



## Landscape trends in small mammal occupancy in the Makira–Masoala protected areas, northeastern Madagascar

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Madagascar's native small mammals (Tenrecidae and Nesomyinae) are understudied. To help fill these knowledge gaps, we analyzed 1,575 detections of small mammals obtained during camera-trap surveys at 7 sites in northeastern Madagascar (2008–2011) using single-season occupancy analyses in program PRESENCE. We estimated landscape occupancy and detection probabilities of tufted-tailed rats (*Eliurus* spp.), red forest rats (*Nesomys* spp.), greater hedgehog tenrecs (*Setifer setosus*), and common tenrecs (*Tenrec ecaudatus*) and examined how these parameters responded to habitat characteristics, habitat degradation, and the trap success of native and exotic carnivorans. Only *Nesomys* showed a marked difference in mean occupancy between intact ( $\psi = 0.71 \pm SE 0.06$ ), intermediately degraded ( $\psi = 0.23 \pm SE 0.05$ ), and degraded ( $\psi = 0.34 \pm SE 0.06$ ) forest sites. Only *Nesomys* and *Setifer* occupancy was strongly influenced by habitat characteristics; *Nesomys* occupancy was positively related to distance away from forest edge ( $\beta = 1.39 \pm SE 0.27$ ) and percent rainforest cover ( $\beta = 1.89 \pm SE 0.39$ ), and *Setifer* occupancy negatively related to average canopy height ( $\beta = -0.52 \pm SE 0.25$ ). We found trap success of exotic carnivorans had little influence on small mammal occupancy and detection probabilities (with the exception of *Eliurus*). We suggest that camera traps are a valid method for studying aspects of small mammal ecology, but caution researchers to consider characteristics of camera traps (e.g., trigger speed) to increase potential inference.

Key words: camera trap, exotic predator, habitat degradation, Nesomyidae, rodent, tenrec, Tenrecidae

A basic goal of ecology is to understand the factors that influence species' distributions (Guisan and Thuiller 2005). Because species distributions are driven by environmental and physiological needs and constrained by interspecific interactions (Hutchinson 1957), habitat characteristics and climate (Lehtonen et al. 2001; Kamilar and Tecot 2016), the presence of sympatric species (Case and Bolger 1991; Wisz et al. 2013; Wells et al. 2014), and anthropogenic pressures (Peres 2001; Wijesinghe and Brooke 2005; Kamilar and Tecot 2016) can all influence whether a species is present at a site (Guisan and Thuiller 2005). Habitat degradation, in particular, can negatively affect species presence at a site by increasing the vulnerability of habitat patches to

hunting (Peres 2001) and invasion by exotic species (Laurance and Uuseche 2009). To provide baseline ecological knowledge to advance conservation and management programs, it is necessary to determine how habitat characteristics, sympatric species, and anthropogenic pressures influence the distribution of understudied taxa.

Madagascar is a global biodiversity hotspot with high rates of endemism and intense anthropogenic pressures (Myers et al. 2000; Brooks et al. 2002, 2006). Madagascar's native species include 2 diverse, small mammal groups—rodents of the subfamily Nesomyinae (27 species) and tenrecs of the family Tenrecidae (32 species)—each originating from

separate single-colonization events and showing 100% endemism (Olson and Goodman 2003; Poux et al. 2005; Everson et al. 2016). Understanding what factors influence the distribution of Malagasy small mammals is important as these animals are seed dispersers or seed predators (Soarimalala and Goodman 2011; Dammhahn et al. 2013), predators of invertebrate pest species (Peveling et al. 2003), prey for a variety of native predators (Karpanty and Goodman 1999; Goodman 2012), and components of the local bushmeat trade (Golden 2009; Jenkins et al. 2011; Gardner and Davies 2014). Few studies have examined what factors influence the distribution of small mammals in Madagascar's species-rich northeastern region (Stephenson 1995; Andrianjakarivelo et al. 2005) despite locally unsustainable hunting rates (Golden 2009) and the potential negative influence of exotic carnivorans (domestic dog *Canis familiaris*, feral cat *Felis silvestris*, and small Indian civet, *Viverricula indica*) on small mammals (Farris et al. 2015c).

We detected 6 endemic small mammal taxa (Supplementary Data SD1 and SD2) during photographic sampling of 7 sites in the Makira–Masoala protected area complex, northeastern Madagascar (2008–2011; Table 1 and Fig. 1), with tufted-tailed rats (*Eliurus* spp.; hereafter, *Eliurus*), red forest rats (*Nesomys* spp.; hereafter, *Nesomys*), greater hedgehog tenrecs (*Setifer setosus*; hereafter, *Setifer*), and common tenrecs (*Tenrec ecaudatus*; hereafter, *Tenrec*) being detected most often. These 4 taxa can be found across much of Madagascar in both disturbed and undisturbed forests (Eisenberg and Gould 1970; Andrianjakarivelo et al. 2005; Goodman et al. 2013). *Setifer* and *Tenrec* both exhibit seasonal torpor, the extent of which depends on local conditions, geographic area, age, and sex (Gould and Eisenberg 1966; Eisenberg and Gould 1970; Levesque et al. 2013). *Setifer* and *Tenrec* are consumed widely as bushmeat (Ganzhorn et al. 1990; Golden 2009). The conservation status of Madagascar's small mammals is poorly known, as scant information is available on their population trends, ecology, and threats to enable assessments for most taxa (Soarimalala and Goodman 2011; Goodman et al. 2013).

Focusing on these 4 taxa, our objectives were to: 1) estimate occupancy and detection probabilities across the

Makira–Masoala landscape, 2) examine the variation in small mammal occupancy probabilities across a habitat degradation gradient, and 3) determine the influence of habitat characteristics and the presence of native and exotic carnivorans on small mammal occupancy and detection probabilities. Based on what is known of their ecology, we hypothesized that occupancy probability of small mammals would be similar at intact, intermediately degraded (hereafter, intermediate), and degraded forest sites (Lehtonen et al. 2001; Andrianjakarivelo et al. 2005; Goodman et al. 2013). We also hypothesized that *Setifer* and *Tenrec* occupancy would be positively related to distance away from a village in response to hunting pressure (Golden 2009), and that the occupancy and detection probabilities of all 4 small mammal taxa would be negatively related to trap success for feral cats (Medina et al. 2011; Table 2). A final objective was to monitor trends in annual occupancy probabilities of small mammals using long-term camera-trapping data from 1 resurveyed site (2008–2015; Supplementary Data SD3).

