with the transects constructed in the unfenced forest, the selected trails were approximately 1 km in length running east-west from the river, parallel, and separated by 200 m. I selected trees along transects in the unfenced forest and established trails in Parcel 1 every 50 m and recorded their dbh (diameter at breast height) and height.

Weekly sampling of food abundance took place during the last four weeks of the study. Sampled trees along transects and trails were marked with flagging tape and examined for the presence or absence of fruits, flowers, immature or mature leaves. In order to compare insect abundance, sweep net sampling using a 33 cm diameter net was conducted at three 10 m x 10 m plots along trails and transects in both forests. Beat traps were also set under trees within these plots. Total number of insect captures was tallied for each forest.

The research team conducted 246 hours of walks in Parcel 1 and the unfenced forest to locate mouse lemurs. Walks were evenly distributed throughout the night, with half of the walks occurring between 1800 and 2400 and the other half between 2400 and 0600. At a pace of approximately 2 km per hour, researchers traveled on trails, transects, clearings, and animal paths while using their headlamps to scan the forests for mouse lemurs. When mouse lemurs were located, we recorded the time and their behaviors using continuous focal sampling until they went out of sight.

I examined variation in forest structure and resource availability between the two forests using a proportions t-test. A chi-square test was used to determine: i) if the total number of insects captured in each habitat differed and ii) if differences existed in the number of encounters with mouse lemurs between Parcel 1 and unfenced forest throughout the night. I used only the time and behavior of a mouse lemur upon initial encounter to avoid oversampling the behaviors of well-habituated mouse lemurs. The level of significance for all analyses was set at $p < 0.05$.

RESULTS

The trees in the unfenced habitat were smaller and shorter on average than trees in Parcel 1 in terms of dbh (Parcel 1_{Mean} = 17.5 cm, n =70, SD = 23.3 cm; $Unfenced_{Mean}$ = 12.6 cm, n = 66, SD = 16.3cm) and tree height (Parcel 1_{Mean} = 8.1 m, n = 70, SD = 5.5 m; $Unfenced_{Mean}$ = 5.0 m, n = 66, SD = 2.2 m), but these differences were not significant. Although the presence of mature and immature leaves declined in both forests during this study, a higher percentage of trees in Parcel 1 contained both mature and immature leaves in comparison to the unfenced habitat during three of the four weeks of surveys (week 1: t-1 = -3.104, df = 95, p = 0.001; week 2: t-1 = -1.588, df = 77.8, p = 0.059; week 3: t-1 = -1.735, df = 92.6, p = 0.043; week 4: t-1 = -1.674, df = 107.7, p = 0.048). The total number of insects captured in both habitats was low (Parcel 1_n = 20; $Unfenced_n$ = 15) and did not differ significantly between habitats (chi-square = 0.7, df = 1, p = 0.4). Abundance of trees producing fruits or flowers in both forests was low (n < 3) during each week of sampling for each forest and precluded statistical testing.

The frequency of mouse lemur encounters in both forests was similar before midnight when they were encountered 206 times in Parcel 1 and 193 times in the unfenced forest (chi-square = 0.424, df = 1, p = 0 .515). Upon initial encounter, mouse lemurs in Parcel 1 traveled most frequently (49% of initial encounters), followed by resting (28% of initial encounters),

foraging (21% of initial encounters), and other (2% of initial encounters). Those in the unfenced habitat also traveled most frequently (43% of initial encounters), followed by resting (39% of initial encounters), foraging (15% if initial encounters), and other (3% of initial encounters).

After midnight, mouse lemurs in the unfenced habitat were encountered more frequently (n = 210) than mouse lemurs in Parcel 1 (n = 137) (chi-square = 15.357, df = 1, p = 0.001). After midnight, mouse lemurs in Parcel 1 traveled in 43% of initial encounters, rested in 39%, foraged in 17%, and engaged in other behaviors in 1%. Mouse lemurs in the unfenced forest traveled in 44% of initial encounters, rested in 32%, foraged in 23%, and engaged in other behaviors in 1%.

DISCUSSION

In both forests, mouse lemurs were encountered at similar frequencies before midnight. This suggests that a similar number of individuals are roused from torpor to commence traveling and foraging in both forests. After midnight, mouse lemurs in the unfenced habitat were encountered more frequently. Mouse lemurs in the unfenced forest may have been more visible to our research team, however, similar encounter frequencies in both forests before midnight argue against this sample bias. The lower encounter frequency with mouse lemurs in Parcel 1 suggests that many individuals retreat to sleeping nests after midnight while those in the unfenced habitat continue their activity period. This study builds on the work of Rasoazanabary (2011) who documented a higher percentage of active nights for mouse lemurs in another disturbed forest (Ihazoara) near BMSR. An extension of the activity period for mouse lemurs in disturbed forests may contribute to the activity increase observed by Rasoazanabary.

Mouse lemurs in Parcel 1 may be more efficient at foraging, allowing them to retreat to nests earlier in the night. There may be greater food availability in Parcel 1 or lower travel costs due to differences in forest structure between Parcel 1 and the unfenced forest. The similar percentages of time spent traveling by mouse lemurs in both forests argues against differences in travel costs, but more extensive follows of mouse lemurs in each forest are necessary to fully evaluate this. My limited dataset suggest low levels of insects, fruits, and flowers in both forests during this dry season study. However, more extensive phenological monitoring and assessments of plant species composition in the forests, including abundance of trees utilized for gums, are needed. Lower nutritional quality based on differences in tree species composition in each forest may underlie the extension of activity period.

Additionally, higher levels of leaf availability may explain the activity pattern of mouse lemurs in the unfenced habitat. The greater leaf availability in Parcel 1 suggests that more of this forest is shaded throughout the day. Because of a reduction in leaf availability, mouse lemur tree holes in the unfenced forest are likely exposed to more solar radiation during the time of the year when trees have their lowest insulative capacities (Schmid 1998). As a result, tree holes in the unfenced forest may exceed the temperature threshold above which mouse lemurs terminate torpor (Schmid 1998) at earlier times in the day. Because torpor results in energetic savings due to reduced metabolic activity (Schmid and Speakman 2000, Kobbe and Dausmann 2009), mouse lemurs in Parcel 1 may remain in energy-saving torpor longer while those in the unfenced forest are roused from torpor and return to a more active metabolic state earlier in the day. Thus, energy costs may be higher for mouse lemurs in the unfenced habitat, forcing them to remain active longer. Further information regarding daytime temperatures in tree holes in both unfenced and Parcel 1 habitats at BMSR as well as assessments of mouse lemur body temperatures and timing of arousal from torpor in these habitats are needed to test this hypothesis.

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