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Drivers of present and lifetime natural resource use in a tropical biodiversity hotspot

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Abstract

Effective biodiversity conservation requires an understanding of the drivers of natural resource use. Few studies, however, have examined how motivations of natural resource users and attributes of local social organizations affect resource extraction over time. We aimed to identify which characteristics of individuals (taboos, food security, resource-related income), groups (village size, ease of access to education, proximity to park), and institutions (presence of enforcement mechanisms) best predicted use of multiple types of natural resources near a protected area during the past 1.5 years and during respondents' lifetimes. Data were collected in 2013 via semi-structured interviews with 360 people across ten villages along the perimeter of Ankarana National Park (northern Madagascar). All recent and lifetime uses of natural resources examined were higher in villages close to the park and for respondents with a history of earning money from extracting natural resources. In addition, individuals with ancestral meat-related taboos were less likely to have extracted natural resources over their lifetime, while individuals who recently consumed meat were more likely to have extracted natural resources over the past 1.5 years. All other variables were less important in explaining the use of natural resources. The results highlight that some drivers can be consistently important in predicting natural resource use and that simple models can have relatively high explanatory power even in the context of the (sometimes) illegal extraction of five different types of natural resources.

Introduction

The unsustainable anthropogenic use of natural resources is a major cause of global biodiversity loss and habitat degradation (Dirzo & Raven, 2003). Natural resource use, particularly biological resource use (hunting and collecting animals, gathering plants, logging; IUCN, 2016), has led to a decrease in local biodiversity through habitat loss, fragmentation, and degradation (Fahrig, 2003; Lamb, Erskine & Parrotta, 2005; Wright, 2005); hunting (Wilkie *et al.*, 2011); and deterioration of forest ecosystems (Gorchov *et al.*, 1993; Medellin & Gaona, 1999; Kunz *et al.*, 2011). Areas of high anthropogenic natural resource use often overlap with areas of high biodiversity (Brooks *et al.*, 2002). Therefore, effective biodiversity conservation requires an understanding of the drivers of natural resource use (Scales, 2014).

Natural resource use is complex (Solomon, Gavin & Gore, 2015), encompassing both large-scale extraction of a single resource (e.g. industrialized logging) and small-scale, multi-actor extraction (e.g. Kremen *et al.*, 2000). Natural resource use takes place in a complex economic, geographic, political, and cultural landscape and is influenced by economic vulnerability (Lindsey *et al.*, 2013), cultural values (deFrance, 2009), movement of people (Poulsen *et al.*, 2009), and legal context (Lindsey *et al.*, 2013). Natural resource use can sometimes be mitigated, such as via the development of alternative livelihoods and ecotourism (Vos *et al.*, 2016).

Past research on the drivers of natural resource use has often been contradictory (Table 1), partly because the motivations for natural resource use can vary within and between individuals, and change over time in different contexts (Kollmuss & Agyeman, 2002; Kahler & Gore, 2012). While recent studies have begun to evaluate multiple drivers of resource extraction (e.g. Arias *et al.*, 2015), many do not consider drivers of natural resource use at different levels of social organization (individual level; group level such as via social norms; institutional level such as via governance bodies, Manfredo *et al.*, 2014).

Improved understanding of the drivers of natural resource use are needed in biodiversity-rich areas, like Madagascar, that are experiencing rapid anthropogenic habitat change. In Madagascar, 90% of the population lives on <2 USD per day

Table 1 Predictor variables included in at least one of the top-ten ranked models for the four dependent variables (Table 3)

Predictor variable	Indicator	Description	Rationale and Hypothesis
Institutional characteristics			
MnpAg	Enforcement of natural resource laws	Whether there were Madagascar National Parks (MNP) agents stationed in the village (categorical presence/absence variable)	Inadequate enforcement can be a driver for illegal hunting (Lindsey *et al.*, 2013). We hypothesized that villages with MNP agents permanently assigned to the village would have lower extraction rates.
Characteristics of the local village			
DistBou	Distance to natural resources	Distance of the respondent's village from the national park boundary (continuous variable: 0–9.5 km)	Hunting has been shown to be lower (Nuno *et al.*, 2013) or not change (Mackenzie *et al.*, 2011) with distance from the park boundary. Given the low amount of natural resources remaining outside park boundaries in the Ankarana National Park (Gudiel *et al.*, 2016), however, we hypothesized extraction would increase closer to the park boundary.
SecSch	Public services	Whether there was a secondary school present in the village (categorical presence/absence variable). Proxy for public services available to individuals in the village as this correlated with the presence/absence of having a paved road in a village.	Higher education levels have been found to increase prevalence of hunting (Nuno *et al.*, 2013) and more income-generating activities from natural resources (Mackenzie *et al.*, 2011). However, around the Ankarana National Park, secondary schools (and other public services, like wells) have been given to communities as in-kind compensations by MNP. Therefore, we predicted that villages with secondary schools would have lower extraction rates.
Characteristics of the individual respondent			
DivCon	Wealth/social status	Number of types of meat consumed in the past 3 days (scale 0–3), inclusive of both domestic and bush meat. Proxy for individual wealth and social status.	We treated the ability to consume different types of meats as a proxy for individual wealth and social status. Given that poverty has been described as driver for illegal natural resource use (Lindsey *et al.*, 2013), we hypothesized that individuals with the ability to consume different types of meats (as opposed to just one type of meat) would be less likely to illegally extract natural resources.
DivPur	Wealth/social status	Number of types of meat purchased in the past 3 days (scale 0–3). Proxy for individual wealth and social status.	We treated the ability to purchase different types of meats as a proxy for individual wealth. Given that poverty has been described as driver for illegal natural resource use (Lindsey *et al.*, 2013), we hypothesized that individuals with the ability to purchase meat would be less likely to illegally extract natural resources.
Meat	Food security	Whether the respondent had eaten meat in the past 3 days (categorical presence/absence variable). Proxy for food security.	We treated 'access to meat' as a proxy for food security (Reuter *et al.*, 2016*b*). Protein shortages have been described as a driver for illegal hunting (Lindsey *et al.*, 2013; Borgerson *et al.*, 2016). We predicted that individuals without access to meat in the 3 days prior to the interview would be more likely to extract natural resources.
SoldRe	Income	Whether the respondent had ever sold natural resources (scale of 0–6 for six different types of natural resources with one point given to a respondent if he/she had ever sold one of six different types of natural resources).	We hypothesized that respondents with a history of making money from natural resources would be more likely to extract them than their peers (Lindsey *et al.*, 2013).