## MATERIALS AND METHODS

**Study area and camera-trap surveys.**—From 2008 to 2011, we conducted camera-trap surveys at 7 forest sites across the Makira and Masoala protected areas (Fig. 1; Table 1). One of these sites was resurveyed an additional 5 more times between 2010 and 2015 for a total of 6 surveys (Supplementary Data SD3). The Makira–Masoala protected area complex is the largest contiguous protected forest in Madagascar (5,197 km<sup>2</sup> as of 2013, excluding community-managed buffers). Unsustainable and illegal hunting (Golden 2009), habitat loss and degradation (Farris et al. 2015c), negative interactions with exotic carnivorans (Farris et al. 2014, Farris et al. 2015b), and, in a broader geographical sense, climate change (Andriamasimanana and Cameron 2013; Barrett et al. 2013) threaten wildlife across the region. The Makira and Masoala protected areas are home to over 30 small mammal species, including 2 *Nesomys* spp. and 8 *Eliurus* spp. (Supplementary Data SD2). We identified individuals of *Nesomys* and *Eliurus* to genus, as in most instances it is difficult to determine the species in photographs.

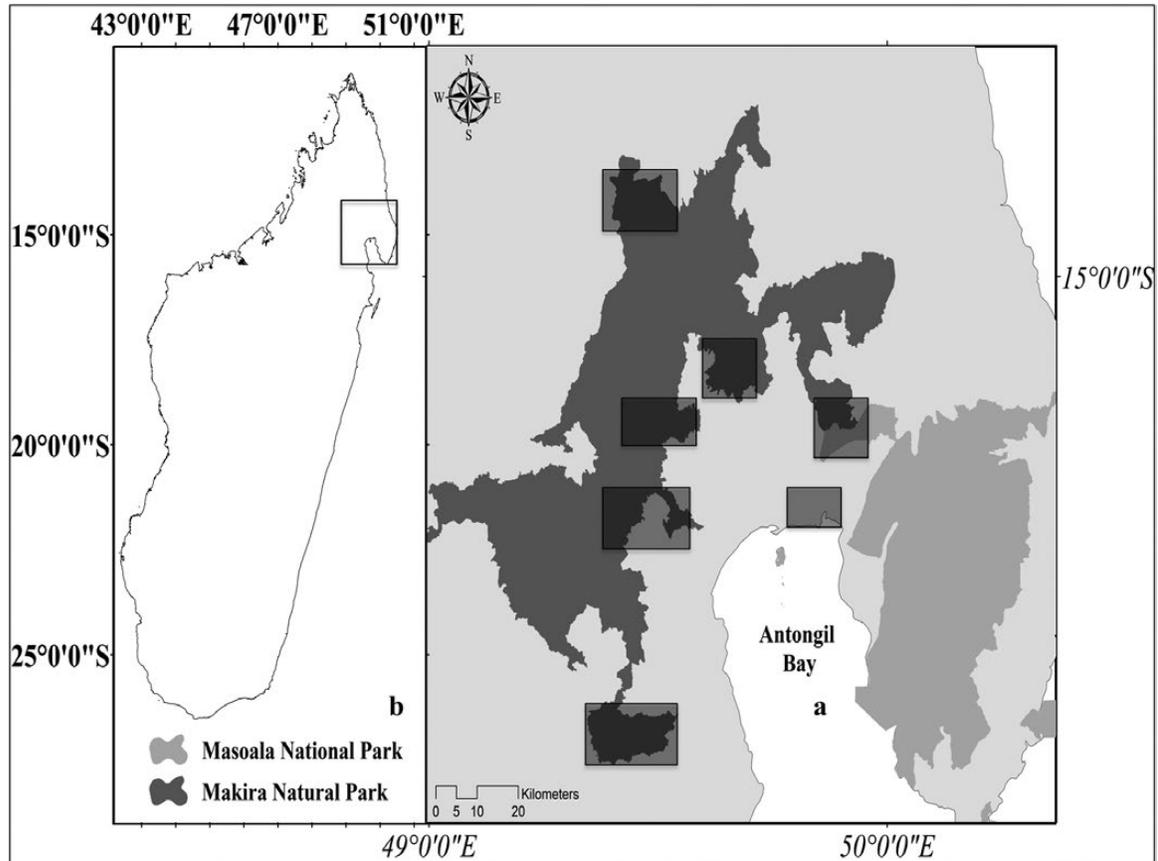
**Table 1.**—Survey details for the camera-trap surveys that surveyed small mammal populations at 7 sites across the Makira–Masoala protected areas in northeastern Madagascar (2008–2011), including trap success rates (TS) for *Eliurus* (E), *Nesomys* (N), *Setifer* (S), and *Tenrec* (T).

Study site (survey dates; season) <sup>a</sup>	Elevation range (m)	Survey duration	No. of camera stations	Total no. of trap nights <sup>b</sup>	TS <sup>c</sup>			
					E	N	S	T
S01 (Mar.–May 2009; HW)	1,000–1,400	61 trap nights	20	989	11.9	18.0	0.38	3.62
S02 (Sept.–Nov. 2008; CW)	360–703	73 trap nights	20	1,315	5.55	17.1	2.74	0.08
S03 (Aug.–Oct. 2009; CW)	380–550	68 trap nights	19	1,067	4.22	3.94	2.25	–
S04 (June–Aug. 2011; CW)	21–385	66 trap nights	23	1,462	3.35	–	0.14	–
S05 (Mar.–May 2011; HW)	324–786	64 trap nights	24	1,509	2.52	0.46	0.20	0.66
S06 (Nov. 2009–Jan. 2010; HD)	580–820	69 trap nights	18	881	5.22	15.7	2.95	0.57
S07 (Dec. 2010–Feb. 2011; HD)	93–507	71 trap nights	24	1,570	0.96	0.13	1.08	0.70

<sup>a</sup> Season that the site was surveyed: HW (hot–wet; Feb.–May), HD (hot–dry; Oct.–Jan.), and CW (cold–wet; June–Sept.—Farris 2014).

<sup>b</sup> Total number of trap nights (i.e., 24-h periods where at least 1 camera was functional at each camera station) summed over all camera stations at the study site.

<sup>c</sup> TS is the number of photographic detections divided by the total number of trap nights for that site multiplied by 100. If a species has no trap success estimate listed for a survey (–), one possible reason may be due to torpor (see Supplementary Data SD2; Soarimalala and Goodman 2011).



