Threats to a rainforest carnivore community: A multi-year assessment of occupancy and co-occurrence in Madagascar

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ABSTRACT

Protected areas (PA) aim to eliminate many of the threats that species face on the greater landscape. In the last three decades, PA's have expanded considerably; however, quantitative assessments of how well they have mitigated threats to habitat and biodiversity are very limited. Habitat bordering PA's and the wildlife that use it are threatened by a wide-range of anthropogenic pressures (e.g., edge effects, fragmentation, and introduced predators) and this situation is particularly acute for low-density, poorly studied carnivore communities. From 2010 to 2015, we photographically sampled within (contiguous forest) and bordering (degraded, fragmented forest) a UNESCO World Heritage rainforest PA in Madagascar - Ranomafana National Park (RNP). We investigated the effects of invasive predators, local people presence, and habitat quality on the endemic rainforest carnivore community using static, dynamic, and co-occurrence models. We found native carnivores to be absent or have a low probability of occurrence in degraded forest bordering the PA, while local people and dogs (*Canis familiaris*) had high occurrence. Madagascar's largest endemic carnivore, the fosa (*Cryptoprocta ferox*) and the much smaller ring-tailed vontsira (*Galidia elegans*), occurrence in RNP declined rapidly over six years; their strong co-occurrence with dogs suggests interspecific competition, direct aggression/mortality, or disease as the cause. We highlight the dangers posed to biodiversity, particularly carnivores, from anthropogenic pressures bordering PA's and present recommendations to address increased human and dog activity, including programs to control dogs and their impact on biodiversity.

1. Introduction

Protected areas (PAs) aim to conserve the world's biodiversity and rarest species, while covering just 15% of earth's terrestrial surface (Farris et al., 2017). The number of PAs has grown considerably in the last three decades, particularly in tropical, developing countries (Naughton-Treves et al., 2005; Tittensor et al., 2014). Since 1992, PAs have increased annually by an average of 2.5% in total area and 1.4% in the total number of sites (Butchart et al., 2010; Rands et al., 2010). By 2006, PAs covered 24,000,000 km², in 133,000 designated areas (Butchart et al., 2010; Rands et al., 2010). However, this positive development for biodiversity conservation needs to be viewed from a balanced perspective. For example, it is estimated that 20% of vertebrate taxa recognized as threatened by the International Union for Conservation of Nature (IUCN) do not live in PAs (Rodrigues et al., 2004). Furthermore, despite formal protection, many PAs do not fully mitigate threats to habitats and biodiversity, due to chronic understaffing, underfunding, and political instability (Brown et al., 2016; Naughton-Treves et al., 2005).

Despite the proliferation of PAs worldwide (Di Marco et al., 2014;

Wolfe et al., 2015), attempts to quantify the effectiveness of these critical areas are greatly limited (Dickman, 2013; Rosenblatt et al., 2014; Tittensor et al., 2014; Valenta et al., 2016a). While data indicate that PAs generally curb forest loss within their boundaries, many areas suffer the effects of deforestation and biodiversity loss from surrounding areas, where managers lack the authority, resources, and funding to respond to adjacent biodiversity threats (Bauer et al., 2015; Lindenmayer et al., 2012). The actions in these bordering areas often harm PAs (e.g., watershed degradation). The failure to develop targeted measures to assess effective conservation and inadequate resources to conduct management activities (i.e., enforcement, boundary demarcation, and compensation to local communities; Bruner et al., 2001) prevents managers and conservationists from evaluating progress and incorporating adaptive management strategies (Panek, 2013).

Developing effective and practical management plans for protecting wildlife within PAs is particularly important for carnivores, as they are fundamental drivers of trophic functioning (Ripple et al., 2014) and can increase ecosystem resilience (Tittensor et al., 2014) through stabilizing consumer populations (Bruner et al., 2001). As a guild, carnivores are arguably the most vulnerable species because of their typical-low densities and wide-ranging movements, which increases their interaction with local human communities (hereafter human), and thus conflict. Human-carnivore conflict can be a significant source of mortality for carnivores living in, but ranging beyond, PAs (Koziarski et al., 2016; Lindsey et al., 2017; Woodroffe and Ginsberg, 1998) and recent research has highlighted the effects of fragmentation, edge effects, and introduced predators on native carnivores (Brodie et al., 2015; Chanchani et al., 2016; Gerber et al., 2012b; Sleeman, 2013; Vanak and Gompper, 2010; Vanak et al., 2013; Young et al., 2011). In particular, forest fragmentation means that wide-ranging carnivores must move among habitat patches and thus face dangers found in the matrix. This results in low fragment occupancy for many native carnivore species, when human and introduced carnivore populations increase (Chanchani et al., 2016; Crooks, 2002; Farris et al., 2015c; Gerber et al., 2012b; Michalski and Peres, 2005). Introduced carnivores (e.g., feral dogs and cats) can greatly intensify pressure on native carnivores as they alter their temporal activity patterns (Farris et al., 2015b; Farris et al., in press; Gerber et al., 2012a), reduce their spatial distribution and habitat use (see Vanak et al., 2013 for review), and decrease prey availability (see Young et al., 2011 for review).

Long-term surveys of carnivores and their prey are critical to recognize when population changes are occurring (i.e., occupancy, density, survival, recruitment) and to identifying the driving factors. Unfortunately, such studies are rare, with most carnivore studies only providing a small snap-shot of the population, thus missing important dynamics. Carnivores are highly sensitive to disturbances at the borders of PAs and are negatively affected by edge effects, poaching, and human-wildlife conflict (Loss et al., 2013; Sleeman, 2013; Wearn et al., 2012; Woodroffe and Ginsberg, 1998). Thus, carnivore population health is likely driven by species-specific tolerances to habitat variation, human presence, habitat fragmentation, invasive carnivore density, and prey distributions. The complexity of the interactions between carnivores and their habitat and prey means that their management must account for the multiplicity of variables driving population health within and around PAs.

