

Patterns of spatial co-occurrence among native and exotic carnivores in north-eastern Madagascar

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Abstract

Human populations continue to increase and encroach on remaining natural habitats worldwide, resulting in greater numbers and larger ranges of commensal exotic carnivores such as cats and dogs. This results in increased interactions with native wildlife. In Madagascar, we know relatively little about the effects of domestic and/or feral dogs and cats on native carnivore populations. We investigated spatial interactions by combining photographic sampling across seven sites with two-species co-occurrence modeling to provide the first assessment of the spatial co-occurrence of native and exotic carnivores in Madagascar, including an examination of habitat characteristics that explain these relationships. Our surveys from 2008 to 2013 accumulated 2991 photo-captures of native and exotic carnivores in 8854 trap nights. We found that native and exotic carnivores in rainforest habitat occur together less often than expected and that exotic carnivores may be replacing native carnivores, particularly in forest areas nearest villages. Six of the native carnivores in this study had higher site use in the absence of exotic carnivores and their species interaction factors (SIF) revealed a lack of co-occurrence (e.g. $SIF < 1.0$). We found that nocturnal and/or crepuscular native carnivores were less likely to co-occur with exotic carnivores. We demonstrate the effectiveness of combining photographic sampling with co-occurrence modeling to investigate the effects of exotic carnivores on an entire community of native carnivores. Our study exposes the strong negative influence of exotic carnivores, ranging from exclusion to complete replacement of native carnivores, and we urgently recommend a combination of targeted educational programs and removal programs to combat the influx of exotic carnivores.

Introduction

Understanding spatial interactions among species (i.e. level of co-occurrence and behavioral responses to co-occurring species) is of great importance to community ecologists. Spatial interactions are important for addressing questions of community membership, including how communities are shaped and structured (via biotic interactions or random assembly), why some species become members of a community and some do not (i.e. inclusion vs. rejection), and which selection criteria are most important for community assembly (Diamond, 1975; Weiher & Keddy, 1999; Wootton & Emmerson, 2005; Ritchie *et al.*, 2009; Lazenby & Dickman, 2013). Investigating co-occurrence and asymmetrical interactions among species, particularly between predator–prey, different sized predators, competitors and native–exotic species, allows researchers to explore concepts such as competitive exclusion, resource partitioning, predator–prey dynamics and ecological constraints (Lockwood, Moulton & Balent, 1999; MacKenzie, Bailey

& Nichols, 2004; Luiselli, 2006; Waddle *et al.*, 2010; Lazenby & Dickman, 2013).

As exotic carnivores (primarily domestic/feral dogs *Canis familiaris* and cats *Felis* sp.) continue to increase worldwide in number and range, their interactions with native wildlife species continue to mount. Globally, research has highlighted the negative impacts of these exotic carnivores, particularly *Ca. familiaris* (Hughes & Macdonald, 2013), on wildlife populations, with recent work highlighting their impacts on Madagascar's endemic Eupleridae carnivores (Gerber, Karpanty & Randrianantenaina, 2012a,b; Farris, 2014; Farris *et al.*, 2014). This recent research has demonstrated the overlap in temporal activity, habitat use, diet and body size among native and exotic carnivores; however, the spatial interactions of native and exotic carnivores, including the variables influencing these interactions, remain little studied for Madagascar and similar habitats worldwide.

Spatial co-occurrence, or two-species occupancy modeling, provides a framework to investigate asymmetrical interactions and/or behavioral responses for co-occurring

species (MacKenzie *et al.*, 2004; Bailey *et al.*, 2009; Richmond, Hines & Beissinger, 2010; Waddle *et al.*, 2010). In particular, these models provide an estimate of co-occurrence between two or more species within a maximum likelihood framework while accounting for imperfect detection (MacKenzie *et al.*, 2004), thus allowing the investigation of ecological interactions. As a result, these models have been used to investigate interactions among a variety of taxa, including mammals (Williamson & Clark, 2011; Lazenby & Dickman, 2013; Farris *et al.*, 2014; Santulli *et al.*, 2014), birds (Bailey *et al.*, 2009; Richmond *et al.*, 2010; Sauer *et al.*, 2013; Haynes *et al.*, 2014), reptiles (Luiselli, 2006; França & Araújo, 2007; Steen *et al.*, 2014) and amphibians (MacKenzie *et al.*, 2004; Waddle *et al.*, 2010; Olson *et al.*, 2012). However, the use of this spatial modeling approach to investigate the influence of exotic carnivores on native wildlife is currently limited (Krauze-Gryz *et al.*, 2012; Santulli *et al.*, 2014).