**Fig. 1.**—The Makira and Masoala protected areas and surrounding land in northeastern Madagascar (a) is the largest contiguous forest in Madagascar (b; 5,197 km<sup>2</sup>, excluding community-managed buffers; box indicates location of area shown in map (a)). The small mammal communities of 7 sites (S01–S07) in the regions outlined by the boxes were photographically surveyed with camera traps from 2008 to 2011 (1 site was resurveyed from 2008 to 2015). Due to sensitivity of the data collected in several of these same areas on hunting by local people, we are unable to provide the exact locations of survey grids.

Four sites were within the Makira protected area; the remaining 3 were outside the Masoala ( $n = 2$ ) and Makira ( $n = 1$ ) protected areas. We ranked our sites from least to most degraded, resulting in 2 intact (S01 and S02), 3 intermediate (S03, S04, and S05), and 2 degraded sites (S06 and S07—see Farris 2014). Camera-trap surveys of the 7 sites consisted of 61–73 trap nights and comprised 18–24 unbaited camera stations spaced 400–600 m apart ( $n = 148$  camera stations total for landscape analyses). Camera-trap surveys at the resurveyed site consisted of 53–75 trap nights and comprised 20–25 unbaited camera stations; we used the same locations and surveyed the site during the same months each year (September, October, and November; Supplementary Data SD3). Each station had 2 camera traps positioned 20–30 cm off the ground on opposite sides of wildlife (0.0–0.5 m wide) or human (> 0.5 m wide) trails and operated 24 h/day. Cameras were arranged so as to provide full coverage of the trail and surrounding area. We used a total of 6 different camera models—DeerCam DC300 and Cuddeback IR (Non Typical, Inc., Green Bay, Wisconsin), Reconyx PC85 and HC500 (Reconyx, Inc., Holmen, Wisconsin), Moultrie D50 and D55 (EBSCO Industries, Inc., Birmingham, Alabama)—with 2 different models at each station to lessen detection biases caused by any single camera model. We visited stations every 5–10 days for maintenance purposes. Based on the camera-trap

data, we created capture histories, where we recorded whether a species was detected (“1”) or not detected (“0”) for each trap night. We collapsed these capture histories so that each survey occasion was equal to 9 trap nights ( $n = 8$  survey occasions total) to improve model convergence for landscape occupancy analyses. The survey occasions for the resurveyed site ranged from 6 to 9 survey occasions.

By convention, a “photographic detection” can be defined as the number of distinctly different individuals of a species detected within a 30-min period (Di Bitetti et al. 2006; Davis et al. 2011). As we were unable to discriminate individual small mammals, each detection event was noted as 1 animal, unless there were multiple animals in the images. We estimated trap success—the number of photographic detections of a species divided by the total number of trap nights for that survey and multiplied by 100 for the 4 focal small mammals, sympatric native and exotic carnivorans, and humans (nonresearchers). Trap nights are the number of 24-h periods that a station had at least 1 camera functional. The 1st author (AJM) identified the tenrecs (*Tenrec* and *Setifer*) to species and the 2nd author (SMG) identified the rodents (*Eliurus* and *Nesomys*) to genus. Because *Tenrec* young show cryptic coloration similar to the sympatric lowland streaked tenrec (*Hemicentetes semispinosus*—Soarimalala and Goodman 2011), we distinguished

**Table 2.**—List of 19 covariates used in single-season occupancy analyses of 4 native small mammal taxa that were detected during camera-trap surveys of 7 sites in the Makira–Masoala protected areas, northeastern Madagascar (2008–2011). Covariates include landscape-level and station-level habitat characteristics, the trap success rates of sympatric native and exotic carnivorans, and the season that the survey was conducted. “ $\psi$ ” indicates we tested the covariate effect on occupancy probability only, “ $p$ ” indicates we tested the covariates effect on detection probability only, “ $\psi/p$ ” indicates we tested the covariates effect on occupancy and detection probability, and “ $\pm$ ” indicates the direction of the hypothesized relationship.

Covariate	Definition	<i>Eliurus</i>	<i>Nesomys</i>	<i>Setifer</i>	<i>Tenrec</i>
distedge	Distance to the nearest forest edge (km) for each camera station		$\psi+$		
distvil	Distance to the nearest village (km) for each camera station			$\psi+$	$\psi+$
%rf	Percentage of forest cover within the study site that is primary rainforest <sup>a</sup>	$\psi+$	$\psi+$		
totpatches	Total number of habitat patches (including rainforest, degraded forest, and matrix or cultivated) within the study site	$\psi-$	$\psi-$		
canht	Average canopy height (m) for each camera station <sup>b</sup>	$\psi+$		$\psi+$	
cancov	Average percent canopy cover for each camera station		$\psi+$		
treedens	Average tree density (stems $\geq 5$ cm/ha) at each camera station	$\psi+$	$\psi-$	$\psi+$	
ba	Average basal area (stems $\geq 5$ cm, m <sup>2</sup> /ha) at each camera station	$\psi-$	$\psi+$		
totusty	Average understory cover (%) from 0.0 to 2.0 m height present for each camera station	$\psi+$	$\psi+$	$\psi+$	$\psi+$
tw	Width (m) of the trail a camera station was centered on at each study site	$p-$	$p-$	$p-$	$p-$
tt	Type of trail (human, game, or non-trail) that each camera station was centered on at each study site	$p+$	$p+$	$p+$	$p+$
crfts	Trap success rate <sup>c</sup> of the native fosa ( <i>Cryptoprocta ferox</i> ) at each camera station	$p-$	$p-$	$p-$	$p-$
ffts	Trap success rate of the native spotted fanaloka ( <i>Fossa fossana</i> ) at each camera station	$p-$	$p-$	$p-$	$p-$
egts	Trap success rate of the native falanouc ( <i>Eupleres goudotii</i> ) at each camera station	$p+$	$p+$	$p+$	$p+$
sects	Sum of the trap success rates of the 3 native small carnivores (ring-tailed vontsira, <i>Galidia elegans</i> ; broad-striped vontsira, <i>Galidictis fasciata</i> ; and brown-tailed vontsira, <i>Salanoia concolor</i> ) at each camera station	$p-$	$p-$	$p-$	$p-$
cafts	Trap success rate of the exotic domestic dog ( <i>Canis familiaris</i> ) at each camera station		$\psi-/p-$	$\psi-/p-$	$\psi-/p-$
fsts	Trap success rate of the exotic feral cat ( <i>Felis silvestris</i> ) at each camera station	$\psi-/p-$	$\psi-/p-$	$\psi-/p-$	$\psi-/p-$
vits	Trap success rate of the exotic small Indian civet ( <i>Viverricula indica</i> ) at each camera station	$\psi-/p-$	$\psi-/p-$	$\psi-/p-$	$\psi-/p-$
seas	The climatological season that the study site was surveyed in: hot–dry (Oct.–Jan.), hot–wet (Feb.–May), and cold–wet (June–Sept.) <sup>d</sup>	$p+$	$p+$	$p+$	$p+$

<sup>a</sup> Landscape-level covariates such as %rf and totpatches were measured within a 500-m buffer around a study site/camera-trapping grid using satellite imagery provided by the Wildlife Conservation Society Madagascar Program and ERDAS Imagine (Intergraph Corporation) and FRAGSTATS (McGarigal et al. 2012; Farris 2014).