Table 1 Continued.

Predictor variable	Indicator	Description	Rationale and Hypothesis
Taboos	Taboo	Whether the respondent had meat-related taboos (categorical presence/absence variable)	Taboos in Madagascar typically restrict or prohibit certain acts for cultural or religious reasons as well as to avoid supernatural repercussions (Jones *et al.*, 2008). Food-related taboos can be against wild or domestic animals. We hypothesized that individuals with taboos would be less likely to hunt animals.
TabAn	Taboo/ethnicity	Whether the respondent had meat-related taboos due to ancestral reasons (categorical presence/absence variable)	Taboos in Madagascar typically restrict or prohibit certain acts for cultural or religious reasons as well as to avoid supernatural repercussions (Jones *et al.*, 2008). Food-related taboos can be against wild or domestic animals. We hypothesized that individuals with ancestral taboos would be less likely to hunt animals and extract other natural resources.
TabDom	Taboo	Whether the respondent had taboos against any type of domestic meat (categorical presence/absence variable)	Taboos in Madagascar typically restrict or prohibit certain acts for cultural or religious reasons as well as to avoid supernatural repercussions (Jones *et al.*, 2008). We hypothesized that individuals against domestic meats would be more likely to hunt and extract wild animals and other natural resources.

Other variables were measured and considered but excluded from analyses and from this table as they correlated with each other.

(World Bank, 2013) and natural resources wood (Innes, 2010), non-timber forest products (NTFPs; Novy, 1997), mining (Walsh, 2005), and animals (Golden *et al.*, 2011) – are regularly extracted for personal use, cultural reasons, and economic gain (Reuter *et al.*, 2016*a*,*b*). Extraction occurs legally and illegally, inside and outside protected areas (Reuter *et al.*, 2016*a*,*b*), involving people of different ethnicities, religions, and socioeconomic backgrounds (Walsh, 2005; Innes, 2010; Golden *et al.*, 2011). Natural resource use behaviors are not static (e.g. illegal logging increased following the 2009 coup d'état; Innes, 2010) and extraction is often considered unsustainable (Walsh, 2005; Innes, 2010; Golden *et al.*, 2011).

This study identifies individual, group, and institutional characteristics important for predicting natural resource use near a protected area over time. We used Ankarana National Park (northern Madagascar) as a case study, focusing on several types of natural resource use (wood extraction, hunting and mining). Based on past studies (Table 1), we aimed to understand how characteristics of the individual respondent, the respondent's group, and local institutions would influence reported rates of natural resource use both in the recent past and over respondents' lifetimes.

Materials and methods

Study site

Surveys were conducted in villages along the Ankarana National Park perimeter (*a priori* defined as within 10 km of the park boundary, Gilles & Reuter, 2014) in May–June 2013 (Table 2). The park was established in 1956 as a *Réserve Spéciale* (Cardiff & Befourouack, 2003), is the fifth-most visited park in Madagascar (Christie & Crompton, 2003), and had 13,730 visitors in 2012 [Madagascar National Parks (MNP), pers. comm.]. Park boundaries and the prohibitions against natural resource use within these boundaries have not changed substantially since establishment (more information regarding the park's history presented in Appendix S1).

Economic opportunities include farming for rice and cash crops, ranching, ecotourism (near the main park entrance, eastern side of the park) (Gezon, 1997; Walsh, 2005), and the extraction of natural resources including the mining/sale of sapphires (near the north-eastern section of the park, Walsh, 2005), harvest/sale of wood (Gudiel *et al.*, 2016), wild meat (Reuter *et al.*, 2016*b*), and other NTFPs (medicinal plants, K. E. Reuter, pers. obs.). The local population is predominantly of the Antankarana ethnic group (Gezon, 1997); villages on the eastern border now include substantial numbers of other Malagasy ethnic groups that have immigrated due to the sapphire mining trade and ecotourism (Walsh, 2005).

Interviews during a pilot study in 2012 with 79 individuals in three of the villages (Appendix S2) indicated that communities differed in perceptions of the presence of conflict between the communities and the protected area, community involvement in the park, factual knowledge about the park and about conservation, and that perceptions of the park were more negative at farther distances from the main park entrance (Table S1). Of those who perceived a conflict between the communities and the protected area, the cause was often identified as prohibitions on natural resource use within park boundaries (Appendix S2). Data from interviews in 2012 are not included in subsequent analyses.

Natural resource use

This study focused on five common types of natural resource extraction: wood extraction for (1) firewood, (2) construction, and (3) charcoal production; (4) hunting of animals; and (5) sapphire mining. These are illegal to use/extract within park boundaries, which is often clearly marked (communities know it is illegal to use resources inside the boundary, Gilles & Reuter, 2014). The use of these resources is also prohibited in unmarked buffer zones that include forests adjacent to and outside of park boundaries, as part of agreements between the park and local communities (MNP, pers. comm.). MNP agents are stationed in several villages near the park or buffer zones. MNP manages natural resources in the park and buffer zones, setting rules and restricting access, and patrolling for evidence of illegal resource use.