Madagascar contains some of the highest levels of biodiversity and endemism in the world (Ganzhorn et al., 2001), but is home to only nine native carnivore species. These species are endemic and range in conservation status from Least Concern to Endangered (Goodman, 2012; IUCN, 2014). A wide-range of anthropogenic threats has resulted in Madagascar being one of the world's top conservation priorities (Mittermeier et al., 2004; Schwitzer et al., 2014). While 21 national parks have been designated in Madagascar (IUCN, 2015), surveys and population estimates of carnivores are lacking for most of these Pas. For example, Farris and Gerber (unpublished data) estimate that < 20% of PAs have robust surveys, consisting of more than opportunistic sight-

ings or rapid assessments, of carnivore populations. Research from five PAs highlights the threat posed to endemic carnivores as the result of degradation, fragmentation, and human disturbance (Farris et al., 2015c; Gerber et al., 2012b; Wierzbowska et al., 2016), poaching and bushmeat consumption (Farris et al., 2015c; Golden, 2009; Golden et al., 2014; Robley et al., 2014), and introduced carnivores (Farris et al., 2015a; Farris et al., 2015b; Gerber et al., 2012b, a). The long-term effects of these factors and the effectiveness of PAs to diminish their effects remain unstudied.

Here, we provide a six-year evaluation of the effects of invasive predators, human encroachment, and habitat quality on population trends for five native carnivores in one of Madagascar's most important PAs and a UNESCO World Heritage site, Ranomafana National Park (RNP). We document the spatial distribution of native carnivores (fosa *Cryptoprocta ferox*, falanouc *Eupleres goudotii*, spotted fanaloka *Fossa fossana*, ring-tailed vontsira *Galidia elegans*, and broad-striped vontsira *Galidictis fasciata*) over time, by investigating the factors influencing native and introduced carnivore species distributions in contiguous forest and human-dominated sites. Quantifying the effects of spatial habitat variation, edge effects, and species interactions on native carnivores, allows us to evaluate the effectiveness of management actions for carnivore conservation. We hypothesized that all five native carnivores would have higher occupancy in contiguous forest inside the PA, while dogs (*Canis familiaris*) and human occupancy would be higher in degraded forest outside the PA and distance to edge would negatively influence native carnivore occupancy and positively influence dogs and human occupancy. We also hypothesized that native carnivore occupancy would experience little overall change, while dog and human occupancy would show slight increases over the six-years. This prediction is based upon trends observed across the RNP region with growing human and dog populations. Finally, we hypothesized that all native carnivores would demonstrate a lack of co-occurrence, defined as "apparent spatial avoidance" (whether behavioral or habitat-mediated), with both dogs and humans inside the PA.

2. Methods

2.1. Study site

We conducted this study at Ranomafana National Park (41,000 ha) in southeastern Madagascar (21°16′S, 47°20′E; Fig. 1). A small percentage of this submontane rainforest site was selectively logged from 1986 to 1989, but in 1991 the area was designated as a PA (Wright et al., 2012). RNP protects 13 lemur and five carnivore species (fosa *Cryptoprocta ferox*, falanouc *Eupleres goudotii*, spotted fanaloka *Fossa fossana*, ring-tailed vontsira *Galidia elegans*, and broad-striped vontsira *Galidictis fasciata*). This PA, which is bisected into two parcels by the Namarona River and a paved road, is one of four long-term research sites in Madagascar (Wright et al., 2012).

2.2. Photographic sampling

Our photographic sampling results from two efforts: (1) Tropical Ecology Assessment and Monitoring network (TEAM - www.teamnetwork.org; Data Set Identifier: TEAM-DataPackage-20131011121105_2883) surveys (2010–2015) within contiguous forest within the boundaries of the PA and (2) Mad Dog Initiative (MDI; www.maddoginitiative.com) surveys (2014–2015) within degraded, fragmented forest outside the PA (Fig. 1; Table 1). For the first surveys, we followed TEAM protocol (TEAM Murphy et al., in press) and surveyed at 40 (2015) to 60 (2010) sites between the months of August and April (Fig. 1). For the degraded, fragmented forest surveys, we surveyed 23 sites between September and October (2014) and 25 sites between June and July (2015).

At each station we placed one or two cameras on opposing sides of small unmaintained (0–0.5 m) or maintained (> 0.5 m) trails and
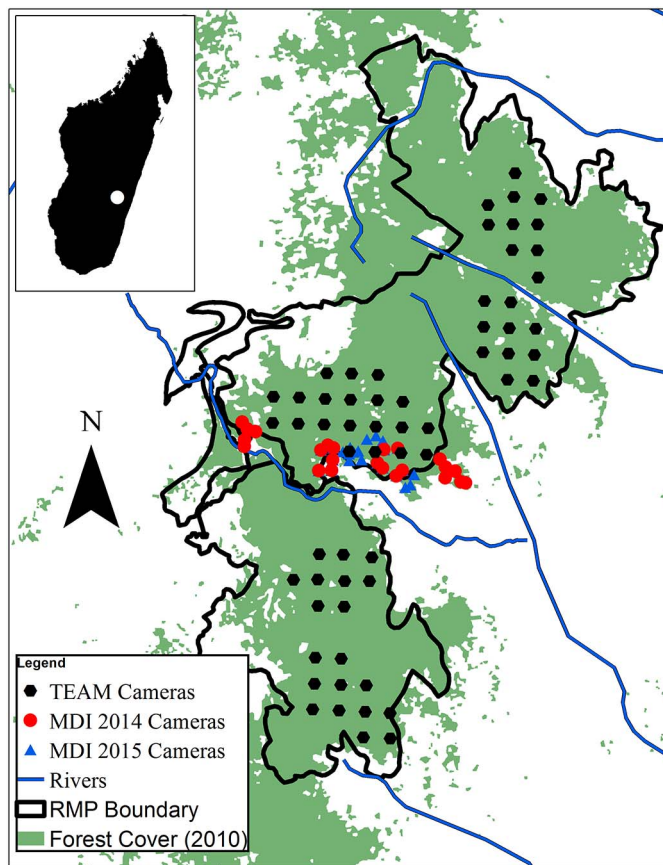
Fig. 1. Map of Ranomafana National Park, including location of camera grids from Tropical Ecology and Assessment Monitoring (TEAM) network (2010–2015; black dots) and Madagascar Dog Initiative (MDI) for 2014 (red dots) and 2015 (blue triangles) photo surveys. A portion of the cameras for MDI surveys overlapped for 2014 and 2015. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