Our goal was to provide the first assessment of the spatial co-occurrence of native and exotic carnivores within a complex native-exotic carnivore community. To achieve this goal, we photographically sampled carnivores across a rainforest landscape with varied levels of degradation and human disturbance and estimated co-occurrence and/or co-detection between all species pairings. We included camera station-level and landscape-level habitat variables, ground-dwelling, co-occurring wildlife (i.e. birds and small mammals) and human presence as covariates for all native, endemic Eupleridae carnivores (fosa *Cryptoprocta ferox*, falanouc *Eupleres goudotii*, spotted fanaloka *Fossa fossana*, ring-tail vontsira *Galidia elegans*, broad-stripe vontsira *Galidictis fasciata* and brown-tail vontsira *Salanoia concolor*) and exotic carnivores (domestic dog *Ca. familiaris*, domestic/feral cat *Felis* sp. and small Indian civet *Viverricula indica*) pairings that had sufficient captures for model convergence. Based on the previous findings on native and exotic carnivore habitat use and spatial interactions from our previous work using single-season occupancy (Farris & Kelly, 2011; Farris *et al.*, 2012, in press) and two-species occupancy modeling (Farris *et al.*, 2014, 2016), we expected to find a lack of co-occurrence among native and exotic carnivores as contiguous, undisturbed forest increased and strong co-occurrence where forest became more degraded, patchy and/or fragmented and where exotic carnivore and human activity increased.

Methods

Study site

The Masoala-Makira landscape, which consists of the newly designated Makira Natural Park (372 470 ha of protected area and 351 037 ha of community management zone) and Masoala National Park (240 000 ha), represents the largest protected area landscape in Madagascar (Kremen, 2003; Holmes, 2007). This landscape is estimated to have the highest level of biodiversity in Madagascar, but faces numerous anthropogenic threats, including exotic carni-

vores, poaching, human encroachment and fragmentation (Holmes, 2007; Golden, 2009; Farris *et al.*, 2014; Golden *et al.*, 2014). We photographically sampled carnivores from 2008 to 2013 at seven sites having various levels of degradation and fragmentation across the Masoala-Makira landscape (Supporting Information Appendix S1). These seven study sites were selected as part of an ongoing research project investigating the effects of habitat fragmentation and degradation, exotic species and human encroachment on Madagascar's native carnivores and lemurs (Farris & Kelly, 2011; Farris *et al.*, 2012, 2014). At two of the seven study sites, we conducted repeated surveys, resulting in a total of 13 surveys across the landscape.

Photographic sampling

We established camera grids, consisting of 18–25 camera stations per grid, at each of the seven study sites across the Masoala-Makira landscape (Fig. 1) and surveyed each site an average of 67 days \pm SD 8.10 (min = 53 days; max = 71 days). The length of these surveys was chosen to ensure an adequate number of captures and recaptures for reliable estimation of population parameters based on suggestions from a number of sources (Maffei *et al.*, 2011). Surveys across these seven sites were conducted over the three seasonal periods for this region; however, despite changes in temporal activity across seasons (Farris *et al.*, 2015), season was not important for predicting occupancy or detection across the landscape (Farris *et al.*, 2014, 2015). We placed two digital (Reconyx PC85 & HC500, Holmen, WI, USA; Moultrie D50 & D55, Calera, AL, USA; Cuddeback IR, Greenbay, WI, USA) and/or film-loaded (DeerCam DC300) remote-sensing cameras on opposing sides of human (0.5–2.0-m wide) and game (<0.5-m wide) trails to capture both flanks of passing wildlife at each camera station. We spaced camera stations approximately 500 m apart based on the small home ranges of Madagascar's carnivores, excluding *Cr. ferox* (Goodman, 2012). We offset cameras to prevent mutual flash interference and we paired each camera with a different opposing brand or model of camera to compensate for inefficiency in detection speed, flash or photo quality of various camera models. We checked cameras every 5–10 days to change batteries, memory cards and/or film, and to ensure proper functioning. We placed cameras 20–30 cm off the ground and allowed them to run 24 h day⁻¹. We used no bait or lure.