Survey materials

Data were collected using semi-structured interviews (Rietbergen-McCracken & Narayan, 1998). Survey materials and sampling design were approved by the Temple University Institutional Review Board (Protocol Number: 21414, May 2013). Surveys were authorized by the Madagascar Ministry of Environment, Waters and Forests and MNP. Individuals were asked about their natural resource extraction and purchase within the protected area and along the perimeter. Individuals were asked about the location in which extraction or purchase had taken place, to ascertain whether such activities took place within 10 km of the protected area. Survey materials can be found in Appendix S3. Natural resource extraction within the park is illegal; natural resource extraction along the perimeter of the park is sometimes illegal. Therefore, respondents may have under-reported their extraction of natural resources.

We interviewed 360 people across 10 villages (Table 2). Some villages were located near two of the three official park entrances. Villages were spread evenly along the west, north, and east sides of the park and were broadly representative of all villages bordering the park in terms of distance from the park boundary, village population (the largest and some of the smallest towns on the perimeter, Table 2), and access to infrastructure. Time and resources limited surveys along the southern park perimeter.

Interviews lasted 7.5 ± 0.3 min (mean $\pm$ 95% CI). Households were sampled systematically (as in Reuter *et al.*, 2016*a*,*b*), sampling every fifth household in smaller communities and with random sampling stratified by administrative unit in the largest community (Town D, Table 2). One person per household was interviewed. Researchers received permission to conduct interviews from the highest-ranking, locally elected official, who then announced the researchers' presence to the village. Thereafter, face-to-face recruitment methods were used, whereby researchers approached households and requested permission to interview the head-of-households (males and females with major buying power for household goods). Individuals were informed that they could decline to participate or answer any question asked, or end the interview; informed consent was received prior to the interview's start. If an eligible individual refused or if no one was present, we moved on to the next household. Only adults (18+ years) were interviewed; respondent gender was not recorded and therefore not controlled for in analyses. Respondents typically provided information for their entire household. No identifying information was collected. We did not track whether individuals involved in pilot interviews (in 2012) were also interviewed in 2013. Interviews were completed by a team of two people (one international researcher; one Malagasy translator not known to the respondents) in the interviewee's language of choice (French or the local Malagasy dialect). Most interviews were conducted in the local Malagasy dialect; some interviewees partially answered questions in French.

Table 2 Characteristics of communities surveyed in 2013

Village	Interview sample size	Village population	Distance from park boundary (km)
A	30	2500–3000	0.90
B	30	1500–2000	2.82
C	34	1500–2000	0.00
D	90	3000+	9.50
E	30	100–500	0.63
F	29	100–500	0.50
G	28	100–500	2.99
H	30	100–500	0.57
I	29	100–500	3.95
J	30	100–500	4.04

Villages are identified using codes, to protect the anonymity. The population of each village is depicted as a range in this table in order to protect anonymity.

Analysis

We ran generalized linear models on the 2013 data with a Gamma distribution, accounting for over-dispersion, and a log-link function, to examine which factors potentially affected reported rates of natural resource use. We examined four different response variables: Direct Lifetime Use, Direct Recent Use, All Lifetime Use, and All Recent Use. Direct use was the respondent's history of personally extracting natural resources from within the protected area and its perimeter. Indirect use also included acquisition of natural resources from another individual who sourced them from the protected area and its perimeter. Lifetime use was any use during the respondent's lifetime. Recent use was during the ~1.5 years before interviews were conducted.

Dependent variables were calculated as indices (Appendix S4). Direct Use Indices were calculated by summing the following estimates of natural resource extraction for each respondent: (1) number of trees cut down for one housing project; (2) number of trees cut down per year for charcoal; (3) number of times trees were cut down per year for commercial timber; (4) number of trips/year into the park to dig sapphires; and (5) the number of wild animals caught per year. The All Use indices summed: (1) all of the estimates of natural resource extraction included in the Direct Use Indices; (2) the number of trees purchased for one housing project; (3) the number of trees purchased per year to make charcoal; (4) the number of times trees were purchased per year for commercial timber; (5) the number of large (50 kg) bags of charcoal purchased per year; (6) the number of times sapphires were purchased per year; and (7) the number of wild animals purchased per year. After summing natural resource extraction by respondent, indices were scaled from 0 to 1 prior to analyses; data were not otherwise transformed during the summing or scaling of indices. Additional details on the calculation of indices are in Appendix S4.

We determined Spearman's rank correlations among variables and only retained the predictor variables that were not strongly correlated ($r < 0.80$) or that were most important in explaining natural resource use. Predictor variables are listed in Table 1.

We used an information theoretic approach and applied model selection based on Akaike's information criterion (AICc), followed by multimodel inference and averaging (Burnham & Anderson, 2002) implemented in the R (version 3.1.0) package glmulti (Calcagno & de Mazancourt, 2010). We assessed each model's relative probability, and its structural goodness of fit using AICc weights and the per cent of deviance explained by the model. The relative importance of each predictor variable was measured as the sum of the Akaike weights over the six top-ranked models containing the parameter of interest (Conroy & Brook, 2003). We excluded interaction terms as they made the models less stable and did not change interpretation of coefficients. We validated the top-ranked model by using leave-one out cross-validation, which is used to estimate the mean model-predictor error by successively omitting one observation from the training dataset and using it for validation.

Results

We measured extraction and purchase rates and other data regarding five types of natural resource use within the park and the perimeter (Tables S2 and S3). Natural resource use was high in all towns interviewed; 71 ± 7% of respondents had directly extracted natural resources at least once in the park or its perimeter, though this differed significantly by town (Pearson chi-square, d.f. = 9, $\chi^2 = 33.718$, $P = 0.0001$; Table S2). Not all respondents extracted all types of natural resources; the per cent of respondents who had extracted natural resources differed by the type/use of natural resource (Table S2).