checked cameras every 5–10 days to change memory cards and batteries (if required). We placed cameras (Reconyx PC85 & HC500, Wisconsin, 109 USA; Moultrie D50, D55, & M550, Alabama, USA; Cuddeback IR, Wisconsin, USA) 10–30 cm off the ground and did not use bait or lure. We surveyed each station site between 30 and 60 days (Table 1). Spacing between cameras varied between the two surveys with TEAM surveys ranging from 1.2 to 2.0 km and MDI surveys ranging between 0.3 and 1.0 km between camera stations. Finally, for use as covariates in our modeling, we measured the distance of each camera station to the nearest forest edge and nearest village.

2.3. Data analysis

For each occupancy (ψ) modeling approach described below, we created capture histories for each species by recording whether there

were one or more detections (1) and/or no detections (0) for each trap night. We defined a capture event as all photos taken of a given species at a single camera station within 30-min; a time previously chosen to ensure independence between events (Di Bitetti et al., 2006). We defined a trap night as the 24-h in which at least one camera trap at a site was properly functioning. For TEAM data, we used each trap night as a sampling period, while for MDI data, we collapsed trap nights for each survey into six-day sampling periods to improve model convergence. For each modeling approach, we created a priori models based on the aforementioned hypotheses, used Akaike information criterion [corrected for small sample sizes (AICc)] for model selection (Burnham and Anderson, 2002), and reported all top-ranking models (ΔAICc < 2.0). We investigated the hypotheses using three occupancy-modeling approaches (static, dynamic, and co-occurrence) depending on the available data. All occupancy modeling was analyzed using Program MARK (MacKenzie et al., 2002; White and Burnham, 1999) and account for false negatives (i.e., imperfect species detections).

2.4. Static (single-season) occupancy

Given that edge forest surveys were conducted at different sites outside the PA for only two years (2014–2015), we used single-season, single-species (hereafter 'static') occupancy modeling to estimate probabilities of occupancy and detection for five native carnivores, dogs (*Canis familiaris*), and humans. For each of these species we considered models that varied in detection by distance to village, distance to edge, and time. We also considered models that varied in occupancy by distance to village and edge. For each species having sufficient captures we provide model-averaged estimates of occupancy (White and Burnham, 1999). However, for species having low capture rates we provide naïve occupancy (e.g., number of site-level detections divided by the total number of sites; not accounting for imperfect detection) (MacKenzie et al., 2002).

2.5. Dynamic (multi-season) occupancy

For contiguous surveys within RNP (TEAM surveys) we used multi-season, single-species (hereafter 'dynamic') occupancy modeling in Program MARK (MacKenzie et al., 2006; White and Burnham, 1999), where 'season' refers to subsequent yearly surveys. This explicitly models yearly changes in the probability of occupancy and probabilities of local colonization (γ) and extirpation (ε). Local colonization is defined as the probability of an unoccupied site during time t becoming occupied at t_{+1}. Conversely, local extirpation is defined as the probability of a previously occupied site during time t becoming unoccupied at t_{+1} (MacKenzie et al., 2006). This modeling approach uses a robust design, meaning parameters (occupancy, detection, colonization, and extirpation) are geographically 'closed' to movement (e.g. immigration and/or emigration) during surveys, but 'open' between surveys or years (MacKenzie et al., 2006). Models include distance to nearest village and distance to edge of the forest as covariates on detection and occupancy parameters. For each species,

Table 1
Summary of photographic surveys conducted at sites within and bordering the Ranomafana National Park, Madagascar from 2010 to 2015 by the Tropical Ecology Assessment and Monitoring (TEAM) network and Madagascar Dog Initiative (MDI).

Site name	Survey date	# Cam stations	# Native carnivore photos	# Dog photos	# Human photos	Habitat
TEAM 2010	Aug–Nov, 2010	60	1125	33	355	Contiguous, secondary forest
TEAM 2011	Aug–Dec, 2011	59	2167	32	983	Contiguous, secondary forest
TEAM 2012	Sept–Jan, 2012	59	1589	19	299	Contiguous, secondary forest
TEAM 2013	Nov–Mar, 2013	59	682	27	700	Contiguous, secondary forest
TEAM 2014	Dec–Apr, 2014	55	181	62	693	Contiguous, secondary forest
TEAM 2015	Oct–Feb, 2015	40	455	10	1012	Contiguous, secondary forest
MDI 2014	Sept–Oct, 2014	23	107	520	3660	Degraded, edge forest
MDI 2015	June–July 2015	25	156	181	793	Degraded, edge forest

Table 2

Model averaged estimates of occupancy (psi) and detection (p) for five native carnivores, domestic dogs, and humans resulting from static (single-season, single-species) occupancy estimation using photographic surveys of degraded and edge rainforest bordering Ranomafana National Park by the Madagascar Dog Initiative (MDI) from 2014 and 2015.

Species	2014		2015	
	psi (SE)	p (SE)	psi (SE)	p (SE)
Fosa (*C. ferox*)	0.47 (0.35)	0.20 (0.08)	0.12[a]	-
Falanouc (*E. goudotii*)	0 (0)	0 (0)	0.08[a]	-
Spotted fanaloka (*F. fossana*)	0.66 (0.17)	0.28 (0.07)	0.63 (0.21)	0.35 (0.05)
Ring-tailed vontsira (*G. elegans*)	0.17[a]	-	0.12[a]	-
Broad-striped v. (*G. fasciata*)	0.09[a]	-	0.04[a]	-
Domestic dog (*C. familiaris*)	0.87 (0.15)	0.41 (0.06)	0.90 (0.12)	0.45 (0.07)
Human, local (*H. sapien*)	0.91 (0.09)	0.71 (0.06)	0.71 (0.30)	0.58 (0.04)

- = Indicates data too sparse to estimate detection probability (p).

