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The times they are a changin': Multi-year surveys reveal exotics replace native carnivores at a Madagascar rainforest site

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ABSTRACT

Surveys across multiple seasons or years are necessary to evaluate the effects of dynamic processes on long-term persistence of wildlife populations, such as effects of exotic species on native species populations. Unfortunately, multi-year surveys are rare, particularly for rainforest carnivore populations, and managers often rely on single-season/year, 'snapshot' surveys that produce static estimates of population parameters. Here we provide results using single-species, multi-year occupancy modeling from a six-year survey (2008–2013) of a rainforest carnivore community at a 15 km^2 area study site within the newly established Makira Natural Park, Madagascar. We demonstrate a precipitous decline in the native carnivore community with four of the six native carnivores (falanouc *Eupleres goudotii*, ring-tailed vontsira *Galidia elegans*, broad-striped vontsira *Galidictis fasciata*, and brown-tailed vontsira *Salanoia concolor*) decreasing by at least 60% over this six-year period. In addition, we observed two exotic carnivores (small Indian civet *Viverricula indica* and feral cat *Felis* species) colonize this study site with *Felis* species increasing in occupancy from 0 to 0.68 by the final year. Further, we demonstrate how variables associated with human encroachment (i.e. distance to forest edge and nearest village) are most important for explaining these trends in native carnivore extirpation and exotic carnivore colonization. These findings provide additional evidence on the threat posed to native carnivore populations by the expansion of exotic carnivores worldwide. We highlight the striking increase in extirpation, and the factors influencing such changes, for native carnivores. In this manuscript, we point to the limited number of multi-year surveys to evaluate dynamic processes on long-term persistence of native wildlife populations, as well as the lack of exotic carnivore control programs in threatened ecosystems in many developing nations as factors limiting our ability to effectively conserve biodiversity across the globe.

1. Introduction

Long-term persistence of species is the ultimate goal of conservation and management science. Dynamic processes affecting long-term persistence include not just intrinsic demographic processes (birth, immigration, death, emigration), but also extrinsic factors including, but not limited to, climate change, habitat change, disease, and additional metrics associated with human encroachment (Bellard et al., 2012; Garcia et al., 2014; Rybicki and Hanski, 2013; Sleeman, 2013). Multi-year and/or multi-season surveys are required to both measure dynamic processes and determine factors that influence persistence and local dynamics of target species (MacKenzie et al., 2006; Magurran et al., 2010; Rosenblatt et al., 2014). Multi-year surveys allow researchers to investigate environmental drivers and rates of change for various population parameters (Clutton-Brock and Sheldon, 2010; MacKenzie et al., 2003), providing valuable insight into species viability (Dickman, 2013; Lindenmayer et al., 2012).

Unfortunately, long-term or multi-year surveys are especially rare for elusive species occupying tropical forest ecosystems. Tropical environments are important for conservation as they are often associated with high levels of biodiversity; however, high point estimates of biodiversity do not necessarily equate to long-term persistence of species (Sales et al., 2015). Tropical rainforest ecosystems continue to be fragmented and/or degraded as a result of resource demands associated with a burgeoning human population (Hansen et al., 2013). In addition, tropical forest ecosystems face mounting pressure from additional anthropogenic factors including climate change, pathogens, bushmeat hunting and consumption, and exotic species (Laurance, 2015). Despite

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a large increase in the number of protected areas across the tropics in the last three decades (Naughton-Treves et al., 2005), attempts to quantify the effectiveness of these protected areas in conserving these ecosystems and the species therein, remain sparse (Beaudrot et al., 2016; Dickman, 2013). To develop targeted management plans that address these wide-ranging anthropogenic pressures, scientists require long-term or multi-year surveys to evaluate and monitor population trends and ensure the effectiveness of resulting management strategies.

Studies of rainforest carnivore populations are often restricted to single-year photographic (camera-trap) surveys with the aim of estimating population parameters (i.e. occupancy, abundance, and/or density). These single-year, 'snapshot' surveys, which provide static parameter estimates (e.g., occupancy and/or density), are of great importance to conservationists working to develop targeted management plans, as these estimates are lacking for many rainforest carnivore communities. However, given the dynamic, ongoing anthropogenic pressures threatening rainforest ecosystems, snapshot estimates may misinform managers regarding the capacity of a forest site to sustain these species (Krauss et al., 2010; MacKenzie et al., 2006; Sales et al., 2015). For example, static estimates may provide a pattern in species occurrence across the landscape, but they fail to identify complex processes such as impending declines via extinction debt (Essl et al., 2015; Kuussaari et al., 2009; Wearn et al., 2012). As a result, static estimates may result in misrepresentative conclusions, which can impair and mislead management efforts (Krauss et al., 2010; Kuussaari et al., 2009).

Madagascar's carnivores (*Eupleridae*) are perhaps the most threatened and least studied carnivore family in the world (Brooke et al., 2014). Recent research has highlighted the threats posed to endemic carnivores as a result of forest loss, degradation, and fragmentation (Farris et al., 2015d; Gerber et al., 2012b; Kotschwar et al., 2014), bushmeat hunting and consumption (Farris et al., 2015d; Golden, 2009; Goodman, 2012; Jenkins et al., 2011), exotic carnivores (Farris et al., 2015a,b,c; Gerber et al., 2012a,b), and alien, invasive prey species (Brown et al., 2016). However, studies on these threatened carnivores to date are confined to single-year, static estimates. Long-term, multi-year surveys are needed to better understand the impacts of dynamic processes on this endemic carnivore community. Our goal was to provide the first multi-year assessment of Madagascar's rainforest carnivore community. To that end, our first objective was to estimate single-species, multi-year occupancy and evaluate changes in occupancy, local extirpation, and colonization. Our second objective was to evaluate the importance of various habitat, landscape, and co-occurring species variables on parameter estimates.