Table 3 Top-ranked generalized linear models testing potential predictors of natural resource use for 360 respondents across ten villages

Model	No. of variables	AICc	ΔAICc	w_i
Direct Lifetime Use				
1 + 2+7 + 8	4	−244.31	0	0.25
1 + 3+7 + 8	4	−243.39	0.91	0.16
1 + 7+8	3	−243.29	1.02	0.15
1 + 7+8 + 9	4	−242.86	1.44	0.12
1 + 4+7 + 8	4	−242.52	1.79	0.10
1 + 5+7 + 8	4	−242.36	1.94	0.10
Direct Recent Use				
1 + 3+7 + 8	4	−169.14	0	0.29
1 + 2+7 + 8	4	−168.72	0.42	0.23
1 + 3+7	3	−167.37	1.77	0.12
1 + 7+8	3	−167.15	1.98	0.11
1 + 2+7	3	−166.31	2.82	0.07
All Lifetime Use				
1 + 2+5 + 7+8	5	−262.61	0	0.26
1 + 2+4 + 7+8	5	−262.51	0.10	0.24
1 + 2+7 + 8	4	−261.87	0.74	0.18
1 + 2+7 + 8+10	5	−261.72	0.89	0.16
1 + 3+7 + 8	4	−260.39	2.22	0.08
1 + 2+7 + 10	4	−258.03	4.59	0.03
All Recent Use				
1 + 3+7 + 10	4	−200.62	0	0.15
1 + 3+7 + 8	4	−200.62	0	0.15
1 + 3+5 + 7	4	−200.16	0.46	0.12
1 + 2+7 + 8	4	−200.16	0.47	0.12
1 + 3+6 + 7	4	−200.12	0.50	0.11
1 + 3+7	3	−199.97	0.65	0.11

Results of model selection (ΔAICc < 2), with corrected Akaike's information criterion (AICc) and Akaike weights (w_i). The values are derived from model averaging and multimodel inference based on the best-ranked models according to AICc.

1, DistBou: distance of the respondent's village to the park boundary; 2, DivCon: number of types of meat consumed in the past 3 days; 3, DivPur: number of types of meat purchased in the past 3 days; 4, Meat: whether the respondent had eaten meat in the past 3 days; 5, MnpAg: whether there were Madagascar National Park agents stationed in the village; 6, SecSch: whether there was a secondary school present in the village; 7, SoldRe: extent to which the respondent had ever sold natural resources (scale of 0–6); 8, TabAn: whether the respondent had meat-related taboos due to ancestral reasons; 9, TabDom: whether the respondent had taboos against any type of domestic meat; 10, Taboos: whether the respondent had any type of meat-related taboo.

According to model selection and multimodel inference among the candidate models, the best overall predictors for explaining Direct Use and All Use within the park and its perimeter were the distance of the respondent's village from the park boundary and a respondent's history of selling natural resources (Table 3; Fig. 1). The distance of the respondent's village from the park boundary had a negative sign, indicating that natural resource use was higher in villages in closer proximity to the park boundary. The respondent's