Camera station-level habitat and landscape sampling

To measure camera station-level habitat features (Supporting Information Appendix S1) for use in occupancy models, we sampled vegetation at each camera station by walking 50-m transects in three directions (0, 120 and 240 degrees) starting at each camera station. At 25 and 50 m on each transect, we used the point-quarter method (Pollard, 1971) to estimate tree density and basal area, recording DBH for

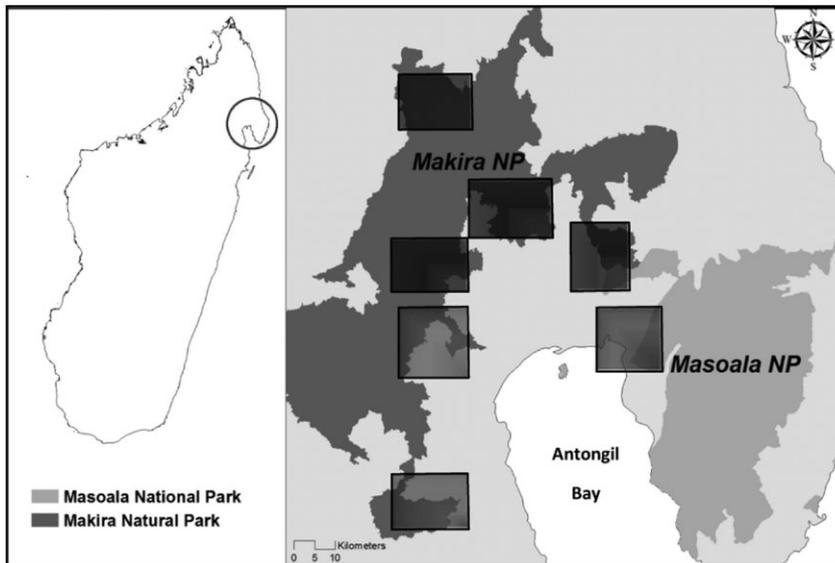


Figure 1 Map of the Masoala-Makira landscape including the outline of the study areas in which the surveys were conducted at seven study sites. Photographic surveys occurred from 2008 to 2012. We are unable to provide the detailed locations of our trap arrays due to the sensitivity of bushmeat data collected at some of the study areas.

any stem/tree ≥ 5 -cm diameter. At 20 and 40 m, we established a 20-m perpendicular transect to the established 50-m transect and we measured understory cover at three levels (0–0.5, 0.5–1.0 and 1.0–2.0 m) by holding a 2-m pole perpendicular to the ground at 1-m intervals and recording presence (1 = vegetation touching pole) or absence (0 = no vegetation touching pole) of understory cover (Davis, Kelly & Stauffer, 2011). Finally, at each 10-m interval along each transect, we estimated canopy height and percent cover. We used these station-level habitat covariates for use in our landscape and site-specific occupancy models for Madagascar's small-bodied native carnivores.

To understand how landscape-level features (Supporting Information Appendix S1) influence carnivore co-occurrence, we used Landsat satellite imagery (2004, 2006 and 2009) and classified the following cover types using Erdas Imagine (Intergraph Corporation, Madison, AL, USA): rainforest, degraded forest and matrix (non-forest area exhibiting early succession, cultivation or open fields for cattle). We placed a 500-m (landscape-level) buffer around individual camera stations, dissolved these individual buffers and clipped the classified imagery for each of the resulting seven camera grid buffers (each providing an approximately 10–15-km² area) for analysis in program FragStats (McGarigal, Cushman & Ene, 2012). For *Cr. ferox*, we used a 2000-m buffer around individual camera stations, rather than the initial 500-m buffer, to extract more meaningful, species-specific landscape covariates given the estimated home range of this larger carnivore species (Hawkins & Racey, 2005).