<sup>b</sup> Station-level habitat was measured around a camera station using 3 habitat transects centered on the camera station and then averaged for the station (Farris 2014).

<sup>c</sup> Trap success is the number of photographic detections of a species divided by the total number of trap nights multiplied by 100.

<sup>d</sup> Season of survey was determined by taking temperature and precipitation measurements during surveys (Farris et al. 2015c).

between the 2 species using size, coloration, and whether a *Tenrec* adult was also captured during the detection event. If we were unable to confidently identify a photographed small mammal, it was excluded from the occupancy analyses.

**Landscape and annual occupancy analyses.**—We estimated small mammal occupancy and detection probabilities across the Makira and Masoala protected areas, determined the influence of habitat characteristics and trap success for carnivorans on small mammal occupancy and detection, and examined variation in small mammal occupancy across a habitat degradation gradient using single-season occupancy analysis in program PRESENCE (v 7.8—MacKenzie et al. 2005; Hines 2006). We conducted a Pearson’s correlation on 41 possible covariates (i.e., landscape-level and station-level habitat characteristics, trap success for native or exotic carnivorans, trap success for humans, and the season the survey was conducted; Supplementary Data SD4). Based on the literature, we picked the most biologically relevant variables from pairs of highly correlated covariates ( $|r| > 0.70$ ) and discarded the others. Of the remaining uncorrelated covariates, we chose 19 (Table 2) to include in our landscape-level occupancy models based on a priori hypotheses and then

normalized these final covariates within PRESENCE. We built occupancy models by first determining what covariate(s) influenced detection probability for each small mammal taxa while holding occupancy probability constant. Once we determined the top detection model (i.e., Akaike information criterion [ $\Delta AIC$ ] = 0.0), we included covariate(s) on occupancy. We then conducted goodness-of-fit tests on our most parameterized model and corrected for overdispersion ( $\hat{c} \geq 3.0$ —Lebreton et al. 1992). We considered models competing if they had a quasi-AIC ( $\Delta QAIC$ )  $\leq 2.0$ , and parameter and beta estimates were model-averaged unless the top model was strongly supported (model weight  $\geq 80\%$ —Akaike 1973). Covariates were determined as having a strong influence on occupancy or detection if the 95% confidence intervals (CIs) of the model-averaged beta estimates did not overlap with 0. We determined the mean occupancy probability for each small mammal for intact, intermediate, and degraded forest sites. If 95% CIs overlapped between estimates, there was no evidence for a difference among mean occupancy probabilities at the 3 forest types.

We estimated annual occupancy probabilities for 3 of the 4 small mammal taxa—*Eliurus*, *Nesomys*, and *Setifer*—at our

resurveyed site (S02) using multi-season occupancy analyses in PRESENCE. We did not estimate annual occupancy probabilities for *Tenrec* due to extremely low number of detections at the site ( $n = 2$ ) and we did not include covariates in these models due to low number of detections. As we could not measure the extent of model fit because there are no validated goodness-of-fit tests for dynamic occupancy models (Mackenzie et al. 2005; Fiske and Chandler 2011), we present these results in the Supplementary Data SD5 and SD6). We considered models competing if they had a  $\Delta\text{AIC} \leq 2.0$ , and parameter estimates were model-averaged unless the top model was strongly supported (model weight  $\geq 80\%$ —Akaike 1973).

This study conforms to published ASM guidelines for the use of wild mammals in research (Sikes et al. 2016).

## RESULTS

We obtained 1,575 photographic detections of small mammals during 8,793 trap nights. Total trap success for small mammals over all surveys for all species, including photographic detections of small mammals we could not identify, was 17.91 detections per 100 trap nights. We could not identify approximately 20% of the photographic detections of small mammals ( $n = 204$  diurnal and  $n = 106$  nocturnal); of the remaining photographic detections that could be identified, *Nesomys* had the most detections and the highest trap success ( $n = 592$ ; 6.73 detections per 100 trap nights), followed by *Eliurus* ( $n = 384$ ; 4.37 detections per 100 trap nights), *Setifer* ( $n = 112$ ; 1.27 detections per 100 trap nights), and *Tenrec* ( $n = 65$ ; 0.74 detections per 100 trap nights). *Eliurus* and *Setifer* were detected at all 7 sites, whereas *Tenrec* was only detected at 5 sites. We also detected the introduced black rat (*Rattus rattus*) at 4 sites ( $n = 10$ ; 0.11 detections per 100 trap nights).

**Landscape occupancy and detection.**—*Nesomys* and *Tenrec* both had 1 competing ( $\Delta\text{QAIC} \leq 2.0$ ) model, whereas *Setifer* and *Eliurus* had 2 and 3 competing models, respectively (Table 3). *Eliurus* had the highest landscape occupancy