[a] Indicates naïve occupancy estimate used. Naïve estimate does not account for imperfect detection and is calculated by dividing the number of detections by the number of sites surveyed.

we report annual estimates of occupancy and a single estimate of local colonization and extirpation over the six years. Finally, we provide projections of occupancy trends for this carnivore community, assuming continued dynamics, by calculating the occupancy equilibrium (λ) for each species using the following equation from MacKenzie et al. (2006):

$$\lambda_t = \gamma/(\gamma + \varepsilon).$$

2.6. Dynamic (multi-season) co-occurrence

We investigated co-occurrence between native carnivores, dogs, and humans by fitting multi-season, two species occupancy models to contiguous forest data within RNP (TEAM surveys). We used the conditional parameterization (Richmond et al., 2010) and designated the introduced species (dog and human) as the 'dominant' species (A) and the native carnivore as the 'subordinate' species (B) to estimate parameters (Appendix I). In addition, we estimated a species interaction factor (SIF) for each species combination. An SIF of 1.0 indicates no interaction (e.g. species use space independent of one another), while an SIF > 1.0 indicates co-occurrence (e.g. occur together more often than expected if independent) and an SIF < 1.0 indicate avoidance (e.g. occur together less often than expected if independent) (Steen et al., 2014). We consider a value of SIF < 1.0 to be evidence of "apparent spatial avoidance" and a value of SIF > 1.0 to be "apparent spatial attraction". However, the lack of covariates in these models prevents us from investigating whether these patterns are due to

Fig. 2. Dynamic (multi-season) occupancy trends across Ranomafana National Park, Madagascar from 2010 to 2015 for A) fosa *Cryptoprocta ferox*; B) ring-tailed vontsira *Galidia elegans*; and C) human, local *Homo sapien*. Photographic data were collected from 60 camera sites by the Tropical Ecology Assessment and Monitoring (TEAM) network.

competitive or behavioral interactions or may be a mediating factor, such as the environment. We analyzed all possible combinations of three native carnivores (fosa, spotted fanaloka, and ring-tailed vontsira), dogs, and humans. Insufficient captures of falanouc and broad-
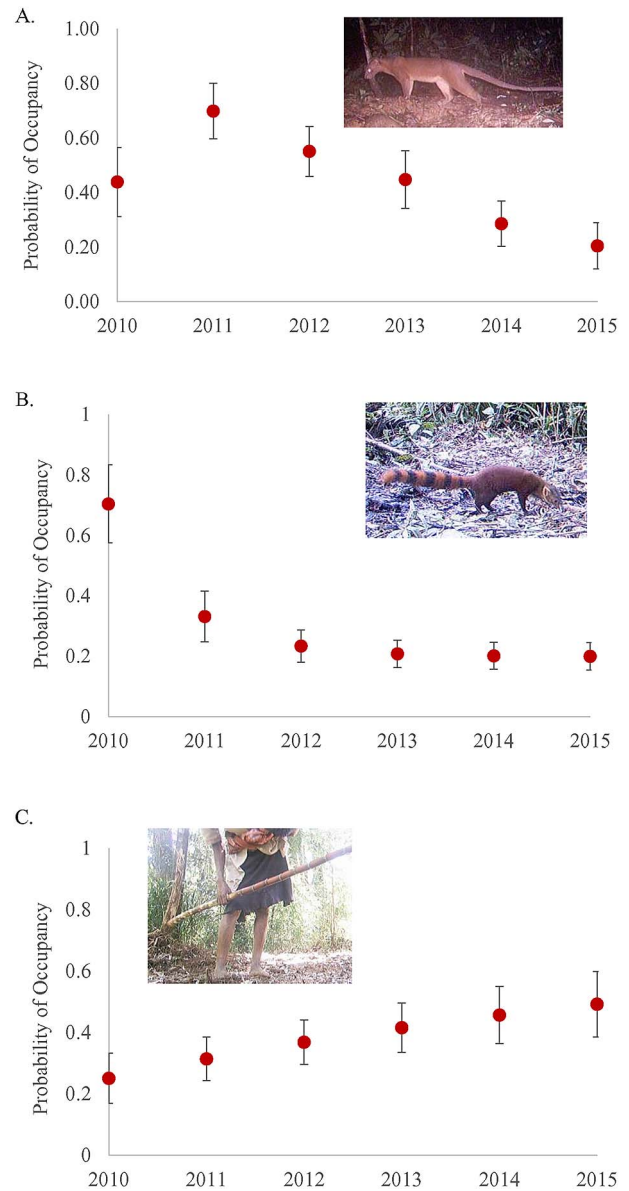
Table 3

Estimates of occupancy, local colonization (gam), and local extirpation (eps) for five native carnivores, domestic dogs, and humans resulting from dynamic (multi-season, single-species) occupancy estimation from photographic surveys within Ranomafana National Park by the Tropical Ecology Assessment and Monitoring (TEAM) network from 2010 to 2015.