Using program FragStats, we created the following landscape-level covariates and clipped imagery from each buffered camera grid (~10–15 km²) for use in our occupancy models: (1) number of patches (#Patches): total number of rainforest, degraded forest and matrix patches (based on habitat classifications from satellite imagery) within the buffer; (2) largest patch index (LPI): the percentage of total

buffered area comprised by the largest rainforest patch; (3) landscape shape index (LSI): the standardized measure of total edge adjusted for the size of the buffered area (McGarigal *et al.*, 2012); (4) percent rainforest within the buffered area (%Rain); (5) percent matrix or non-forest, cultivated area within the buffered area (%Matrix); (6) total rainforest core area (Core): the sum of the core areas (accounting for edge of depth of 500 m) of each rainforest patch within the buffer; (7) total edge (TotEdge) (in m ha⁻¹) (McGarigal *et al.*, 2012). Further, we provided an average distance of each camera station to the nearest forest edge (Avg. Dist. to Edge) and to the nearest village (Avg. Dist to Village; Supporting Information Appendix S1) using satellite imagery.

Co-occurring species activity

We defined a 'capture event' as all photographs of unique individuals of a given species within a 30-min time period (Di Bitetti, Paviolo & De Angelo, 2006). Further, we defined a trap night as a 24-h period during which at least one of the two cameras at a camera station is functioning properly. We calculated the trap success (TS) for each species by dividing the number of capture events by the number of trap nights at each camera station, minus malfunctions and multiplied by 100. We calculated TS to provide an encounter rate of co-occurring humans and/or prey species (birds, small mammals) for use as covariates in our co-occurrence models.

Co-occurrence analysis and modeling

We created capture histories for each of the six native and three exotic carnivore species using daily capture events to determine the presence or absence of each species at each camera station. Using these capture histories, we investigated the spatial interactions between native and exotic carnivores via co-occurrence modeling. We used the psiBa

parameterization for the single-season, two-species occupancy model presented by Richmond *et al.* (2010) and modeled co-occurrence in program PRESENCE (Hines, 2006). This parameterization provides eight estimable parameters, including the occupancy of the dominant species (ψ_A), occupancy of the subordinate species where the dominant is present (ψ_{BA}) and absent (ψ_{Ba}), the probability of detection for the dominant species (p_A) and subordinate (p_B) given the other is absent, the probability of detecting dominant given both present (r_A) and the probability of detecting subordinate where dominant is present (p_{BA}) and absent (p_{Ba}).

It should be noted that occupancy in this study is more likely representative of probability of site use (prob[used|occupied]) rather than true occupancy (prob[occupied]) given that our 'sites' are point locations of camera traps. The 500-m spacing may ensure independence of our sites for small- and medium-sized carnivores, but true occupancy is the product of whether the greater area is occupied (which we do not have information about) and whether the species is actually present at the site. We therefore, use 'site use' in lieu of 'occupancy' throughout the paper. Similarly, detection should be interpreted as the probability a species is detected, given the site is occupied and used during each occasion (prob[detected|site occupied and used]). Despite this qualifier, our approach is still valid considering our focus was to explore co-occurrence and habitat co-variate effects among carnivores rather than total occupancy *per se*.

Madagascar's exotic carnivores have been shown to negatively influence occupancy and density of native carnivores (Gerber *et al.*, 2012a,b). Further, these exotic carnivores have a larger body size than the majority of the native carnivores (Farris, 2014). As a result, we used the exotic (E) carnivores as the dominant and the native (N) carnivore as the subordinate for all carnivore pairings, which, in turn, allowed us to investigate how site use by native carnivores changes in the presence (denoted ψ_{NE}) and absence (ψ_{Ne}) of exotic carnivores. In addition to these parameters, we derived a species interaction factor (SIF) for each carnivore pairing based on the formula provided by Richmond *et al.* (2010). This SIF measures interaction between two species to determine if habitat use and selection are due to random processes, thus indicating independent occurrence (SIF = 1.0), or if co-occurrence is greater (SIF > 1.0) or less (SIF < 1.0) than expected under independence (Steen *et al.*, 2014). We used the 'deltamethod' function in the msm package in program R (Team, 2010), using estimates of mean and the variance-covariance matrix from PRESENCE, to calculate the SIF and we incorporated covariate values and corresponding confidence intervals for each carnivore pairing.