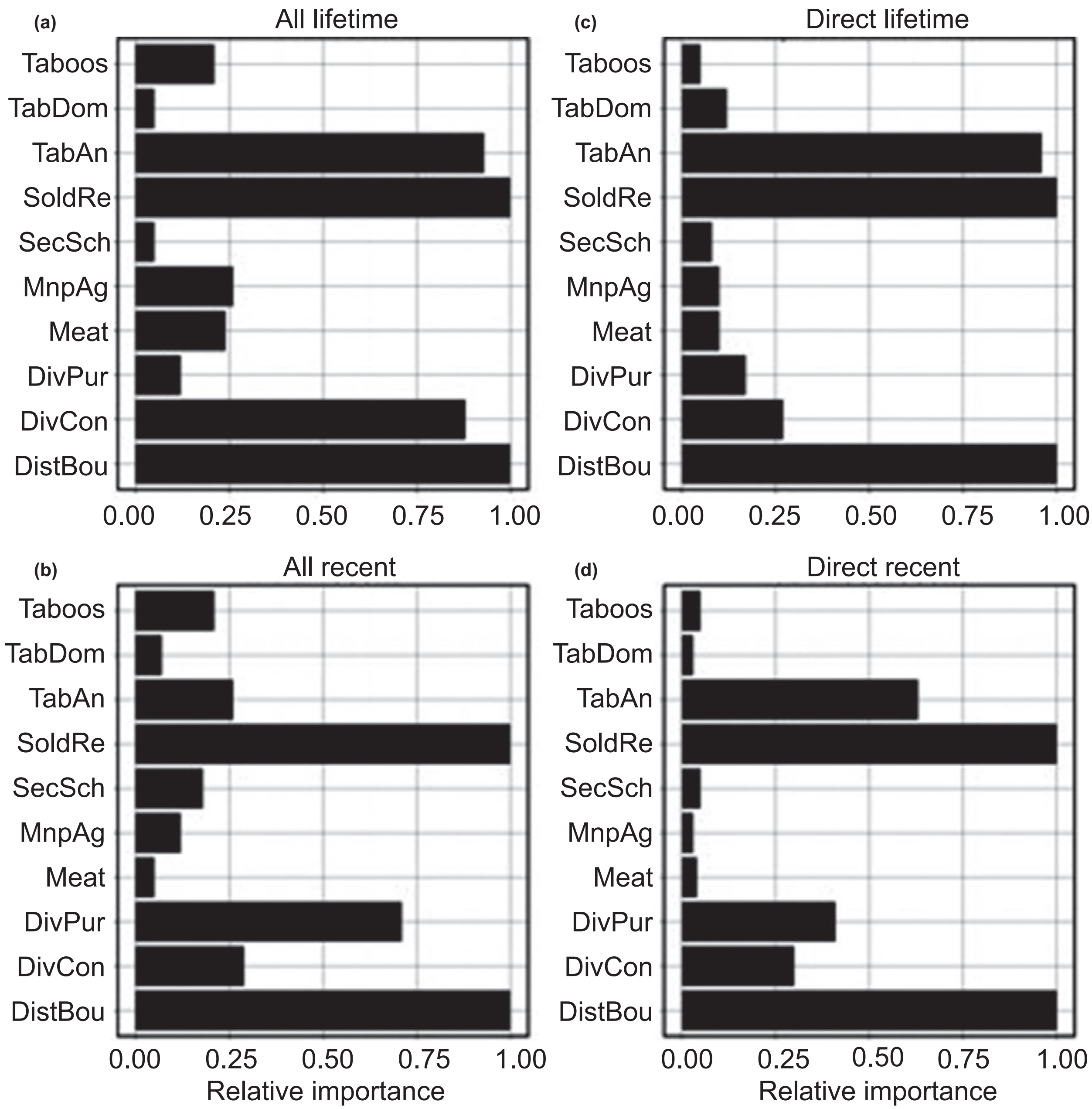

Figure 1 Relative importance of variables in predicting natural resource use, including: (a) All Lifetime Use – respondent has personally extracted or purchased natural resource anytime in his/her lifetime; (b) All Recent Use – respondents has personally extracted or purchased natural resources in 1.5 years prior to the interview; (c) Direct Lifetime Use – respondent personally extracted resources anytime in his/her lifetime; and (d) Direct Recent Use – respondent personally extracted resources in 1.5 years prior to the interview. DistBou: distance of the respondent's village to the park boundary; DivCon: number of types of meat consumed in the past 3 days; DivPur: number of types of meat purchased in the past 3 days; Meat: whether the respondent had eaten meat in the past 3 days; MnpAg: whether there were Madagascar National Park agents stationed in the village; SecSch: whether there was a secondary school present in the village; SoldRe: extent to which the respondent had ever sold natural resources (scale of 0–6); TabAn: whether the respondent had meat-related taboos due to ancestral reasons; TabDom: whether the respondent had taboos against any type of domestic meat; Taboos: whether the respondent had any type of meat-related taboo. The values are derived from model averaging and multimodel inference based on the best-ranked models according to Akaike's information criterion (AICc). Higher values indicate higher importance of the factor.

history of selling natural resources had a positive sign, indicating that respondents with a more extensive history of earning money from natural resources would be more likely to extract natural resources. Other important predictor variables varied according to the response variable (Table 3; Fig. 1). Ancestral taboos were important in the lifetime use of natural resources and in Direct Recent Use of natural resources (Fig. 1). Specifically, individuals with ancestral taboos were less likely to hunt animals and extract other natural resources. The number of types of meat consumed in the past 3 days was another important predictor for All Lifetime Use and the number of types of meat purchased in the past 3 days was important for All Recent Use (Fig. 1). These variables had a positive sign, meaning that respondents who had consumed or purchased different types of meats had extracted or purchased more natural resources. All other predictor variables (Table 1) were less important (Table 3; Fig. 1).

The top-ranked models had an AICc weight of 0.25, 0.29, 0.26 and 0.15 for each response variable, respectively (Table 3). The per cent of deviance explained for the top-ranked models was 58.3%, 64.1%, 60.4% and 52.3% implying good explanatory power of these models, but also suggesting that other factors beyond those evaluated here also influence natural resource use. Using the 10-fold cross-validation, our top-ranked models had a mean prediction error of 28% (Direct Lifetime Use), 36% (Direct Recent Use), 27% (All Lifetime Use), and 31% (All Recent Use), which was comparable to the per cent of deviance explained.

Discussion

This study provides evidence that the income generated from natural resource extraction (an individual characteristic) and proximity to protected area boundaries (group characteristic) are the most important predictors of natural resource use. Secondary variables related to natural resource extraction included the ability for respondents to purchase and consume meat (both interpreted as proxies for wealth, though other relationships between meat purchase/consumption and natural resource use are possible) and ancestral taboos. This study also provides evidence that ongoing enforcement and infrastructure development initiatives (e.g. school buildings, such as those provided by MNP to communities) may not be adequate for reducing natural resource use in the park at current levels of effort; proxies for these two initiatives did not strongly predict natural resource extraction (Fig. 1).

Most survey respondents (71 ± 7%) had extracted natural resources from within the park/perimeter before. This is not surprising given the proximity of the communities to the protected area and that the cost to procure natural resources from unprotected areas can be significant (Emerton, 1999). The problem of ongoing natural resource use is not unique to our study site. In East Africa, almost 50% of national parks – where all resource use is forbidden – were ineffective at maintaining or increasing forest area (Pfeifer *et al.*, 2012). Nevertheless, in countries like Madagascar, where much of the primary vegetation has been removed, protected areas will continue to be advocated (e.g. Lemur Action Plan, Schwitzer *et al.*, 2014) as one of the more effective methods of biodiversity conservation (Bruner *et al.*, 2001).

A history of income generation from natural resources correlated positively with their continued extraction. This may reflect the dependence that some (particularly poorer) households had on the protected area for income (in the absence of alternative livelihoods; Walsh, 2005). But, this variable may obscure nuances in the link between wealth and natural resource-related income generation. For example, sapphires are extracted for money-making only, whereas wood and meat are extracted for consumption and sale. Studies from Cambodia and South Africa suggest patterns of natural resource use vary by socio-economic status (Ender, 2016; Shackleton & Shackleton, 2006).

Extraction of natural resources from the park and perimeter decreased at greater distances from the park boundary. This may be because there are relatively few resources remaining outside the park (Gilles & Reuter, 2014; Gudiel *et al.*, 2016). Villages more distant from the park boundary, however, did not simply shift their extraction away from the park perimeter. With the exception of wood cut for construction, 100% of all other natural resource extraction reported by respondents in this study occurred within the park perimeter (albeit at decreasing levels with increasing distance from the park boundary, Table S2). Distance from a park boundary does not have a consistent relationship with natural resource extraction; extraction can first increase and then decrease with distance (Nuno *et al.*, 2013) or not correlate with distance at all (Mackenzie, Chapman & Sengupta, 2011).