2. Methods

2.1. Study site

From 2008 to 2013, we conducted photographic surveys at 24 locations over ~15 km^2 area to sample the carnivore community at a study site within Makira Natural Park (NP), Madagascar (Fig. 1). We are unable to reveal the precise location of this site due to permit requirements resulting from previous work on bushmeat hunting at this location. This study site was established in 2007 as a long-term research study site as it protects at least 12 species of lemurs (Murphy et al., 2016; Rasolofoson et al., 2007), including the critically endangered silky sifaka and red-ruffed lemur *Varecia rubra*. Previous work at this study site (Farris and Kelly, 2011; Farris et al., 2012, 2014) has reported the presence of six native carnivore species, including (with current IUCN Red List status) the fosa *Cryptoprocta ferox* (Vulnerable), falanouc *Eupleres goudotii* (Vulnerable), spotted fanaloka *Fossa fossana* (Vulnerable), ring-tailed vontsira *Galidia elegans* (Least Concern), broad-striped vontsira *Galidictis fasciata* (Vulnerable), and brown-tailed vontsira *Salanoia concolor* (Vulnerable) (IUCN, 2016). Surveys across this region have revealed exotic carnivores (domestic dog *Canis familiaris*, domestic/feral cat *Felis* species, and small Indian civet *Viverricula indica*) to overlap both temporally and spatially with native carnivores and thus potentially negatively impact native carnivore populations (Farris et al., 2015a,b). While the period of colonization is unknown, it is believed that *C. familiaris* and *Felis* species were introduced by the first human colonizers and *V. indica* was introduced by traders during the Islamic period (between 700 and 1200; Goodman, 2012).

The study site is located near the Antainambalana River and lies adjacent to two villages having population sizes of approximately 1500 and 2300. This steep terrain, low elevation rainforest study site is positioned along a hard edge where forest has been cleared for cattle (zebu) grazing and cultivation. Degraded forest and invasive plant species are prominent along the edge, but the forest transitions into secondary forest growth within approximately 100 m. We found evidence of forest cutting and lemur hunting each year within the study site; however, these forms of anthropogenic disturbance were rare and not widespread. Human trails are present throughout the forest with two

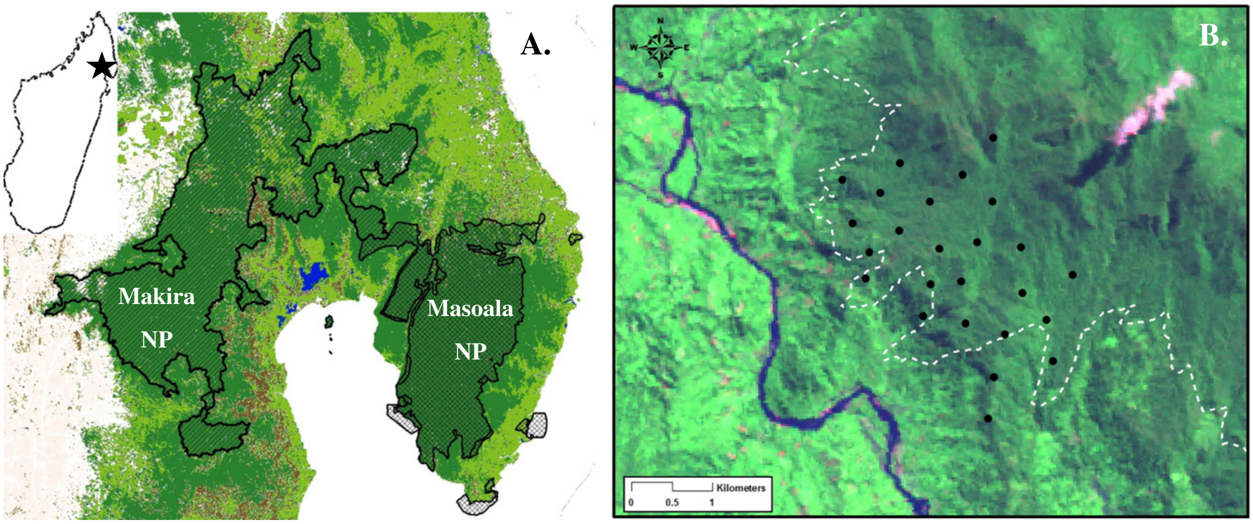

Fig. 1. Land cover maps revealing A) the location of the Makira Natural Park (left) and Masoala National Park (right) and B) the camera trap (black circles) layout used for photographic surveys from 2008 to 2013 and the park boundary (white dashed line) for Makira Natural Park. Maps include forest cover (dark green), degraded forest and/or non-forest (light green), and the location of the Antainambalana River (dark blue).

prominent trails leading directly into the core forest with secondary human trails and game trails branching from these primary trails.

Construction of a permanent research cabin took place within the forest study site in 2012. This construction consisted of clearing a patch of secondary forest (~2500 m^2) and creating a new trail to the construction site. During construction, human and dog activity increased greatly at the building site and on the primary trail leading into the forest. This newly constructed housing structure is used intermittently by researchers and tourists, but there is no permanent presence at the research cabin. Additional forms of disturbance include the presence of zebu (*Bos taurus*) and exotic bush pigs (*Potamochorerus larvatus*) within the study site; however, their presence (noted by signs of disturbance, scat, and camera trap photos) does not appear to be widespread with most activity occurring within 2 km of the forest edge.