These two-species, single-season occupancy models allow us to investigate the level of co-occurrence between two sympatric carnivores; however, no attempt has been made to determine if these co-occurrence relationships are habitat or non-habitat-mediated. Following the recent methods developed by Peoples (2015), we included three specific models

within our model set to differentiate between habitat-mediated and non-habitat-mediated co-occurrence. Using model ranking, we can provide insight on whether: (1) carnivore co-occurrence is independent and site use is explained by habitat [$\psi_{NE} = \psi_{Ne}(\text{Habitat})$]; (2) carnivores co-occur, either positively or negatively, regardless of habitat [$\psi_{NE} \neq \psi_{Ne}(\cdot)$]; or (3) carnivores co-occur and their interactions change across habitat [$\psi_{NE} \neq \psi_{Ne}(\text{Habitat})$]. In these models, 'Habitat' signifies top habitat or landscape covariates based on single-season occupancy modeling from Farris *et al.* (in press).

To evaluate the effect of station-level habitat, landscape-level features, prey species and human presence on native-exotic carnivore co-occurrence and co-detection, we used the most influential covariates from existing single-season, single-species occupancy modeling for each individual carnivore (Farris, 2014). We created *a priori* models for each native-exotic carnivore pairing and we used Akaike information criterion, corrected for small sample sizes (AICc), for model selection (Akaike, 1973). For each carnivore pairing, we reported all top-ranking models ($\Delta\text{AIC} < 2.0$).

For any carnivore pairing having insufficient captures to estimate co-occurrence using the single-season, two-species occupancy modeling, we used single-season, single-species occupancy models to estimate the site use and detection (given site use) of the native carnivore species and we used the encounter history of the exotic carnivore as a covariate to assess the effect of exotic carnivore presence on native carnivore site use and detection. We combined all surveys across the seven study sites to estimate native-exotic carnivore co-occurrence. At sites having repeated surveys across years, we used the survey having the highest cumulative total number of native-exotic carnivore captures for the carnivore pair being assessed. This provided a total of 152 camera stations across the Masoala-Makira landscape to estimate native-exotic carnivore co-occurrence.

Results

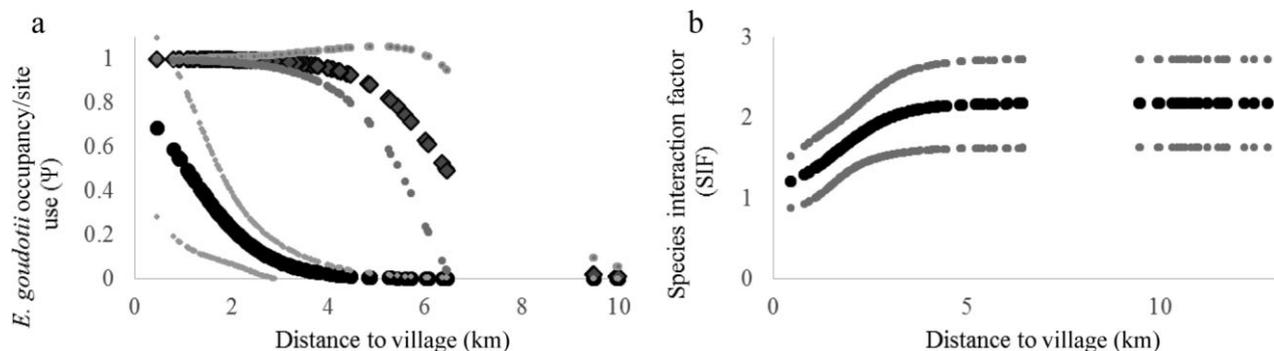
From 2008 to 2013, we captured all six native and three exotic carnivore species known to occupy the Masoala-Makira landscape (Farris *et al.*, 2012; Goodman, 2012). We surveyed an average of 1264 trap nights per site accumulating a total of 8854 trap nights across our seven study sites and a total of 2991 photo-captures of native and exotic carnivores. Of the 18 native-exotic carnivore pairings, we were unable to estimate the spatial co-occurrence and/or co-detection for six pairings due to insufficient captures. For these six carnivore pairings, we attempted the use of single-season, single-species occupancy models to assess the influence of the exotic predator on native carnivore site use; however, due to insufficient captures, these models did not converge or models revealed poor fit ($c\text{-hat} > 3.0$).