Proxies for wealth (Table 1) were often retained in models that explained natural resource use. Wealthier respondents (i.e. those who had consumed/purchased more types of meats) had extracted or purchased more natural resources in their lifetime. Natural resource use rates are sometimes higher among households that have regular employment (Nuno *et al.*, 2013) or are more educated (Mackenzie *et al.*, 2011). Alternatively, the link between wealth and natural resource consumption may be observed because wealthier individuals: (1) achieved that status by selling natural resources; or (2) felt comfortable using natural resources (and reporting that use to researchers) because they had the resources to avoid penalties associated with illegal behavior.

Ancestral taboos played a role in lifetime extraction rates; individuals with ancestral taboos were less likely to extract natural resources. Ancestral taboos are often described as limiting natural resource extraction in Madagascar (Jones, Andriamarovololona & Hockley, 2008; Westerman & Gardner, 2013). However, ancestral taboos may be breaking down (Jones *et al.*, 2008) and the transition from traditional to institutional religion can influence some types of natural resource use (both permitting and prohibiting use; Reuter *et al.*, 2016*b*).

The variable related to park enforcement did not predict natural resource use. Other proxies (e.g. number of patrols or arrests) may have better predicted natural resource use (though patrols are irregular and arrests are rare, K. E.

Reuter, unpubl. data). Nevertheless, the results suggest that current enforcement levels do not prevent extensive natural resource use within the park. Similarly, respondents in pilot interviews (Appendix S2) often described park enforcement as ineffective and respondents in villages with permanent MNP agents continued to use natural resources (Gilles & Reuter, 2014). The limited effectiveness of enforcement may be because the park has less than 25 full-time employees for an area of 18,225 ha not including buffer zones (MNP, pers. comm.). The effectiveness of MNP agents at enforcement may also be decreased because: (1) their incomes are lower than others benefitting from the park (e.g., tour guides, hotel owners); (2) they live near people that they are meant to be reporting on (Sodikoff, 2009); and (3) they do not have direct enforcement authority, relying on regional police teams that are often occupied with other priorities. It may also be that communities lacked a complete understanding of the natural resource use/extraction rules as related to the protected area (seen elsewhere in Madagascar, Keane *et al.*, 2011) though we did not assess this. Finally, the limited response to enforcement we observed may be a local manifestation of a broader issue; nationally, there are limited consequences of enforcement for a range of legal and illegal natural resource uses (Sommerville *et al.*, 2010). In this study, the continued extraction of natural resources from the park suggests that offenders were apprehended infrequently enough, punishment of apprehended individuals were unlikely enough, or income gained from extracted natural resources was great enough to dissuade extraction.

Regarding the presence of public services, the variable used in this study (‘SecSch’) did not predict natural resource use. This is important because social development projects (e.g. schools, water wells) are one of the main benefits to the communities around the park funded by park revenues. Many respondents (Appendix S2) felt that the social development projects were not adequately targeted. If these projects continue to be implemented in the future, and if the aim is to incentivize communities not to extract natural resources within the park, then the types of projects implemented may need to be re-considered, increased in scale, or better targeted to encourage those individuals engaged most intensively in extractive activities to change their behavior. The effectiveness of in-kind and monetary incentives to dissuade natural resource use, however, are debated, as they often do not respond to different stakeholders’ needs and interests (Berkes, 2004; Guerbois *et al.*, 2013; Poudyal *et al.*, 2016). In payments for ecosystem services programs, for instance, behavior changes in forest use behavior can be due to either the payments or the monitoring associated with the project (Sommerville *et al.*, 2010). Therefore, the link between incentives and enforcement must be considered especially if they do not directly target high natural resource users.

Caveats

This study has several caveats. First, we acknowledge that the calculation of the indices (metrics used; index scaling) could have influenced the results of this study. The metrics used in this study were informed by the pilot study and represent the format in which respondents could most accurately quantify their natural resource use. Regarding the scaling of the indices, we acknowledge that combining and summing the different types of natural resource use is equating them such that the cutting down of five trees is equivalent to, for example, hunting of five animals (although different types of natural resource use require different time/resources per unit extracted). To modify the indices by weighting some types of natural resource use heavier than others would have required additional data on effort by resource users that was unavailable to us. Given that we aimed to understand the motivations of natural resource use broadly, our simple indices capture major variation in resource use while quantifying variables for which measurement can be replicated (in Madagascar and elsewhere). Second, the caveats of respondent recall periods of natural resource use are discussed in the literature (Reuter *et al.*, 2016*a*,*b*); long recall periods are recommended in the case of rare or uncommon events. However, the frequency of natural resource use varied by extraction type (Table S2). Different recall periods for different types of natural resource extraction could have solicited more accurate information from interviewees but might have served to complicate interviews. Third, like other studies (e.g. St. John *et al.*, 2011), respondents could have provided incomplete information about their natural resource use.

Conclusion

We examined drivers of natural resources use over two points in time, finding that while some drivers were always important in predicting natural resource use, others differed in importance depending on the response index. While future studies should examine other factors that may influence natural resource extraction, the simple models in this study had a relatively high explanatory power even in the context of sometimes illegal and occasional extraction of five different types of natural resources.

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References

Arias, A., Cinner, J.E., Jones, R.E. & Pressey, R.L. (2015). Levels and drivers of fishers' compliance with marine protected areas. *Ecol. Soc.* **20**, 19.

Berkes, F. (2004). Rethinking Community-based conservation. *Conserv. Biol.* **18**, 621–630.