2.2. Photographic sampling

We conducted photographic sampling by establishing a camera trap grid consisting of 24 camera stations (only 20 camera stations were used in initial survey in 2008) throughout the study site. Each camera station consisted of two digital (Reconyx PC85 & HC500, Wisconsin, USA; Moultrie D50, D55, & M550, Alabama, USA; Cuddeback IR, Wisconsin, USA) and/or film-loaded (DeerCam DC300) remote sensing cameras placed approximately 10–30 cm off the ground to capture passing wildlife. When possible, we paired cameras with a different model and/or brand to account for differences in trigger speed, flash, or photo quality. We programed cameras to take up to three photos when triggered (dependent upon model) and set cameras to high sensitivity. We placed camera stations on opposing sides of existing human and/or game trails within all available habitat types (contiguous forest, degraded forest, edge habitat, and non-forest or early succession growth locally termed *savoka*). We placed camera stations both inside the Makira NP ($n = 19$) and outside the protected area within a local community managed forest area ($n = 5$; Fig. 1) and we checked cameras every 3–5 days to ensure proper function and to change memory cards or film. The boundary of the protected area and/or community managed zone is not marked and camera stations located outside the protected area boundary were more likely to be located in degraded habitat due to their close proximity to the forest edge.

To eliminate seasonal variation we surveyed this site between August and November every year from 2008 to 2013, excluding 2009 when a coup d'état occurred in Madagascar. To provide adequate photo captures for estimating detection while ensuring a closed population, we surveyed for an average of 65 (± SD 10) days per survey. Elevation within the camera grid ranged from 350 m to 690 m. We spaced camera stations at approximately 500 m intervals (min. = 328 m and max. = 606 m) as this is equal to or larger than the estimated home range of native carnivore species (Goodman, 2012), excluding the larger-bodied fosa *Cryptoprocta ferox*, which allowed us to estimate the true occupancy of these smaller carnivore species. We did not use any bait or lure during our surveys. The data collected and analyzed for this manuscript have been archived with the Wildlife Conservation Society (WCS Program, 2300 Southern Boulevard Bronx, New York 10460). These data can be made available upon request by contacting the lead author.

2.3. Data analyses

2.3.1. Trap success

We defined a capture event as all photos taken of a given species within a 30-minute period. This time period was chosen to ensure independence between unique capture events (Di Bitetti et al., 2006). We defined a trap night as a 24-hr period in which at least one camera trap at a given camera station was properly functioning and collecting data. We calculated grid-level trap success for all native and exotic carnivores per survey/year by dividing the total number of capture events for a given survey/year by total trap nights and multiplied by 100. This grid-level trap success value provided us with an estimate of activity for all native and exotic carnivore species across the entire study site for comparison across years. In addition, for use in our occupancy models we also calculated station-level trap success for each camera station for each year of the survey. This station-level trap success provided us with a measure of activity at each individual camera station to evaluate how activity of a given species may influence the occupancy, colonization, and/or extirpation of our target carnivore species.

2.3.2. Multi-year occupancy estimation

To evaluate changes in native and exotic carnivore populations across this six-year time period and to gain inference on processes influencing the carnivore community within this site, we used single-species, multi-season occupancy modeling, where season refers to subsequent years (hereafter multi-year estimation). We explicitly modeled potential changes in the occupancy over time using colonization and local extirpation probabilities (MacKenzie et al., 2006), where colonization is the probability that an unoccupied site (i.e. camera station) during year t will become occupied at $t_{+1,}$ and extirpation is the probability that a site that was occupied during year t will become unoccupied at t_{+1} (MacKenzie et al., 2006). This modeling approach allows for the state of parameters (occupancy, detection, colonization, and extirpation) to change between surveys or years, but these parameter states are 'closed' both geographically and demographically within survey/year (MacKenzie et al., 2006), similar to Pollock's robust design in mark-recapture studies (Pollock, 1982).

To model multi-year occupancy we created capture histories for each native and exotic carnivore species where 1 signifies detection and 0 is no detection and we collapsed these capture occasions into six day intervals to improve model convergence. This is resulted in $n = 9$ (min; 2013) to $n = 14$ (max; 2012) capture occasions per year. To investigate factors influencing extirpation probabilities of native carnivores, we estimated occupancy and extirpation directly and derived colonization (e.g. seasonal occupancy and extinction parameterization; MacKenzie et al., 2006). To investigate factors influencing colonization probabilities of exotic carnivores, we estimated occupancy and colonization directly and derived extinction (e.g. seasonal occupancy and colonization parameterization; MacKenzie et al., 2006). We accounted for all model assumptions for single-species, multi-season (i.e. multi-year) occupancy modeling, including 1) no un-modeled heterogeneity in parameters; 2) sites are 'closed' demographically and geographically within the survey period; 3) detection is independent; and 4) target species are accurately identified (MacKenzie et al., 2006). To evaluate variables influencing changes in model parameters across years, we included the following camera station level covariates into our multi-year occupancy models: distance to edge (m), distance to village (km), canopy height (m), percent canopy cover, elevation (m), trail width (m), trail type, and percent total understory. In addition, we included covariates that varied by survey occasion and year, including: human (non-researcher), dog, cat, bush pig, and small mammal, station-level trap success. For exotic carnivore models we excluded dog and cat trap success. We normalized all variables, thus allowing resulting beta values from models to be compared.

We established our a priori models, based on species-specific, biologically relevant information, we ran these models in program PRESENCE (Hines, 2006), and used Akaike Information Criterion (AIC) and model selection to rank models (Akaike, 1973). We reported all competing models (ΔAIC $\leq$2.0) and evaluated the importance and/or effect of covariates on carnivore occupancy and detection using beta estimates from our highest-ranking model. If 95% confidence interval limits did not overlap among years we considered this evidence of changes in occupancy among years. Where multi-year occupancy model convergence was not possible for a given species (due to low capture rates), we used single-season occupancy modeling (hereafter single-year occupancy) and provided individual estimates of occupancy for each survey year.