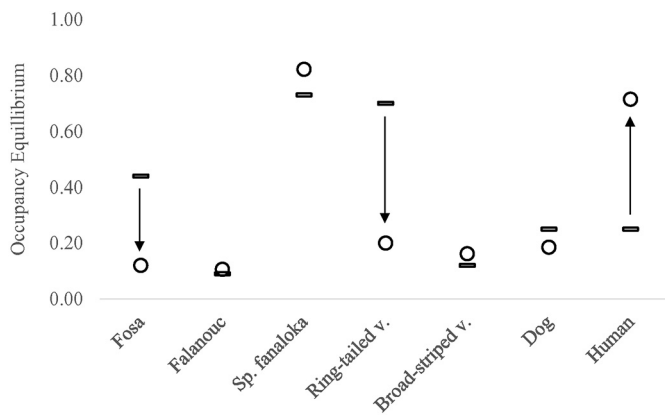| Species	2010	2011	2012	2013	2014	2015	gam	eps
Fosa (*C. ferox*)	0.44 (0.13)	0.70 (0.10)	0.55 (0.09)	0.45 (0.11)	0.29 (0.08)	0.20 (0.08)	0.06 (0.05)[a]	0.44 (0.17)[a]
Falanouc (*E. goudotii*)	0.09 (0.08)	0.10 (0.04)	0.10 (0.04)	0.11 (0.05)	0.11 (0.05)	0.11 (0.05)	0.07 (0.04)	0.59 (0.26)
Spotted fanaloka (*F. fossana*)	0.73 (0.08)	0.78 (0.07)	0.80 (0.08)	0.81 (0.09)	0.82 (0.10)	0.82 (0.10)	0.46 (0.11)	0.10 (0.08)
Ring-tailed vontsira (*G. elegans*)	0.70 (0.13)	0.33 (0.08)	0.23 (0.05)	0.21 (0.05)	0.20 (0.05)	0.20 (0.05)	0.15 (0.05)	0.60 (0.11)
Broad-striped v. (*G. fasciata*)	0.13 (0.08)	0.16 (0.07)	0.16 (0.07)	0.16 (0.07)	0.16 (0.07)	0.16 (0.07)	0.17 (0.08)	0.88 (0.12)
Domestic dog (*C. familiaris*)	0.25 (0.11)	0.21 (0.08)	0.20 (0.07)	0.19 (0.08)	0.19 (0.08)	0.19 (0.08)	0.10 (0.05)	0.44 (0.19)
Human (*H. sapien*)[b]	0.25 (0.08)	0.31 (0.07)	0.37 (0.07)	0.42 (0.08)	0.46 (0.09)	0.49 (0.11)	0.10 (0.03)	0.04 (0.06)

[a] Top model included colonization (gam) and extirpation (eps) varying by season; the single estimate provided for these two parameters is the estimate from 2015 only.

[b] Human only.

Fig. 3. Occupancy equilibrium (**O**) plotted in relation to probability of occupancy at year one (■) for five native carnivores, dogs, and humans over a six year period within contiguous forest at Ranomafana National Park, Madagascar. Arrows indicate the measure and direction of change in occupancy over this six-year period.

striped vontsira prevented us from including these two native carnivores in co-occurrence analyses.

3. Results

The contiguous forest surveys within RNP resulted in 6199 individual photos of the five native carnivores, 183 photos of dogs, and 4042 photos of humans (Table 1). The degraded, edge forest surveys resulted in 263 photos of four native carnivores (broad-stripe vontsira were absent), 701 photos of dogs, and 4453 photos of humans (Table 1).

3.1. Static occupancy

The number of captures of native carnivores in degraded, edge forest only allowed occupancy estimates of two carnivores in 2014 (fosa $\psi = 0.47 \pm$ SE 0.35 and spotted fanaloka $\psi = 0.66 \pm$ SE 0.17) and one native carnivore in 2015 (spotted fanaloka $\psi = 0.63 \pm$ SE 0.21). Dog and human occupancy were considerably higher than native carnivores, with little change in these two parameters across years (Table 2). Dog and human detection were higher than native carnivores' detection and increased with distance from the forest edge (dogs) and distance to village (humans; Table 2; Appendix II).

3.2. Dynamic occupancy

The dynamic occupancy analyses of contiguous forest showed high annual probabilities of local extirpation for both fosa and ring-tailed vontsira ($\varepsilon = 0.44 \pm$ SE 0.17 and $\varepsilon = 0.60 \pm$ SE 0.11, respectively; Table 3; Appendix III) which resulted in strong decreases in occurrence for both native carnivores over the six years (Fig. 2A–B). Spotted fanaloka, falanouc, and broad-striped vontsira occupancy changed very

little and neither falanouc, nor broad-striped vontsira occupancy ever exceeded $\psi = 0.20$ for any of the six years (Table 3). All native carnivores, excluding spotted fanaloka, had local extirpation probabilities far exceeding local colonization probabilities (Table 3).

Dogs showed only a slight decrease in occupancy over the six years with an extirpation probability ($\varepsilon = 0.44 \pm$ SE 0.19) higher than their colonization probability ($\gamma = 0.10 \pm$ SE 0.05). Humans showed a considerable increase in occupancy over the six years (Fig. 2C) with colonization ($\gamma = 0.10 \pm$ SE 0.03) higher than extirpation ($\varepsilon = 0.04 \pm$ SE 0.06; Table 3). If dynamics continue, equilibrium occupancy is expected to decrease sharply for fosa and ring-tailed vontsira and increase sharply for humans (Fig. 3). Our estimates found falanouc and broad-striped vontsira at equilibrium, with spotted fanaloka showing a slight increase and dogs showing a slight decrease in occupancy over the six years (Fig. 3).

3.3. Dynamic co-occurrence

Fosa show positive co-occurrence with dogs at contiguous forest sites within RNP with higher occupancy at sites where dogs are detected (psiBA; Table 4), resulting in a positive SIF between the two carnivores (Fig. 4A). Spotted fanaloka and dogs show little relationship in co-occurrence, with spotted fanaloka occupancy being slightly lower at sites where dogs are detected (psiBA; Table 4). Ring-tailed vontsira and dogs show positive co-occurrence in 2010, but no relationship by 2015 (Fig. 4B). Humans show little relationship with native carnivores within RNP with the three native carnivores having slightly higher occupancy at sites where humans are detected (Table 5). However, humans and dogs show exceedingly high levels of co-occurrence with occupancy of dogs highest at sites where humans are detected (psiBA) compared to where humans are not detected (psiBa); resulting in a SIF value ranging from 1.77 ($\pm$ SE 0.41; 2015) to 2.92 ($\pm$ SE 1.51; 2010; Table 5; Fig. 4C).