Five of the native-exotic carnivore relationships exhibited independent relationships and site use was best predicted by habitat or landscape [$\psi_{NE} = \psi_{Ne}(\text{Habitat})$; SIF = 1.0], while the remaining seven pairings had strong co-occurrence relationships that were influenced by a

Table 1 Probability of spatial co-occurrence between exotic and native carnivores, including the probability of occupancy (ψ) and detection (r) with (NE) and without (Ne) the co-occurring exotic predator

Species	ψ NE (SE)	ψ Ne (SE)	r NE (SE)	r Ne (SE)	SIF	CI
<i>Canis familiaris</i> and <i>Cryptoprocta ferox</i>	0.51 (0.06)	0.51 (0.06)	0.22 (0.02)	0.22 (0.02)	0.95	0.77–1.13
<i>Ca. familiaris</i> and <i>Fossa fossana</i>	0.43 (0.05)	0.43 (0.05)	0.29 (0.03)	0.29 (0.03)	1.00	–
<i>Ca. familiaris</i> and <i>Eupleres goudotii</i>	0.23 (0.05)	0.69 (0.11)	0.07 (0.03)	0.22 (0.04)	0.51	0.29–0.73*
<i>Ca. familiaris</i> and <i>Galidictis fasciata</i>	0.24 (0.06)	0.90 (0.15)	0.08 (0.02)	0.08 (0.02)	0.59	0.41–0.77*
<i>Ca. familiaris</i> and <i>Salanoia concolor</i>	0.31 (0.05)	0.31 (0.05)	0.01 (0.005)	0.01 (0.005)	0.91	0.90–0.92
<i>Felis catus</i> and <i>Cr. ferox</i>	0.85 (0.03)	0.85 (0.03)	0.14 (0.04)	0.07 (0.01)	0.98	0.88–1.08
<i>Fs. catus</i> and <i>E. goudotii</i>	0.43 (0.03)	0.07 (0.03)	0.04 (0.01)	0.04 (0.01)	1.90	1.49–2.31*
<i>Fs. catus</i> and <i>S. concolor</i>	0.13 (0.04)	0.13 (0.04)	0.02 (0.01)	0.02 (0.01)	1.00	–
<i>Viverricula indica</i> and <i>Fo. fossana</i>	0.33 (0.11)	0.72 (0.31)	0.36 (0.05)	0.36 (0.05)	0.50	0.0–1.01
<i>V. indica</i> and <i>E. goudotii</i>	0.11 (0.05)	0.64 (0.19)	0.33 (0.05)	0.33 (0.05)	0.22	0.10–0.34*
<i>V. indica</i> and <i>Ga. elegans</i>	0.14 (0.06)	0.86 (0.27)	0.25 (0.04)	0.25 (0.04)	0.26	0.24–0.28*
<i>V. indica</i> and <i>Gs. fasciata</i>	0.11 (0.08)	0.89 (0.22)	0.06 (0.03)	0.06 (0.03)	0.21	0.19–0.23*

The spatial interaction between each exotic and native predator is described by the species interaction factor (SIF) where lack of co-occurrence is denoted by $SIF < 1.0$ and co-occurrence by $SIF > 1.0$, as long as the confidence intervals (CIs) on SIF do not overlap 1.0 (indicated by the asterisk). Photographic sampling of carnivores occurred across the Masoala-Makira landscape from 2008 to 2013.

**Figure 2** Level of co-occurrence between the native falanouc *Eupleres goudotii* and exotic domestic/feral cat *Felis* sp., including (a) the probability of occupancy (i.e. site use) (Ψ) for *E. goudotii* with (gray diamonds) and without (black circles) *Felis* sp. as a function of distance to village (km) and (b) the species interaction factor (SIF) revealing strong co-occurrence between *Felis* sp. and *E. goudotii* as distance to village increases. SIF of 1.0 denotes independent occurrence, while $SIF > 1.0$ indicates co-occurrence. Gray dashed lines show the 95% confidence intervals. Photographic sampling of carnivores occurred across the Masoala-Makira landscape from 2008 to 2013.