In these cases, we did not report estimates of colonization or extirpation for these species. Finally, to estimate projections in occupancy trends (assuming observed dynamics from 2008 to 2013) we calculated the occupancy equilibrium (λ) for each species using the following equation from MacKenzie et al. (2006), where γ represents probability of colonization and ε represents probability of extirpation:

$$\lambda t = \gamma/(\gamma + \varepsilon)$$

3. Results

Our five photographic surveys from 2008 to 2013 resulted in an average of 1337 (±SD 130) trap nights per survey/year and provided a total of 32,861 captures of wildlife and humans (non-researchers), including 2791 captures of six native carnivores and 363 captures of three exotic carnivores. *Fossa fossana* had the highest grid-level trap success of any carnivore, native or exotic, across all surveys; however, their activity per 100 trap nights decreased considerably from 2008 (13.91 ± SE 2.64) to 2013 (3.59 ± SE 1.05). *Galidictis fasciata* had the lowest grid-level trap success of any native carnivore, followed closely by *Salanoia concolor* (Table 1). *Cryptoprocta ferox* had the lowest change in grid-level trap success across the six-year sampling period. For exotics, *C. familiaris* had the highest initial grid-level trap success, but its activity (as measured by trap success) decreased over this six-year period. *Felis* species had the greatest increase in grid-level trap success of any carnivore species with no captures in 2008 and up to 2.01 (±SE 0.60) by 2012 (Table 1). Overall, birds and small mammals showed the greatest change in grid-level trap success with birds decreasing from 62.85 ± SE 9.26 (2008) to 8.43 ± SE 2.94 (2013) and small mammals decreasing from 42.31 ± SE 6.84 (2008) to 3.52 ± SE 1.52 (2013).

Our multi-year occupancy results revealed that four of the six native carnivore species (*E. goudotii, G. elegans, G. fasciata*, and *S. concolor*) had strong declines in occupancy over this six-year period (Fig. 2A). In particular, *E. goudotii, G. fasciata*, and *S. concolor* showed at least a 60% decrease in occupancy from 2008 to 2013. As a result, each of these native carnivores had high probabilities of local extirpation (i.e. sites previously occupied became unoccupied in subsequent years) with *S. concolor* and *G. fasciata* having the highest extirpation estimates (0.49 ± SE 0.13 and 0.60 ± SE 0.12, respectively; Table 2). Conversely, *C. ferox* showed little to no change in occupancy during this same time frame (Fig. 2A) and *F. fossana*, showed only a slight decrease in occupancy from 2008 (1.0 ± SE 0.0) to 2013 (0.80 ± SE 0.08; Fig. 2A). As a result, these two carnivores had moderate (0.14 ± SE 0.05 for *F. fossana*) or low (0.02 ± SE 0.05 for *C. ferox*) probabilities of local extirpation (Table 2). Due to low capture rates, we had to estimate single-year occupancy for *G. elegans* and use naïve occupancy estimates (imperfect detection not accounted for) for three of the years (2010 − 2012).

For exotic carnivores we found that *C. familiaris* occupancy decreased slightly from 2008 (0.47 ± SE 0.17) to 2013 (0.27 ± SE 0.10; Fig. 2B) and, as a result, had a moderate probability of local colonization (0.24 ± SE 0.11; i.e. probability that an unoccupied site became occupied in subsequent years; Table 2). Conversely, *Felis* sp. exhibited a large increase in occupancy from 0.0 in 2008 to 0.68 (±SE 0.16) by 2013 (Fig. 2B) and a high probability of local colonization (0.52 ± SE 0.23; Table 2). We did not have sufficient captures of *V. indica* to estimate multi-year or single-year occupancy. This exotic carnivore was not captured in 2010 and 2013 and had no more than two captures in other years (Table 1).

Understory cover and year of survey had the greatest influence on carnivore detection followed by type of trail (Table 2). Understory cover was positively associated with *C. ferox* and *S. concolor* detection, but negatively associated with *F. fossana* and *G. fasciata* detection. *Canis familiaris* detection had a strong positive association with human trails ($\beta = 3.42$ ± SE 1.08) while *E. goudotii* detection varied little between human and game trails ($\beta = 0.80$ ± SE 0.33). Distance to edge of the forest had the greatest influence on native carnivore occupancy (Table 2) with occupancy decreasing near villages for *C. ferox* ($\beta = 0.86$ ± SE 1.23) and *G. fasciata* ($\beta = 5.57$ ± SE 3.79). However, for other native carnivores distance to edge had less support (lower AIC weight) than constant occupancy (Table 2). For native carnivores, *G. fasciata* probability of extirpation decreased with increasing distance to edge ($\beta = -2.80$ ± SE 1.18) while *S. concolor* extirpation increased with increasing distance to edge ($\beta = 2.07$ ± SE 1.07; Fig. 3A). *Fossa fossana* local extirpation probability was best explained by human (non-researcher) trap success ($\beta = 0.12$ ± SE 0.001; Table 2). For exotic carnivores, the probability of local colonization for *C. familiaris* was best explained by distance to nearest village ($\beta = -2.55$ ± SE 1.17) with sites within 2 km of local villages having a considerably higher probability of colonization (Fig. 3B).

Based on estimates of colonization (γ) and extirpation (ε) for each native and exotic carnivore we found the occupancy expected at equilibrium was lower than the observed occupancy for *C. ferox*, *E. goudotii*, *G. fasciata*, and *S. concolor* (Fig. 4), indicating strong decreasing population trends. Alternatively, the occupancy at equilibrium for *Felis* sp. was higher than the observed occupancy, showing an increasing population. For both native *F. fossana* and exotic *C. familiaris* the occupancy expected at equilibrium was similar to the observed occupancy, suggesting these two carnivores are in equilibrium (Fig. 4). Our inability to calculate colonization and extirpation probabilities for *G. elegans* prevented us from calculating its occupancy equilibrium.

Table 1
Summary of photographic surveys and activity levels (calculated as grid-level trap success TS per 100 trap nights) of native and exotic (in bold) carnivores, as well as birds, small mammals, and bush pigs by year at the study site within the Makira Natural Park, Madagascar.