4. Discussion

With the global expansion of PAs, the need for reliable assessments to evaluate threats to habitat and biodiversity increase. These assessments and evaluations are exceedingly important for poorly studied, rare carnivore populations. Here we provide an evaluation of population trends and spatial distributions of a native carnivore community, introduced dogs, and humans within and bordering an important rainforest PA. Our findings point to the effectiveness of a PA to conserve rainforest habitat and protect some members of a native carnivore community; however, our results also indicate an alarming shift in equilibrium occupancy for two native carnivores and humans over a six-year period. In our analysis, the increase in human occupancy over this six-year period is a measure of human encroachment, which is related to a wide-range of anthropogenic activities (ex. logging, resource extraction, hunting, and mining), which have shown to negatively affect native carnivore occupancy in multiple regions of

Table 4
Dynamic co-occurrence results for domestic dog (species A; *Canis familiaris*) and three native carnivore species (species B), including the probability of occupancy for native (B) when dogs are present (BA) and absent (Ba) and the species interaction factor (SIF) for each species combination. Photographic data were collected from 2010 to 2015 by the Tropical Ecology Assessment and Monitoring (TEAM) network from 60 camera sites within the Ranomafana National Park, Madagascar.

Species combination	K	2010	2011	2012	2013	2014	2015
Dog - Fosa	psiBA	0.14 (0.13)	0.68 (0.18)	0.45 (0.11)	0.49 (0.12)	0.45 (0.11)	0.45 (0.12)
	psiBa	0.43 (0.12)	0.41 (0.09)	0.33 (0.06)	0.30 (0.06)	0.27 (0.06)	0.25 (0.06)
	SIF	0.39 (0.35)	1.50 (0.31)	1.28 (0.31)	1.53 (0.37)	1.57 (0.40)	1.64 (0.44)
Dog - Spotted fanaloka	psiBA	0.69 (0.08)	0.62 (0.10)	0.63 (0.10)	0.67 (0.10)	0.68 (0.10)	0.68 (0.10)
	psiBa	0.41 (0.24)	0.67 (0.08)	0.75 (0.09)	0.76 (0.08)	0.76 (0.09)	0.76 (0.09)
	SIF	1.06 (0.08)	0.95 (0.11)	0.88 (0.12)	0.90 (0.09)	0.91 (0.09)	0.91 (0.08)
Dog - Ring-tailed vontsira	psiBA	–	0.42 (0.13)	0.28 (0.13)	0.22 (0.11)	0.20 (0.10)	0.20 (0.09)
	psiBa	0.61 (0.14)	0.31 (0.08)	0.22 (0.05)	0.20 (0.04)	0.20 (0.04)	0.20 (0.05)
	SIF	1.50 (0.27)	1.30 (0.40)	1.24 (0.49)	1.11 (0.50)	1.03 (0.44)	1.00 (0.40)

A.

B.

C.
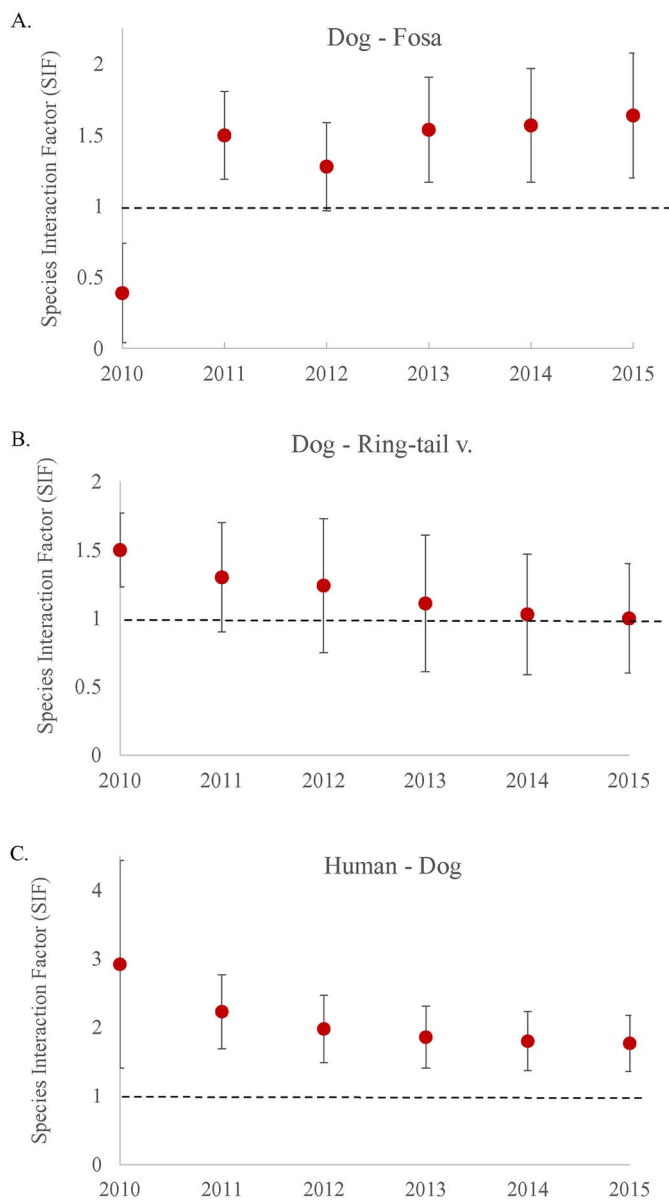
Fig. 4. Species interaction factors (SIF) from 2010 to 2015 resulting from dynamic co-occurrence modeling for A) domestic dog (*Canis familiaris*) and fosa (*Cryptoprocta ferox*); B) domestic dog and ring-tailed vontsira (*Galidia elegans*); and C) human (*Homo sapiens*) and domestic dog. The dashed line at 1.0 indicates lack interaction, or independence in the spatial relationship. Photo data were collected by the TEAM network across Ranomafana National Park, Madagascar.

Madagascar (Farris et al., 2015c; Gerber et al., 2012b). We highlight the need for a better integrative monitoring and protection framework, particularly for carnivores that are at risk due to human conflict occurring on the edge of the park. Carnivores worldwide are threatened by a wide-range of anthropogenic pressures. Our data suggest that introduced carnivores represent a salient threat to native carnivores and the capacity for introduced carnivores to alter the spatial distribution of native carnivores.