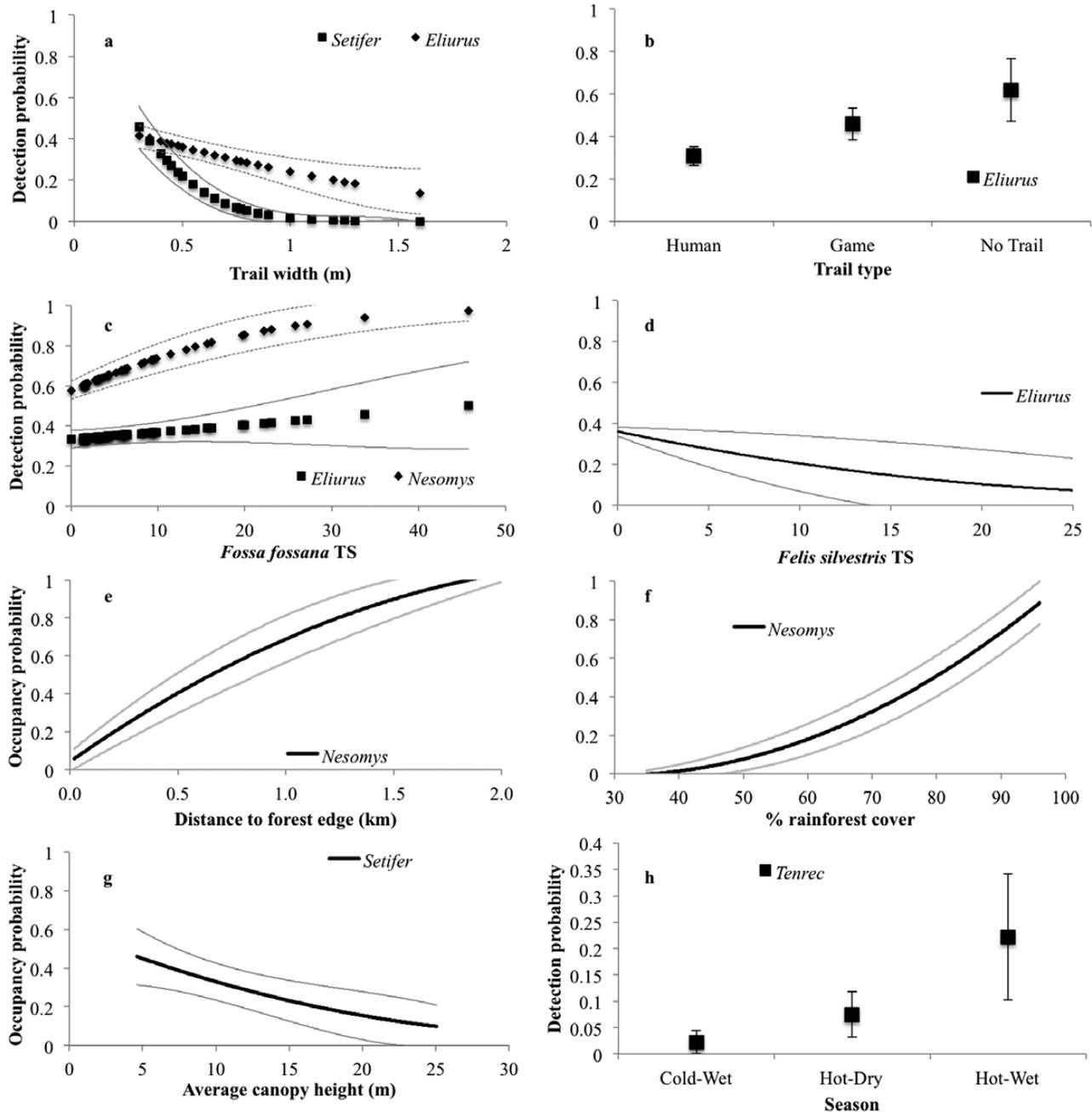
probability ( $\psi = 0.67 \pm SE 0.05$ ) of the 4 small mammal taxa and, although *Eliurus*' top occupancy model included the influence of total number of habitat patches present on the landscape, the relationship was weak (i.e., 95% CI overlapped 0;  $\beta = -0.18 \pm SE 0.18$ ). *Eliurus* landscape detection probability ( $p = 0.31 \pm SE 0.06$ ) was influenced by trail width ( $\beta = -0.38 \pm SE 0.14$ ; Fig. 2a) and type ( $\beta = 0.31 \pm SE 0.09$ ; Fig. 2b), trap success for spotted fanalokas (*Fossa fossana*;  $\beta = 0.11 \pm SE 0.07$ ; Fig. 2c), and trap success for feral cats ( $\beta = -0.20 \pm SE 0.12$ ; Fig. 2d). *Nesomys* had the lowest landscape occupancy probability ( $\psi = 0.38 \pm SE 0.06$ ) and the highest landscape detection probability ( $p = 0.62 \pm SE 0.08$ ) of the 4 small mammal taxa. *Nesomys* occupancy probability was positively related to distance away from forest edge ( $\beta = 1.39 \pm SE 0.27$ ; Fig. 2e) and percent rainforest cover ( $\beta = 1.89 \pm SE 0.39$ ; Fig. 2f), and *Nesomys* detection was positively related to trap success for spotted fanalokas ( $\beta = 0.50 \pm SE 0.14$ ; Fig. 2c).

*Setifer* landscape occupancy and detection probability was  $\psi = 0.42$  ( $SE 0.10$ ) and  $p = 0.23$  ( $SE 0.08$ ), respectively. *Setifer*'s competing models included occupancy as weakly and positively influenced by percent rainforest cover ( $\beta = 0.08 \pm SE 0.17$ ) and trap success for spotted fanalokas ( $\beta = 0.91 \pm SE 0.54$ ); however, average canopy height ( $\beta = -0.52 \pm SE 0.25$ ; Fig. 2g) and trail width ( $\beta = -1.75 \pm SE 0.45$ ; Fig. 2a) had strong negative influences on *Setifer* occupancy and detection probability, respectively. *Tenrec* landscape occupancy probability was  $\psi = 0.46$  ( $SE 0.17$ ), and *Tenrec* had the lowest landscape detection probability ( $p = 0.08 \pm SE 0.05$ ). *Tenrec* occupancy was weakly negatively influenced by tree density ( $\beta = -1.90 \pm SE 1.09$ ), but its detection was strongly influenced by season ( $\beta = 1.06 \pm SE 0.26$ ; Fig. 2h).