Survey	2008	2010	2011	2012	2013
Survey dates	Sept. 02–Nov. 11	Sept. 17–Nov. 16	Aug. 20–Oct. 24	Aug. 1–Oct. 14	Sept. 9–Oct. 28
Trap nights	1315	1257	1383	1536	1198
Fosa (*C. ferox*) TS[a]	3.01 (0.98)	2.18 (0.67)	1.30 (0.49)	1.58 (0.45)	3.39 (0.67)
Spotted fanaloka (*F. fossana*) TS	13.91 (2.64)	11.93 (2.21)	9.04 (2.05)	3.16 (0.84)	3.59 (1.05)
Falanouc (*E. goudotii*) TS	3.08 (0.89)	2.02 (0.66)	2.64 (1.63)	1.18 (0.67)	1.09 (0.75)
Ring-tailed vontsira (*G. elegans*) TS	1.33 (0.45)	1.49 (0.38)	1.00 (0.33)	0.37 (0.20)	0.25 (0.18)
Broad-striped vontsira (*G. fasciata*) TS	2.57 (0.86)	1.13 (0.51)	0.26 (0.20)	0.25 (0.15)	0.25 (0.13)
Brown-tailed vontsira (*S. concolor*) TS	0.98 (0.30)	0.82 (0.43)	1.59 (0.94)	0.39 (0.21)	0.66 (0.38)
Domestic dog (*C. familiaris*) TS	1.97 (1.15)	0.98 (0.52)	1.08 (0.58)	0.65 (0.26)	0.41 (0.20)
Wild/feral cat (*Felis* species) TS	0 (0)	0.20 (0.11)	0.26 (0.12)	2.01 (0.60)	0.92 (0.29)
Small Indian civet (*V. indica*) TS	0.14 (0.14)	0 (0)	0.07 (0.07)	0.14 (0.09)	0 (0)
Total bird[b] TS	62.85 (9.26)	37.06 (4.86)	25.56 (5.44)	11.35 (2.57)	8.43 (2.94)
Total small mammal[b] TS	42.31 (6.84)	27.79 (7.25)	18.12 (2.98)	4.32 (1.29)	3.52 (1.52)
Bush pig (*P. lavartus*) TS	0.07 (0.07)	0.47 (0.47)	0.46 (0.29)	0.69 (0.27)	0.33 (0.19)

[a] TS: trap success is the number of independent photos of a target species across the entire survey grid divided by the trap nights multiplied by 100.

[b] For list of all bird and small mammal species captured during these surveys see (Murphy (2015)).