The creation of PAs help mitigate, but do not eliminate, human-wildlife conflicts. In particular, wide-ranging species, such as carnivores, are often at the center of conflict, which often occur at sites bordering PAs (Koziarski et al., 2016; Lagendijk and Gusset, 2008; Lindsey et al., 2017; Sepúlveda et al., 2014). These human-wildlife conflicts can contribute significantly to carnivore mortality, complicating PA management efforts. We highlight the strong potential for human-wildlife conflict at sites bordering the PA and show that the

largest, most wide-ranging native carnivore, the fosa, had higher occupancy in degraded, edge forest outside the PA. These human-wildlife conflicts may have contributed to the considerable decline in occupancy for fosa and ring-tailed vontsira over this six-years. Similar analyses from the Masoala-Makira landscape in NE Madagascar showed comparable results with fosa having a higher probability of occupancy in forests having some signs of degradation (Farris et al., 2015c). Human-wildlife conflicts occurring on the borders of PAs often include bushmeat hunting and lethal predator control as measures to control livestock loss (Berger, 2006; Woodroffe et al., 2007). Kotschwar et al. (2014) reports that ring-tailed vontsira are killed for bushmeat across the RNP region and almost half of livestock owners across this region had experienced poultry loss to carnivores with fosa and ring-tailed vontsira contributing to these depredation events. Lethal methods for predator control are common, and have been observed in many villages along the eastern region (Farris, personal observation). Both fosa and ring-tailed vontsira, among other native carnivores, are killed unsustainably across the Masoala-Makira region (Farris et al., 2015c; Golden, 2009; Golden et al., 2014). However, annual bushmeat and depredation rates for native carnivores are not yet quantified for the RNP region and, and research is required to assess what role these factors play in the declining trends in fosa and ring-tailed vontsira populations.

Introduced carnivores represent an additional anthropogenic pressure threatening biodiversity within and bordering PAs. The presence of dogs within PAs has resulted in decreases in carnivore and prey populations at multiple sites worldwide (Bergman et al., 2009; Farris et al., 2015a; Galetti and Sazima, 2006; Weston and Stankowich, 2013; Young et al., 2011). In this study, the wide-ranging use of degraded forests by dogs at sites bordering the PA and the strong co-occurrence between dogs and native carnivores within the PA highlights the strong potential for conflict, and may contribute to the precipitous declines observed for fosa and ring-tailed vontsira. Our co-occurrence models and those in similar studies (Farris et al., 2015a; Farris et al., in press), provide a reliable approach for managers to investigate the interactions between introduced and native carnivores. Dogs, and other introduced carnivores, have continually been shown to invade forested habitat worldwide, diminish or extirpate native carnivore populations, and negatively affect ecosystem function (Ritchie et al., 2014; Vanak and Gompper, 2010; Vanak et al., 2013; Young et al., 2011). We provide further evidence of the negative impacts of dogs on native wildlife and point to the alarming increase of introduced carnivores at additional PAs and/or reserves throughout Madagascar, including Mahatsinjo, Ilatsara Reserve, Betampona Reserve, Makira Natural Park, Masoala National Park, and Farankarina Tropical Park (Farris et al., 2015c; Gerber et al., 2012b, F. Rasambainarivo, unpub. data). Studies have also shown that the presence of dogs results in lower occupancy for multiple native carnivores (Farris et al., 2015a), native carnivores altering their temporal activity patterns (Farris et al., 2015b; Gerber et al., 2012a), reduced presence and activity of small mammals (Farris et al., 2015c; Farris et al., 2016), and primates showing apparent avoidance with these introduced predators (Farris et al., 2014). Dogs in Madagascar's forests also have the potential to negatively affect native carnivore populations via disease and pathogen transmission (Pomerantz et al., 2016; Schwitzer et al., 2014). We point to the potential for further expansion of dogs into contiguous forest and continued negative effects on endemic biodiversity at RNP given the widespread occupancy of humans at sites bordering RNP and the strong increase in human occupancy within the park over the six years. In particular, our findings on dog and human detection probabilities increasing with distance to edge likely results from the increase in number of trails and forest access points near the forest edge compared to contiguous forest, thus making detection more difficult near forest edge. Additionally, human and dog detection may have been lower near the forest edge as the result of humans avoiding trails near edge in an effort to diminish their probability of detection by researchers and managers near the protected area.

Table 5
Dynamic co-occurrence results for humans (species A; *Homo sapiens*) and three native carnivore species and domestic dogs (*Canis familiaris*) (species B), including the probability of occupancy for native carnivores and dogs (B) when humans are present (BA) and absent (Ba) and the species interaction factor (SIF) for each species combination. Photographic data were collected from 2010 to 2015 by the Tropical Ecology Assessment and Monitoring (TEAM) network from 60 camera sites within the Ranomafana National Park, Madagascar.

Species combination	K	2010	2011	2012	2013	2014	2015
Human - Fosa	psiBA	0.25 (0.17)	0.34 (0.07)	0.36 (0.07)	0.37 (0.07)	0.38 (0.08)	0.38 (0.08)
	psiBa	0.33 (0.10)	0.30 (0.05)	0.30 (0.05)	0.29 (0.05)	0.29 (0.05)	0.29 (0.05)
	SIF	0.81 (0.52)	1.09 (0.18)	1.17 (0.17)	1.19 (0.18)	1.19 (0.18)	1.19 (0.18)
Human - Spotted fanaloka	psiBA	0.94 (0.06)	0.69 (0.06)	0.63 (0.06)	0.62 (0.07)	0.62 (0.07)	0.62 (0.07)
	psiBa	0.12 (0.08)	0.60 (0.05)	0.60 (0.05)	0.60 (0.06)	0.59 (0.06)	0.59 (0.06)
	SIF	1.43 (0.15)	1.10 (0.06)	1.03 (0.07)	1.03 (0.08)	1.04 (0.08)	1.04 (0.08)
Human - Ring-tailed vontsira	psiBA	0.36 (0.17)	0.29 (0.06)	0.26 (0.06)	0.25 (0.07)	0.25 (0.07)	0.25 (0.07)
	psiBa	0.66 (0.13)	0.26 (0.06)	0.20 (0.04)	0.19 (0.04)	0.19 (0.04)	0.19 (0.04)
	SIF	0.58 (0.28)	1.10 (0.19)	1.22 (0.21)	1.21 (0.23)	1.20 (0.24)	1.20 (0.24)
Human - Dog	psiBA	0.51 (0.20)	0.30 (0.08)	0.25 (0.07)	0.24 (0.07)	0.24 (0.07)	0.24 (0.08)
	psiBa	0.12 (0.09)	0.08 (0.04)	0.08 (0.04)	0.08 (0.04)	0.08 (0.04)	0.08 (0.04)
	SIF	2.92 (1.51)	2.23 (0.54)	1.98 (0.49)	1.86 (0.45)	1.80 (0.43)	1.77 (0.41)