**Small mammal occupancy across a habitat degradation gradient.**—Estimates of mean occupancy probabilities for *Eliurus* (intact =  $0.68 \pm SE 0.05$ , intermediate =  $0.67 \pm SE 0.05$ , and degraded =  $0.68 \pm SE 0.05$ ), *Setifer* (intact =  $0.44 \pm SE 0.11$ , intermediate =  $0.37 \pm SE 0.08$ , and degraded =  $0.48 \pm SE 0.09$ ), and *Tenrec* (intact =  $0.55 \pm SE 0.20$ , intermediate =  $0.30 \pm SE$

**Table 3.**—Competing ( $\Delta\text{QAIC} \leq 2.0$ ) single-season landscape occupancy models for *Eliurus*, *Nesomys*, *Setifer*, and *Tenrec*, which were detected during camera-trap surveys at 7 sites in the Makira–Masoala protected areas (northeastern Madagascar; 2008–2011). Included are model weight ( $w_i$ ) and likelihood, number of model parameters ( $k$ ), and model deviance. Covariates with a strongly supported (95% confidence intervals of the beta estimates did not overlapped zero) relationship with occupancy or detection are denoted as positive “(+)” or negative “(–)”; if the relationship with the covariate is not denoted, then the strength and direction of the relationship could not be determined. Description of covariates included in models (also seen in Table 2): totpatches = total number of rainforest, degraded forest, and matrix habitat patches within the 500-m camera-trap grid buffer; tw = width (m) of the trail a camera station was centered on at each study site; tt = the type of trail (no trail, game trail, or human-made trail) that the camera station was focused on; fsts = trap success rate of feral cats (*Felis silvestris*); ffts = trap success rate of spotted fanalokas (*Fossa fossana*); %rf = percent of landscape consisting of rainforest; distedge = distance (km) of camera station from nearest forest edge; canht = average canopy height at camera station; treedens = average tree density at camera station; seas = seas camera-trap survey occurred in (cold–wet = 1, hot–dry = 2, hot–wet = 3); survey = detection varies by survey occasion.  $\Delta\text{QAIC}$  = quasi-Akaike information criterion.

Species	Model	$\Delta\text{QAIC}$	$w_i$	Likelihood	$k$	Deviance
<i>Eliurus</i>	$\psi(\text{totpatches}), p(\text{survey} + \text{tw}(-) + \text{tt}(+) + \text{fsts}(-) + \text{ffts}(+))$	0.00	0.19	1.00	14	938.5
	$\psi(\cdot), p(\text{survey} + \text{tw}(-) + \text{tt}(+) + \text{fsts}(-) + \text{ffts}(+))$	1.72	0.08	0.42	12	951.6
	$\psi(\cdot), p(\text{survey} + \text{tw}(-) + \text{tt}(+))$	1.79	0.08	0.41	11	956.4
<i>Nesomys</i>	$\psi(\%rf (+) + \text{distedge}(+)), p(\text{survey} + \text{ffts}(+))$	0.00	1.00	1.00	12	555.7
<i>Setifer</i>	$\psi(\text{canht}(-) + \text{ffts}), p(\text{survey} + \text{tw}(-))$	0.00	0.52	1.00	12	441.0
	$\psi(\text{canht}(-) + \%rf + \text{ffts}), p(\text{survey} + \text{tw}(-))$	1.41	0.26	0.49	13	440.3
<i>Tenrec</i>	$\psi(\text{treedens}), p(\text{seas}(+) + \text{tt})$	0.00	0.90	1.00	5	238.36



**Fig. 2.**—Response of the occupancy and detection probabilities of 4 native small mammals to landscape- and station-level habitat and carnivoran TS (trap success for carnivorans, from camera-trap surveys) covariates that strongly influenced their occupancy or detection (i.e., beta estimates did not show a 95% confidence interval overlap): a) *Setifer* and *Eliurus* detection probabilities and trail width (m); b) *Eliurus* detection probability and trail type (human, game, and no trail); c) *Nesomys* and *Eliurus* detection probabilities and trap success for spotted fanalokas (*Fossa fossana*); d) *Eliurus* detection probability and trap success for feral cats (*Felis silvestris*); e) *Nesomys* occupancy probability and distance to nearest forest edge (km); f) *Nesomys* occupancy probability and percent rainforest cover; g) *Setifer* occupancy probability and average canopy height (m); and h) *Tenrec* detection probability and season that the survey was conducted in (cold–wet, hot–dry, and hot–wet). Small mammals were detected during camera-trap surveys of 7 forest sites in the Makira–Masoala protected areas, northeastern Madagascar (2008–2011).

0.14, and degraded =  $0.67 \pm SE 0.18$ ) were similar across the habitat degradation gradient. Only *Nesomys* showed a difference in mean occupancy probabilities at intact ( $\psi = 0.71 \pm SE 0.06$ ), intermediate ( $\psi = 0.23 \pm SE 0.05$ ), and degraded ( $\psi = 0.34 \pm SE 0.06$ ) forest sites.

**Annual occupancy probability trends.**—*Eliurus*, *Nesomys*, and *Setifer* each had 2 competing ( $\Delta AIC \leq 2.0$ ) models

(Supplementary Data SD5). The top model for *Eliurus* had local colonization and local extirpation constant throughout the years, and detection probability varying yearly. *Nesomys* also had yearly variations in detection probability, in addition to local colonization and local extirpation varying each year. *Setifer*'s top model included local colonization varying yearly, and local extirpation and detection probability constant

(Supplementary Data SD5). *Eliurus* had similar occupancy probability estimates in the initial ( $\psi = 0.85 \pm SE 0.10$ ) and final ( $\psi = 0.56 \pm SE 0.08$ ) survey years at the resurveyed site, as did *Setifer* (initial =  $0.57 \pm SE 0.13$  and final =  $0.37 \pm SE 0.11$ ), although *Setifer* had a very low occupancy probability in 2013 ( $\psi = 0.08 \pm SE 0.05$ ). *Nesomys* had a much lower occupancy estimate in the final year ( $\psi = 0.29 \pm SE 0.09$ ) compared to the initial year ( $\psi = 0.71 \pm SE 0.10$ ; Supplementary Data SD6).

## DISCUSSION

It is important for conservationists and managers to examine what factors influence species' distribution and detection, especially for understudied species such as Madagascar's native small mammals. Identifying and evaluating these factors will lead to more effective adaptive management plans to ensure long-term protection of these threatened populations. We hypothesized that *Setifer* and *Tenrec* occupancy probabilities would be higher at camera stations that were further from villages and that all small mammal occupancy would be higher at camera stations with lower trap success for feral cats. We also hypothesized that small mammal detection would be negatively related to trap success for exotic carnivorans (particularly feral cats and small Indian civets). Contrary to our hypotheses, *Setifer* and *Tenrec* occupancy were not influenced by distance to village, and no small mammal occupancy or detection was negatively related to trap success for exotic carnivorans, except for *Eliurus* detection with trap success for feral cats. Our hypothesis that small mammal occupancy would be similar across the 3 forest types was unsupported for *Nesomys*, which had higher occupancy at intact sites compared to intermediate and degraded sites. We found no response to habitat disturbance for *Eliurus*, *Setifer*, and *Tenrec*, consistent with other studies that show *Setifer* and *Tenrec* to occur outside natural forest habitat and *Eliurus* showing tolerance to forest disturbance (Stephenson 1995; Goodman et al. 2013, 2016).