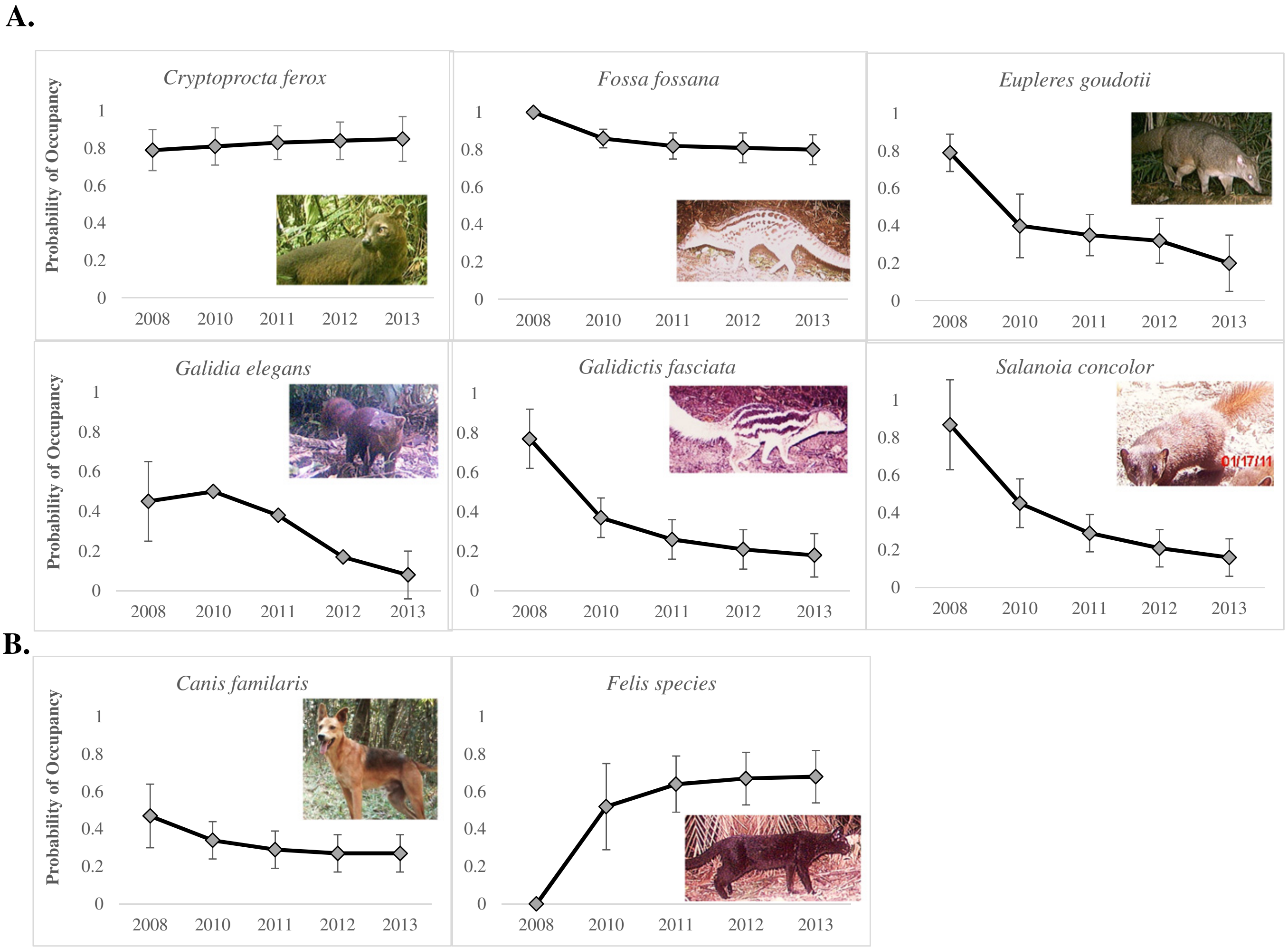

Fig. 2. Line graph demonstrating the multi-year trends in occupancy for A) four native carnivores and B) two exotic carnivores. Photographic surveys were conducted from 2008 to 2013 at a newly established study site within the Makira Natural Park, Madagascar.

4. Discussion

Multi-year surveys are important for developing targeted management and conservation plans as they provide robust estimates of parameters that capture changes in population states resulting from dynamic ecosystem processes. We demonstrate the effectiveness of a multi-year survey and modeling approach to investigate the persistence of a rare, elusive rainforest carnivore community. Alarmingly, we found that four of the six native carnivores in this community decreased in occupancy by at least 60% over a six-year period, resulting in low occupancy equilibrium estimates. In addition, we observed two exotic carnivores (feral cat *Felis* species and small Indian civet *V. indica*) colonize this site, domestic dog occupancy to remain relatively stable, and *Felis* species increase in occupancy from 0 to 0.68 by the final year.

Table 2
Top-ranking models (ΔAIC ≤2) for single-species, multi-year occupancy (psi) estimation for native and exotic (bold) carnivores, including model name, AIC value, ΔAIC, AIC weight (wt.), and estimates (SE) of colonization (gamma), local extirpation (eps), and detection (p). We conducted surveys of carnivores in the Makira Natural Park, Madagascar from 2008 to 2013.

Species	Model	AIC	ΔAIC	AIC wt	γ	ε	p
C. ferox	psi, gamma, eps, p(Under × Year)	322.50	0	0.28	–	0.02 (0.05)	0.13 (0.03)
	psi(Edge), gamma, eps, p(Under × Year)	323.61	1.11	0.16			
F. fossana	psi, gamma, eps(Human), p(Under × Year)	1332.27	0	0.58	–	0.14 (0.05)	0.34 (0.04)
E. goudotii	psi(Human), gamma, eps, p(TrType)	565.82	0	0.21	–	0.31 (0.10)	0.18 (0.03)
	psi, gamma, eps, p(TrType)	566.65	0	0.14			
G. fasciata	psi(Edge), gamma, eps(Edge), p(Under)	334.65	0	0.51	–	0.60 (0.12)	0.11 (0.02)
	psi, gamma, eps(Edge), p(Under)	336.59	1.94	0.19			
S. concolor	psi, gamma, eps(Edge), p(Under × Year)	319.11	0	0.49	–	0.49 (0.13)	0.17 (0.06)
	psi(Edge), gamma, eps(Edge), p(Under × Year)	321.11	2.00	0.18			
C. familiaris	psi, gamma(Village), eps, p(TrType)	287.85	0	0.46	0.24 (0.11)	–	0.08 (0.02)
	psi(Village), gamma, eps, p(TrType)	288.33	0.48	0.36			
***Felis* species**	psi, gamma, eps, p(Year)	332.89	0	0.18	0.52 (0.23)	–	0.06 (0.03)
	psi, gamma, eps, p(Year × TrType)	333.16	0.27	0.16			

Under = percent understory cover; Edge = nearest distance to edge; Human = human (non-researcher) trap success; Cat = feral cat trap success; TrType = trail type; Dog = domestic dog trap success; Village = distance to nearest village colonization (gamma) – probability that a previously unoccupied site becomes occupied in subsequent survey; extirpation (eps) – probability that a site previously occupied becomes unoccupied in subsequent surveys.

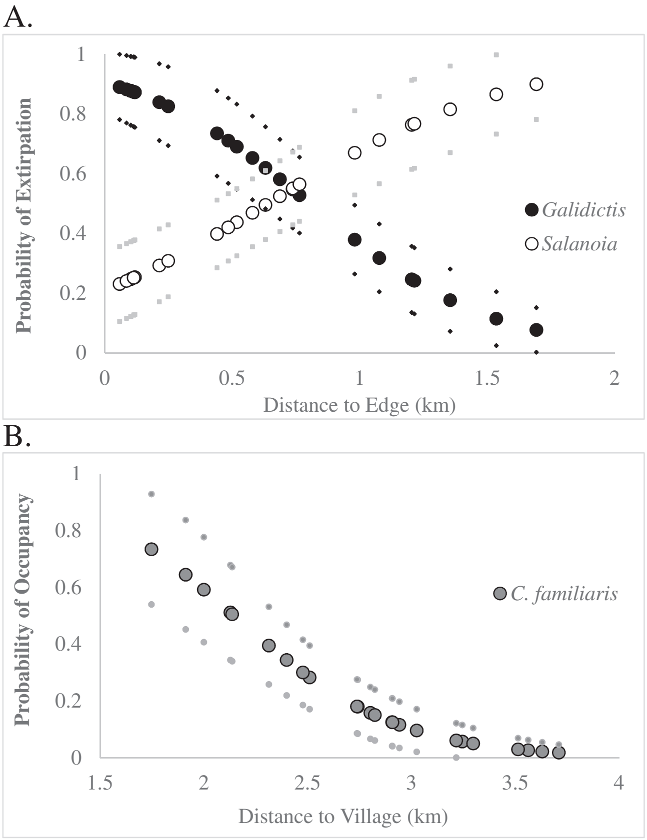

Fig. 3. Graph revealing A) probability of local extirpation in relation to distance to edge for broad-striped vontsira *Galidictis fasciata* and brown-tailed vontsira *Salanoia concolor* and B) probability of colonization for domestic dog *Canis familiaris* in relation to distance to village. Photographic surveys were conducted from 2008 to 2013 within the Makira Natural Park, Madagascar.