Dogs have negative effects on mesocarnivores (Vanak and Gompper, 2010); however, in this study most mesocarnivores showed no change in spatial distribution in relation to dog presence. In particular, the spotted fanaloka had high probability of occurrence in contiguous forests and moderate occurrence in degraded forest, where dog presence was greatest. Farris et al. (2015c) observed similar results across the Masoala-Makira landscape with spotted fanaloka being the most widespread native carnivore and having high occurrence within both contiguous and degraded forests. However, additional research has shown spotted fanaloka to occur in lower density in degraded forest (Gerber et al., 2012b), to be absent from fragmented and highly degraded forests (Farris et al., 2015c; Gerber et al., 2012b), and to have lower probability of occupancy at sites where small Indian civets (*Viverricula indica*) are present (Farris et al., 2015a; Farris et al., in press). Finally, the lack of detections and/or low capture rates for falanouc and broad-striped vontsira resulted in low occupancy estimates within RNP and no estimates from bordering degraded forests. These findings demonstrate the rarity of these two carnivores and correspond with previous research (Farris et al., 2012; Farris et al., 2015c; Gerber et al., 2012b; Goodman, 2012).

Conducting routine, effective management activities and assessing the effectiveness of conservation efforts is critical for effective biodiversity conservation; however, these efforts can vary greatly from one PA to the next. RNP remains one of Madagascar's most important PAs as it protects high levels of biodiversity and is perhaps the most active and productive research site in the country (Johnson et al., 2016). Current management efforts include local school and village-based educational programs, school lunch programs to address food security and malnutrition, reforestation programs, and human health and hygiene programs. However, we underscore the need for targeted action plans to address the sharp declines in fosa and ring-tailed vontsira occupancy and the strong positive co-occurrence with dogs within and bordering the PA over the six years. These negative trends occur within a well-studied, important PA and World Heritage Site and raise concerns about the threats to native carnivores and co-occurring wildlife occupying other PAs who experience less monitoring and enforcement. Additional wildlife surveys, widespread household questionnaires, and diet recalls are needed at RNP to quantify bushmeat consumption, understand and quantify depredation events, understand the activities and resource use of humans, and evaluate the effects of free-roaming dogs on threatened wildlife. The data collected from these expansive research efforts must be used to inform systematic conservation planning (ex. identify conservation goals, implement conservation action on the ground, and improving management decisions) so that managers can effectively address the resource and health needs of local communities, the habitat requirements of native carnivores, and the threats posed to biodiversity from introduced dogs, cats, and livestock. A feral and domestic dog control program, which includes spay/neuter and vaccination efforts, is currently being conducted by the Mad Dog Initiative at villages

bordering RNP. To date, the organization has completed > 300 spay/neuter and vaccination procedures, in addition to conducting household questionnaires to investigate the local husbandry and management practices and the role of dogs in local villages (Valenta et al., 2016b). While these efforts may reduce dog populations over time and diminish disease/pathogen transmission, dogs continue to use the majority of the degraded, edge forest and continue accompanying humans into contiguous forest. The increase in human and dog detections on trails located longer distances from villages and forest edge points to the reliance upon existing trails and the need for humans to travel longer distances into the PA for resource extraction. This finding highlights the need for continued monitoring to determine if current and future management efforts are effective at diminishing human and dog activity within contiguous forest in RNP.

5. Conclusion

Designating protected areas represents an initial step towards effective biodiversity conservation, but it requires additional steps to ensure long-term success. Long-term conservation requires commitments to local communities and enforcement of laws and regulations. Management strategies will have to continually evolve as emerging threats are recognized, which are best understood through long-term scientific monitoring. Evaluating the effectiveness of management efforts to protect biodiversity within PAs is critical for effective long-term conservation. Here we investigate human-wildlife conflicts, highlight the negative effects of introduced carnivores on native wildlife, propose management efforts, and evaluate the effectiveness of an important PA to protect a native carnivore community. We highlight several threats to native carnivore species, provide managers with important data to evaluate management efforts, and support the development of active management plans. Addressing the two-fold increase in human presence and activity within this PA calls for additional enforcement and monitoring. We point to the need for a holistic wildlife conservation and local livelihoods approach by local managers to provide the greatest success in meeting the needs of local people and the long-term protection of the carnivore community at RNP. There is a need for education programs on the threat of domestic pets and livestock to local wildlife, the importance of leaving dogs at home when traveling to the forest, expansion of spay/neuter and vaccination programs, and expansion of community-led programs to address local resource needs. Our findings and recommendations are widely applicable to managers and conservationists working to provide long-term protection of biodiversity.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2017.04.010.

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Glossary

Static occupancy: Single-year occupancy estimation using single-species, single-season models.

Dynamic occupancy: Multi-year occupancy estimation using single-species, multi-season models where season refers to year of survey.

Co-occurrence: Spatial distributions of two co-occurring species calculated by using the conditional (psiBa) parameterization (Richmond et al., 2010) of the two-species, multi-season occupancy models.