Borgerson, C., McKean, M.A., Sutherland, M.R. & Godfrey, L.R. (2016). Who hunts lemurs and why they hunt them. *Biol. Cons.* **197**, 124–130.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, P., Oldfield, S., Magin, G. & Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conserv. Biol.* **16**, 909–923.

Bruner, A.G., Gullison, R.E., Rice, R.E. & da Fonseca, G.A.B. (2001). Effectiveness of parks in protecting tropical biodiversity. *Science* **291**, 125–128.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*. New York: Springer Science and Business Media.

Calcagno, V. & de Mazancourt, C. (2010). glmulti: An R package for easy automated model selection with (generalized) linear models. *J. Stat. Softw.* **34**, 1–29.

Cardiff, S. & Befourouack, J. (2003). The Réserve Spéciale d'Ankarana. In *The natural history of Madagascar*: 1501–1507. Goodman, S.M. & Benstead, J.P. (Eds). Chicago: The University of Chicago Press.

Christie, I.T. and Crompton, D.R. (2003) *Republic of Madagascar: tourism sector study*. Africa Regional Working Paper Series No. 63. Washington: World Bank.

Conroy, S.D.S. & Brook, B.W. (2003). Demographic sensitivity and persistence of the threatened white- and orange-bellied frogs of Western Australia. *Popul. Ecol.* **45**, 105–114.

Dirzo, R. & Raven, P.H. (2003). Global state of biodiversity and loss. *Annu. Rev. Environ. Resour.* **28**, 137–161.

Emerton, L. (1999). *Balancing the opportunity costs of wildlife conservation for communities around Lake Mburo National Park, Uganda*. London: International Institute for Environment and Development.

Ender, C.M. 2016.Assessment of the economic contribution of non-timber forest products to rural livelihoods in Oddar Meanchey, Cambodia. *Cambodian J. Nat. Hist.*, **2016**: 60–70.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Evol. Syst.* **34**, 487–515.

deFrance, S.D. (2009). Zooarchaeology in complex societies: political economy, status, and ideology. *J. Archaeol. Res.* **17**, 105–168.

Gezon, L.L. (1997). Political ecology and conflict in Ankarana, Madagascar. *Ethnology* **36**, 85–100.

Gilles, H. & Reuter, K.E. (2014). The presence of diurnal lemurs and human-lemur interactions within the buffer zone of the Ankarana National Park. *Lemur News* **18**, 27–30.

Golden, C.D., Fernald, L.C.H., Brashares, J.S., Rodolph Rasolofoniaina, B.J. & Kremen, C. (2011). Benefits of wildlife consumption to child nutrition in a biodiversity hotspot. *Proc. Natl Acad. Sci. USA* **108**, 19653–19656.

Gorchov, D.L., Cornejo, F., Ascorra, C. & Jaramillo, M. (1993). The role of seed dispersal in the natural regeneration of rain forest after strip-cutting in the Peruvian Amazon. *Vegetatio* **107**, 339–349.

Gudiel, A., Nieves, S., Reuter, K.E. & Sewall, B.J. (2016). The effect of anthropogenic disturbance on non-native plant species in Madagascar. *J. Trop. Ecol.* **32**, 543–554.

Guerbois, C., Dufour, A.-B., Mtare, G. & Fritz, H. (2013). Insights for integrated conservation from attitudes of people toward protected areas near Hwange National Park, Zimbabwe. *Conserv. Biol.* **27**, 844–855.

Innes, J.L. (2010). Madagascar rosewood, illegal logging and the tropical timber trade. *Madag. Conserv. Dev.* **5**, 6–10.

IUCN. (2016) *Threats classification scheme* (Version 3.2). Available at: http://www.iucnredlist.org/technical-documents/classification-schemes/threats-classification-scheme

Jones, J.P.G., Andriamarovololona, M.M. & Hockley, N. (2008). The importance of taboos and social norms to conservation in Madagascar. *Conserv. Biol.* **22**, 976–986.

Kahler, J.S. & Gore, M.L. (2012). Beyond the cooking pot and pocket book: factors influencing noncompliance with wildlife poaching rules. *Int. J. Comp. Appl. Crim. Justice* **36**, 103–120.

Keane, A., Ramarolahy, A.A., Jones, J.P.G. & Milner-Gulland, E.J. (2011). Evidence for the effects of environmental engagement and education on knowledge of wildlife laws in Madagascar. *Conserv. Lett.* **4**, 55–63.

Kollmuss, A. & Agyeman, J. (2002). Mind the gap: why do people act environmentally and what are the barriers to pro-environmental behavior? *Environ. Educ. Res.* **8**, 239–260.

Kremen, C., Niles, J.O., Dalton, M.G., Daily, G.C., Ehrlich, P.R., Fay, J.P., Grewal, D. & Guillery, R.P. (2000). Economic incentives for rain forest conservation across scales. *Science* **288**, 1828–1832.

Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T. & Fleming, T.H. (2011). Ecosystem services provided by bats. *Ann. N. Y. Acad. Sci.* **1223**, 1–38.

Lamb, D., Erskine, P.D. & Parrotta, J.A. (2005). Restoration of degraded tropical forest landscapes. *Science* **310**, 1628–1632.

Lindsey, P.A., Balme, G., Becker, M., Begg, C., Bento, C., Bocchino, C., Dickman, A., Diggle, R.W., Eves, H., Henschel, P., Lewis, D., Marnewick, K., Mattheus, J., Weldon McNutt, J., McRobb, R., Midlane, N., Milanzi, J., Morley, R., Murphree, M., Opyene, V., Phadima, J., Purchase, G., Rentsch, D., Roche, C., Shaw, J., van der Westhuizen, H., Van Vliet, N. & Zisadza-Gandiwa, P. (2013). The bushmeat trade in African savannas: impacts, drivers, and possible solutions. *Biol. Cons.* **160**, 80–96.

Mackenzie, C.A., Chapman, C.A. & Sengupta, R. (2011). Spatial patterns of illegal resource extraction in Kibale National Park, Uganda. *Environ. Conserv.* **39**, 38–50.