Single-year, static estimates provided from the first year would have provided managers with misleading and incomplete findings, thus missing the dynamic processes threatening native carnivore persistence.

The largest native carnivore, *C. ferox*, had relatively high and stable occupancy across the six-year period; however, we highlight an occupancy equilibrium that falls below observed occupancy, suggesting a decreasing population. *Cryptoprocta ferox* populations may be more stable and tolerant to various forms of anthropogenic disturbance compared to the five other native carnivore species. Conversely, the large home range and daily movements of *C. ferox* likely encapsulates numerous camera stations and potentially the entire camera grid. The spacing of our cameras (~500 m) was selected based on the home ranges of the five smaller-bodied and less expansive native carnivore species. The absence of reliable individual markings on *C. ferox* prevented us from identifying the number of individuals present or the distances moved across years/surveys. As a result, our occupancy estimates for *C. ferox* are more accurately defined as probability of site use rather than true occupancy. To better understand and provide more reliable estimates of yearly changes in *C. ferox* occupancy, we need photographic surveys conducted over larger areas that include a wider range of degradation.

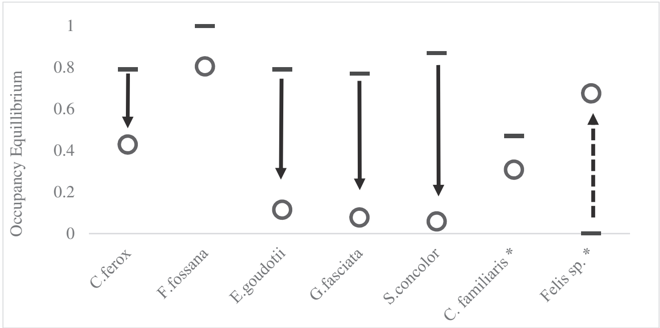

Fig. 4. Occupancy equilibrium (**O**) estimates plotted in relation to probability of occupancy at year one (▬) for five native carnivores and two exotic carnivores (indicated by asterisk) over a six-year period (2008–2013) at a newly established study site within the Makira Natural Park, Madagascar. Arrows indicate the measure and direction of change in occupancy over this six-year period.

The native *F. fossana* also demonstrated little change in occupancy during our study and shows an occupancy in equilibrium, despite the fact that trap success dropped substantially from 2008 to 2013. Thus we caution against the use of trap rates as a proxy for relative abundance because they do not account for imperfect detection. *Fossa fossana* had the highest occupancy of any native or exotic carnivore across the Masoala-Makira landscape (Farris et al., 2015d). Similar photographic surveys at Ranomafana National Park (RNP) in south-east Madagascar revealed *F. fossana* to have a 0.98 (±0.02) probability of occupancy across primary and selectively logged forest sites (Gerber et al., 2012b). However, despite these high estimates across multiple protected areas, we have also found strong temporal and spatial interactions between *F. fossana* and the exotic *V. indica* and that *F. fossana* had lower occupancy at sites where *V. indica* was active (Farris et al., in press). In this study, the limited presence and activity of *V. indica* at this site may explain the stable, high occupancy of *F. fossana* during this six-year period.

Four of the six native carnivore species (*E. goudotii*, *G. elegans*, *G. fasciata*, and *S. concolor*) showed strong decreases in occupancy over this six-year period. Madagascar's small bodied vontsira carnivores appear to be the most susceptible to decline with *G. fasciata* and *S. concolor* exhibiting the greatest declines in occupancy. These two carnivores are the least known members of Madagascar's rainforest carnivore community and most rare, as indicated by the low occupancy across multiple protected areas in Madagascar (Farris et al., 2012, 2015d; Gerber et al., 2012b; Goodman, 2012). Recent research showed that *G. fasciata* has considerably lower occupancy in the presence of multiple exotic predators (Farris et al., 2015b) and *S. concolor* was not detected at sites where exotic predator occupancy, primarily *Felis* sp., was high (Farris et al., 2015d). The dramatic increase in *Felis* species occupancy in our study may explain declines for these two native carnivores. Furthermore, the two native carnivores showed contrasting relationships in probability of local extirpation and distance to forest edge. We found *G. fasciata* are being extirpated (previously captured, but no longer detected) from sites nearest the forest edge while *S. concolor* are being extirpated from sites closer to core forest and located away from the forest edge. Previous work demonstrated how *G. fasciata* had a considerably higher probability of occupancy where small mammal activity was high and *S. concolor* had a higher probability of occupancy where bird activity was high (Farris et al., 2015d). While we are unable to confirm that lower extirpation of *S. concolor* near forest edge is explained by greater numbers of birds at these sites, research by Murphy (2015) has demonstrated multiple birds (ex. Madagascar crested ibis, red-breasted coua, Madagascar wood-rails, and Madagascar turtle-dove) at these same sites have higher occupancy in disturbed forest sites with more patches. Thus the increases in extirpation for these two carnivores may be related to precipitous declines in occupancy of small mammals and birds over this same six-year period.

In the first survey, this study site had a low number of captures, low trap success, and low occupancy of exotic carnivores. *Canis familiaris* was the only exotic carnivore present in the first survey and occupancy decreased slightly across surveys, but error bars overlapped. Farris et al. (2015d) found *C. familiaris* is common and wide-spread across the

Masoala-Makira landscape and occupancy is closely related to human presence. *Canis familiaris* is associated with humans as dogs are used for companionship and service (protection, moving cattle, and hunting) across this region. The increase in *C. familiaris* occupancy in proximity to villages provides further evidence of these relationships. However, it is worth noting that *C. familiaris*-human co-occurrence decreased over this six-year period as captures of *C. familiaris* traveling without humans increased in the final years of the survey. This trend highlights the need for additional research to determine the related implications on native wildlife.