Despite having 3 competing models, total number of habitat patches (a measure of habitat patchiness) was the only covariate to have an influence on *Eliurus* occupancy, but the effect was weak (i.e., beta 95% CIs overlap 0). Lehtonen et al. (2001) found that *E. tanala* occupancy probability in south-central eastern Madagascar was related positively to density of fallen logs and negatively related to density of liana stems. We did not measure these habitat characteristics, thus it is possible that *Eliurus* occupancy in the Makira–Masoala region follows these relationships. All covariates that had a strong influence on *Eliurus* only influenced detection. *Eliurus* detection probability was highest on narrow trails and on non-trails or game trails, which might be due to closer proximity of animals to the camera traps on smaller trails, thus enabling better identification of the small-bodied *Eliurus*. As hypothesized, *Eliurus* were detected less often at camera stations with greater trap success for feral cats. Although there is no published research on diets of feral cats in Madagascar, we have photographic evidence of a feral cat preying on a forest rodent (Supplementary Data SD7) and our previous research across this region has highlighted

strong negative relationships between feral cat occupancy and overall trap success for small mammals (Farris et al. 2015a, 2015c). Our result suggests lowered *Eliurus* activity in areas with greater trap success for feral cats, potentially as a way to evade predation (Lazenby and Dickman 2013). Interestingly, *Eliurus* detection was higher at stations with greater trap success for spotted fanalokas—the opposite of what we hypothesized—despite spotted fanalokas preying on small mammals (Goodman 2012). Further studies into interactions between *Eliurus* and spotted fanalokas are warranted.

*Nesomys* had only 1 competing model, and, as we hypothesized, *Nesomys* occupancy probability was higher at camera stations that were further from the forest edge and at study sites with a higher percentage of primary rainforest cover, similar to results for *N. rufus* in south-central eastern Madagascar (Lehtonen et al. 2001). We found no strong influence of canopy cover or total understory on *Nesomys* occupancy, despite positive relationships to these factors elsewhere (Lehtonen et al. 2001). *Nesomys* was the only small mammal taxa that had a higher mean occupancy estimate at intact forest sites compared to intermediate and degraded forest sites, similar to what other studies have found in the region (Stephenson 1995; Andrianjakarivelo et al. 2005). These patterns in *Nesomys* occupancy could be due to a greater abundance of food resources present in intact, core forest (Ryan et al. 1993; Brown et al. 2009), or negative interactions with domestic dogs and feral cats—which overlap temporally with *Nesomys* and have higher occupancy probabilities at degraded forests (Farris et al. 2015b, 2015c)—that we could not measure solely with trap success. Further surveys should focus on determining the factors influencing habitat use by *Nesomys* in northeastern Madagascar. We also found that *Nesomys* detection, like *Eliurus*, was greater at stations with greater trap success for spotted fanalokas. This is likely to be an indirect, habitat-mediated relationship, as it is unlikely that *Nesomys* and spotted fanalokas interact much due to differences in temporal activity patterns (Ryan et al. 1993; Goodman 2012). Further research into interactions between native carnivorans and native small mammals, and how habitat mediates these interactions, would allow us to determine the reason behind the positive relationships between *Eliurus* and *Nesomys* detection probability and trap success for spotted fanalokas.

Rainforest cover, trap success for spotted fanalokas, and average canopy height all influenced *Setifer* occupancy, yet only average canopy height had a strong influence. Contrary to our hypothesis that *Setifer* occupancy probability would be higher at camera stations with taller trees due to use of tree cavities by *Setifer* as nesting sites (Gould and Eisenberg 1966; Eisenberg and Gould 1970; Levesque et al. 2012), *Setifer* occupancy was actually lower at these camera stations. It is possible that the negative relationship with canopy height was due to use of low branches by *Setifer* as resting sites instead (Levesque et al. 2012) or due to some relationship between canopy height and tree cavities that we did not measure. Further research into habitat use by *Setifer* could address these hypotheses. We also found a negative relationship between *Setifer*

detection and trail width, similar to *Eliurus*, which again may be due to easier identification of small-bodied tenrecs on cameras placed on small trails. Finally, contrary to our hypotheses that *Setifer* occupancy would be negatively related to distance to village and trap success for domestic dogs (Golden 2009), we found no relationship between *Setifer* occupancy or detection and distance to village and trap success for domestic dogs. The lack of relationships between *Setifer* parameters and these 2 factors might be due to the use of passive traps—which can be placed throughout the forest—instead of domestic dogs to hunt *Setifer* and *Tenrec* (Golden 2009; Soarimalala and Goodman 2011).

Similar to *Nesomys*, *Tenrec* only had 1 competing model, but unlike *Nesomys*, *Tenrec* occupancy was not strongly influenced by any covariate, contrary to our hypotheses regarding the negative effect of distance to village and trap success for domestic dogs. We believe that the absence of a relationship between *Tenrec* occupancy and distance to village or trap success for domestic dogs is similar to the reason that there was no relationship between these factors and *Setifer* parameters. The absence of any other covariate having an influence on *Tenrec* occupancy could be due to their use of a variety of habitats (Goodman et al. 2016) or our failure to measure a habitat characteristic significant to *Tenrec* ecology; it might also be due to the sparseness of *Tenrec* detections ( $n = 65$ ), which would influence the ability of the models to find a strong relationship between any covariates and *Tenrec* occupancy. The only relationship that we found was between *Tenrec* detection probability and season, with *Tenrec* detected more often during the “hot-wet” season (February–May) and less often during the “cold-wet” season (June–September). *Setifer* and *Tenrec* are both known to enter torpor during the austral winter (June–September); however, Eisenberg and Gould (1970) suggested that *Setifer* as a species could be active year-round, whereas *Tenrec* spends up to 9 months in terrestrial burrows beginning in March (Nicoll 1985; Soarimalala and Goodman 2011; Lovegrove et al. 2014). This result, and what is known regarding *Tenrec* ecology, corroborates that the time of year a survey is conducted can influence attempts to characterize small mammal occupancy, species richness, and community composition in Madagascar (Stephenson 1994).