Manfredo, M., Teel, T., Gavin, M. & Fulton, D. (2014). Considerations in representing human individuals in social–ecological models. In *Understanding society and natural resources*: 137–158. Manfredo, M.J., Vaske, J.J., Rechkemmer, A. & Duke, E.A. (Eds). Dordrecht: Springer Netherlands.

Medellin, R.A. & Gaona, O. (1999). Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico. *Biotropica* **31**, 478–485.

Novy, J.W. (1997). Medicinal plants of the eastern region of Madagascar. *J. Ethnopharmacol.* **55**, 119–126.

Nuno, A., Bunnefeld, N., Naiman, L.C. & Milner-Gulland, E.J. (2013). A novel approach to assessing the prevalence and drivers of illegal bushmeat hunting in the Serengeti. *Conserv. Biol.* **27**, 1355–1365.

Pfeifer, M., Burgess, N.D., Swetnam, R.D., Platts, P.J., Willcock, S. & Marchant, R. (2012). Protected areas: mixed success in conserving East Africa's evergreen forests. *PLoS ONE* **7**, e39337.

Poudyal, M., Ramamonjisoa, B.S., Hockley, N., Rakotonarivo, O.S., Gibbons, J.M., Mandimbiniaina, R., Rasoamanana, A. & Jones, J.P. (2016). Can REDD+ social safeguards reach the 'right' people? Lessons from Madagascar *Glob. Environ. Change* **37**, 31–42.

Poulsen, J.R., Clark, C.J., Mavah, G. & Elkan, P.W. (2009). Bushmeat supply and consumption in a tropical logging concession in Northern Congo. *Conserv. Biol.* **23**, 1597–1608.

Reuter, K.E., Randell, H., Wills, A.R., Janvier, T.E., Belalahy, T.R. & Sewall, B.J. (2016a). Capture, movement, trade, and consumption of mammals in Madagascar. *PLoS ONE* **11**, e0150305. https://doi.org/10.1371/journal.pone.0150305.

Reuter, K.E., Randell, H., Wills, A.R. & Sewall, B.J. (2016b). The consumption of wild meat in Madagascar: drivers, popularity, and food security. *Environ. Conserv.* **43**, 273–283.

Rietbergen-McCracken, J. & Narayan, D. (1998). *Participation and social assessment: tools and techniques*. Washington: The World Bank.

Scales, I.R. (2014). The future of conservation and development in Madagascar: time for a new paradigm? *Madag. Conserv. Dev.* **9**, 5–12.

Schwitzer, C., Mittermeier, R.A., Johnson, S.E., Donati, G., Irwin, M., Peacock, H., Ratsimbazafy, J., Razafindramanana, J., Louis, E.E., Jr., Chikhi, L.I.C., Colquhoun, I.C., Tinsman, J., Dolch, R., LaFleur, M., Nash, S., Patel, E., Randrianambinina, B., Rasolofoharivelo, T. & Wright, P.C. (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science* **343**, 842–843.

Shackleton, C.M. & Shackleton, S.E. (2006). Household wealth status and natural resource use in the Kat River valley, South Africa. *Ecol. Econ.* **57**, 306–317.

Sodikoff, G. (2009). The low-wage conservationist: biodiversity and perversities of value in Madagascar. *Am. Anthropol.* **111**, 443–455.

Solomon, J.N., Gavin, M.C. & Gore, M.I. (2015). Detecting and understanding non-compliance with conservation rules. *Biol. Cons.* **189**, 1–4.

Sommerville, M., Milner-Gulland, E.J., Rahajaharison, M. & Jones, J.P.G. (2010). Impact of a community-based payment for environmental services intervention on forest use in Menabe, Madagascar. *Conserv. Biol.* **24**, 1488–1498.

St. John, F.A.V., Keane, A.M., Edwards-Jones, G., Jones, L., Yarnell, R.W. and Jones, J.P.G. 2011.Identifying indicators of illegal behaviour: carnivore killing in human-managed landscapes. *Proc R. Soc. Lond. [Biol.]* **279**: 804–812.

Vos, A.D., Cumming, G.S., Moore, C.A., Maciejewski, K. & Duckworth, G. (2016). The relevance of spatial variation in ecotourism attributes for the economic sustainability of protected areas. *Ecosphere* **7**, e01207.

Walsh, A. (2005). The obvious aspects of ecological underprivilege in Ankarana, Northern Madagascar. *Am. Anthropol.* **107**, 654–665.

Westerman, K. & Gardner, C.J. (2013). Adoption of socio-cultural norms to increase community compliance in permanent marine reserves in southwest Madagascar. *Conserv. Evid.* **10**, 4–9.

Wilkie, D.S., Bennett, E.L., Peres, C.A. & Cunningham, A.A. (2011). The empty forest revisited. *Ann. N. Y. Acad. Sci.* **1223**, 120–128.

World Bank. (2013) *Madagascar: measuring the impact of the political crisis*. Available at: http://www.worldbank.org/en/news/feature/2013/06/05/madagascar- measuring-the-impact-of-the-political-crisis

Wright, S.J. (2005). Tropical forests in a changing environment. *Trends Ecol. Evol.* **20**, 553–560.

Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Characteristics of surveyed communities, along with the perceptions and interactions reported by respondents.
Table S2. Direct, lifetime natural resource use as reported by respondents in 2013 (means ± 95% CI, towns are replicates).
Table S3. Indirect, lifetime natural resource use, including data regarding the economic value of natural resources reported by purchasers and sellers in 2013.
Appendix S1. Background information on the Ankarana National Park.
Appendix S2. Results of the pilot interviews in 2012 in three villages surrounding the Ankarana National Park.
Appendix S3. 2013 Interview materials.
Appendix S4. Calculation of dependent variables.