While *C. familiaris* was the only exotic carnivore captured in the first year, we observed three exotic carnivore species by the sixth year with *Felis* sp. having the greatest increase in activity (0 in 2008 to 0.92 in 2013) and occupancy (0 in 2008 to 0.68 in 2013). The generalist diet and high intrinsic rates of increase of feral cats in newly occupied habitat contributes to their ability to swiftly and successfully exploit unoccupied habitats worldwide (Bonnaud et al., 2007, 2011; Loss et al., 2013; Medina et al., 2011). Additional research has revealed that habitat degradation and fragmentation can accelerate the spread of exotic predators and intensify their impacts on native, co-occurring wildlife (Didham et al., 2007; Doherty et al., 2015; Laurance and Useche, 2009; May and Norton, 1996). While this study site is connected to contiguous, primary rainforest it consists of a hard, prominent edge and has patches of degraded, non-forest habitat with recent disturbance. The construction of the new research building at this site also increased human activity and introduced additional, but minimal habitat disturbance. The increase in *Felis* sp. occupancy at this site over this six-year period is likely associated with these forms of anthropogenic disturbance; however, we need additional surveys within contiguous, non-degraded forest sites located long distances from villages and forest edge to further explore this conjecture. The direct and indirect impacts of *Felis* sp. on native wildlife in Madagascar have not been investigated; however, accounts of *Felis* sp. predation on lemurs and other native wildlife in Madagascar exist (Brockman et al., 2008; Goodman, 2003, 2012) and our surveys have revealed *Felis* sp. killing native rodents and lemurs (Z. Farris and A. Murphy, pers. obs.). Further, Murphy (2015) highlighted the negative relationship between *Felis* sp. and multiple native bird species across the Masoala-Makira landscape. Our study and on-going work across this region on carnivores, lemurs, birds, and small mammals suggests the large increases in *Felis* sp. across this region is negatively influencing numerous native wildlife species. Additional research is needed on *Felis* sp. populations including diet analysis, behavioral studies, and more expansive population assessments across both contiguous and fragmented forests.

5. Conclusion

The implications of this study are wide-ranging and we demonstrate the need for multi-year surveys to effectively monitor changes in population parameters across years. Single-year, snapshot surveys and resulting occupancy estimates for this carnivore community would have resulted in misinformed and potentially misguided management plans that failed to bring attention to precipitous declines in occupancy of native carnivore species. For example, instead of expanding border protection and/or the number or range of these snapshot surveys we suggest additional management targeting removal of exotic species and continued monitoring to evaluate the response of native wildlife to these removal efforts. These forms of multi-year surveys have been conducted by the Tropical Ecology Assessment and Monitoring (TEAM) Network (http://www.teamnetwork.org; Conservation International, Arlington, VA, USA) and these data could be used for robust, quantitative, multi-year population assessments (Jansen et al., 2014; Royle et al., 2005). Additionally, these multi-year surveys of carnivore populations have been carried out successfully in various habitats worldwide to investigate demographic trends (Bauer et al., 2015; Di Marco et al., 2014; Rosenblatt et al., 2014), predator-prey dynamics (Panek, 2013; Robley et al., 2014), and anthropogenic influences (Johnson et al., 2016; Wierzbowska et al., 2016; Wolfe et al., 2015). These studies, similar to our findings, provide insight into various dynamic processes that short-term investigations have failed to capture.

Our findings provide insight into the threats posed by anthropogenic disturbance to Madagascar's carnivore populations and are relevant to carnivore populations worldwide. We bring attention to the alarming negative trends in occupancy exhibited by multiple native carnivores across this region with emphasis on eastern falanouc *E. goudotii*, ring-tailed vontsira *G. elegans*, broad-striped vontsira *G. fasciata*, and brown-tailed vontsira *S. concolor*. Special concern is given to *G. fasciata* and *S. concolor* due to their overall rarity, low occupancy across the landscape, their negative associations with multiple anthropogenic pressures, and the limited knowledge of their ecology and natural history. Finally, we provide additional insight into the threat posed by an increasing, wide-ranging exotic carnivore species in Madagascar's eastern rainforests and in similar habitats across the globe. The rapid increase in *Felis* sp. occupancy, combined with previous findings highlighting their negative effects and associations with native birds, small mammals, lemurs, *F. fossana*, *G. fasciata*, and *S. concolor* (Farris et al., 2014, 2015d,b,c), underscores the need for effective, targeted management plans to control populations of feral cats. Additional research is also needed to evaluate the feasibility, acceptance, and effectiveness of expansive village-based education and trap-euthanize programs for *Felis* sp. populations across the Masoala-Makira landscape and similar protected areas in Madagascar.

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Glossary

Camera grid: a collection of camera stations spaced approximately 500 m apart to photographically sample wildlife in a given study site location.

Camera station: a location within the camera grid having two motion sensing cameras on opposing sides of the trail to photographically capture both sides of passing wildlife.

Photographic capture or capture event: all photographs of a given species occurring within a 30 min period.

Trap night: a 24 h period in which at least one of the two cameras at a camera station is functioning properly.

Trap success: a measure or estimate of activity calculated by dividing the number of capture events by the number of trap nights at each camera station, minus malfunctions, and multiplied by 100.

Single-species, multi-season (multi-year) occupancy estimation: use of presence/absence (detection/non-detection) data from repeat sampling occasions of a target species to estimate changes in the probability of site use over time.

Probability of colonization: probability that a site that was previously unoccupied will be occupied during subsequent surveys.

Probability of extirpation: probability that a site that was previously occupied will become unoccupied during subsequent surveys.