In addition to detecting 6 native small mammals, we also detected introduced *Rattus* at 4 sites. *Rattus* is widespread across Madagascar (Soarimalala and Goodman 2011) and it is possible that due to considerable dietary overlap, potential disease transmission, and the possibility of intraguild predation, *Rattus* might negatively impact native small mammals (Goodman 1995; Harris 2008). Despite this, few studies have shown evidence of negative interactions between *Rattus* and native small mammals in Madagascar (Lehtonen et al. 2001; Ramanamanjato and Ganzhorn 2001; Ganzhorn 2003). Our study found *Rattus* to be relatively widespread in the Makira–Masoala region (detected at 4 out of 7 sites) but present at low rates. Future research should examine the nature of any potential interactions between *Rattus* and the native small mammal community.

*Study limitations, implications, and future research.*—While our camera traps were placed low to the ground to detect Madagascar’s relatively small-bodied native carnivorans, it is likely that our ability to detect and identify Madagascar’s small mammals was influenced by species characteristics (e.g., body size) and characteristics of camera traps such as trigger speed (Glen et al. 2013), whether a camera had white-flash or infrared capabilities (Glen et al. 2013; Meek and Vernes 2016), and photo quality (Glen et al. 2013; Rovero et al. 2013). These influences could have caused us to underestimate the presence of the smaller-bodied taxa (e.g., *Microgale* spp. and *H. semispinosus*; Supplementary Data SD1 and SD2; Anile and Devillard 2016). Despite this, we obtained relatively high detection rates of small mammals across the Makira–Masoala protected areas to use in examining how habitat and sympatric carnivorans influence distributions of native small mammals in Madagascar.

In addition, our efforts to examine annual trends in small mammal distribution at a resurveyed site (Supplementary Data SD5 and SD6) were hampered by the lack of validated goodness-of-fit tests for dynamic occupancy models (Mackenzie et al. 2005; Fiske and Chandler 2011). We saw what may be a downward trend in *Nesomys* occupancy; however, we urge caution in extrapolating this result until goodness-of-fit tests are developed for multi-season occupancy models to address potential overdispersion. We suggest that livetrapping and mark–recapture methods be used to monitor the trends in small mammal populations and recommend these methods for any future studies aiming to examine annual changes in small mammal abundance or density at resurveyed sites.

Our findings provide important information on habitat associations of native small mammals (e.g., *Nesomys* and percent rainforest cover) and factors that influence small mammal detection by camera trap (e.g., *Tenrec* and season of survey). We were surprised to find no clear response of small mammal occupancy to trap success for feral cats, but we believe that further studies using other methods (i.e., examining diets of feral cats, estimating trends in abundance of small mammals at sites with feral cats) are necessary before stating that there is no negative effect of feral cats—or other exotic carnivorans—on populations of native small mammals (Bonnaud et al. 2011; Medina et al. 2011; Farris et al. 2015a). Our results showing higher *Nesomys* occupancy at intact forests, and higher occupancy probabilities at camera stations further from forest edge and at sites with higher percentage of primary rainforest cover, suggest that *Nesomys* distribution is connected to intact habitat and raises concerns about the future status of this species as habitat is further degraded in the region. Conservation and management organizations should focus on determining the reasons for this relationship between *Nesomys* and intact habitat and determine how best to manage *Nesomys* populations in the face of continued habitat disturbance and loss. Finally, based on the information we were able to obtain using incidental observations, we suggest that camera traps are a valid method for obtaining valuable knowledge on distributions of small mammals, but that future surveys should take into careful consideration characteristics of

camera traps (e.g., trigger speed or photo quality) to increase inference possible for small mammal ecology.

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### SUPPLEMENTARY DATA

**Supplementary Data SD1.**—Representative camera-trap photographs of the 6 endemic small mammals detected during camera-trap surveys at 7 sites in the Makira–Masoala protected areas in northeastern Madagascar (2008–2011): A) tufted-tailed rat (*Eliurus* sp.), B) lowland streaked tenrec (*Hemicentetes semispinosus*), C) shrew tenrec (*Microgale* sp.), D) red forest rat (*Nesomys* sp.), E) greater hedgehog tenrec (*Setifer setosus*), and F) common tenrec (*Tenrec ecaudatus*).

**Supplementary Data SD2.**—Natural history information on the 6 small mammal taxa—*Eliurus*, *Hemicentetes*, *Microgale*, *Nesomys*, *Setifer*, and *Tenrec*—detected during camera-trapping surveys of 7 sites across the Makira–Masoala protected areas in northeastern Madagascar (2008–2011).

**Supplementary Data SD3.**—Survey details for the initial and subsequent camera-trap surveys of small mammal populations at one resurveyed site in the Makira protected area (northeastern Madagascar, 2008–2015). We show trap success rates (TS) for 4 of the 6 native small mammals—*Eliurus* (E), *Nesomys* (N), *Setifer* (S), and *Tenrec* (T)—that were detected at the site, as these were the 4 we attempted to estimate annual occupancy probabilities using multi-season occupancy models in the program PRESENCE for (see **Supplementary Data SD5** and **SD6**).

**Supplementary Data SD4.**—List of 41 potential covariates that could have been used in landscape single-season occupancy analyses of 4 native small mammal taxa that were detected during camera-trap surveys of 7 sites in the Makira–Masoala protected areas, northeastern Madagascar (2008–2011). Based on the results of a Pearson’s correlation and what we know of small mammal ecology in Madagascar, we narrowed this list of covariates down to 19 that we used in the single-season occupancy analyses.

**Supplementary Data SD5.**—Competing ( $\Delta\text{AIC} \leq 2.0$ ) multi-season annual occupancy models for *Eliurus*, *Nesomys*, and *Setifer* at 1 of the 7 sites surveyed using camera traps in the Makira–Masoala protected areas (northeastern Madagascar; 2008–2015). Included are model weight ( $w_i$ ) and likelihood, and number of model parameters ( $k$ ). We were unable to run dynamic occupancy models for *Tenrec* due to very low detections through the years.

**Supplementary Data SD6.**—Annual occupancy probabilities as estimated by multi-season models in program PRESENCE for A) *Eliurus*, B) *Nesomys*, and C) *Setifer* at the resurveyed forest site, 1 of the 7 forest sites photographically sampled with camera traps for small mammals in the Makira–Masoala protected areas, northeastern Madagascar (2008–2015). Error bars are 95% confidence intervals.

**Supplementary Data SD7.**—Camera-trap image of a feral cat (*Felis silvestris*) preying on an unidentified small mammal in the Makira and Masoala protected areas, northeastern Madagascar.

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