habitat or landscape variable [ψ NE \neq ψ Ne (Habitat); Table 1]. We found that numerous native carnivores co-occur less often with exotic carnivores than expected under independence (ψ Ne $>$ ψ NE; Table 1). In particular, native carnivores had lower or equal site use in the presence of *Ca. familiaris* and lower site use in the presence of *V. indica*. Only one native carnivore, *E. goudotii*, had a higher site use in the presence of an exotic carnivore, *Felis* sp. (Table 1; Fig. 2). In addition, the corresponding SIF provide further evidence of these negative relationships ($SIF < 1.0$) for carnivore pairings (Table 1). Six of the native–exotic carnivore pairings revealed a lack of co-occurrence (i.e. occurred together less than expected under independence). Of those six pairings, four occurred between the exotic *V. indica* and native carnivores and two between *Ca. familiaris* and native carnivores, while *Felis* sp. had the one co-occurrence relationship with *E. goudotii* (Fig. 2). Nocturnal and/or crepuscular native carnivores were more likely to show lack of co-occurrence with exotic carnivores ($n = 5$ pairings; Table 1; Figs 2–4). In particular,

E. goudotii and *S. concolor* were the least likely native carnivores to co-occur with exotic carnivores (Table 1; Figs 3 and 4).

Canis familiaris and *Felis* sp. had the highest number of independent relationships ($n = 3$, $n = 2$; respectively), while for native species, *Cr. ferox* and *S. concolor* had the highest number of independent relationships (2 each; Table 1). These independent relationships occurred among the three largest bodied and most wide-ranging species (*Ca. familiaris*, *Felis* sp. and *Cr. ferox*; Farris, 2014) and the most rare and elusive carnivore (*S. concolor*) (Farris *et al.*, 2012).

We found that landscape variables, particularly number of patches ($n = 5$ co-occurrence relationships) and distance to nearest village ($n = 3$ co-occurrence relationships), were most important for explaining spatial co-occurrence for native and exotic carnivores (Supporting Information Appendix S2). Bird trap success, percent rainforest and percent matrix were the only other variables present in the top-ranking models (Supporting Information Appendix S2). Our results revealed

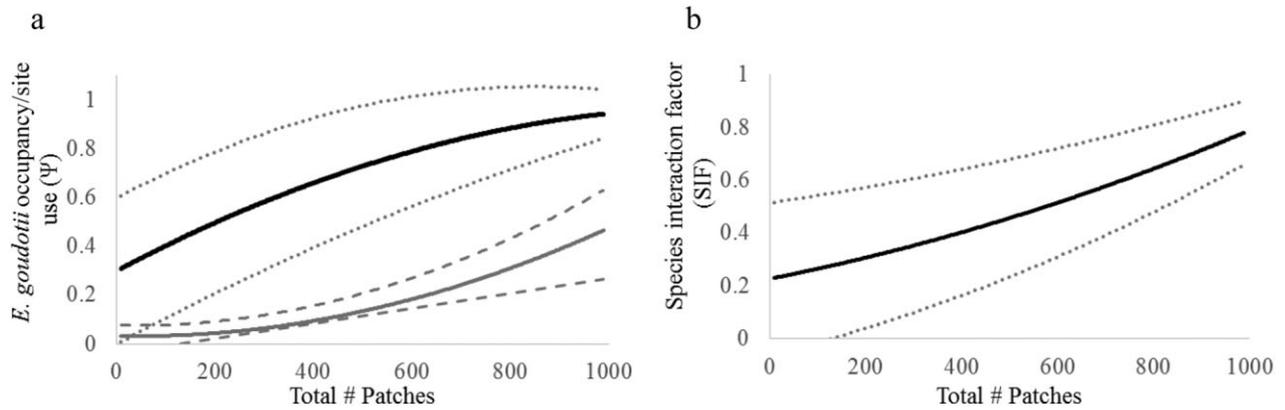


Figure 3 Level of co-occurrence between the native falanouc *Eupleres goudotii* and exotic dog *Canis familiaris*, including (a) the probability of occupancy (i.e. site use) (Ψ) for *E. goudotii* with (gray line) and without (black line) *Ca. familiaris* as a function of total number of patches and (b) the species interaction factor (SIF) revealing evidence of spatial segregation of *E. goudotii* by *Ca. familiaris* in forest habitat where number of patches is low. SIF of 1.0 denotes independent occurrence, while SIF < 1.0 indicates lack of co-occurrence. Gray dashed lines show the 95% confidence intervals. Photographic sampling of carnivores occurred across the Masoala-Makira landscape from 2008 to 2013.

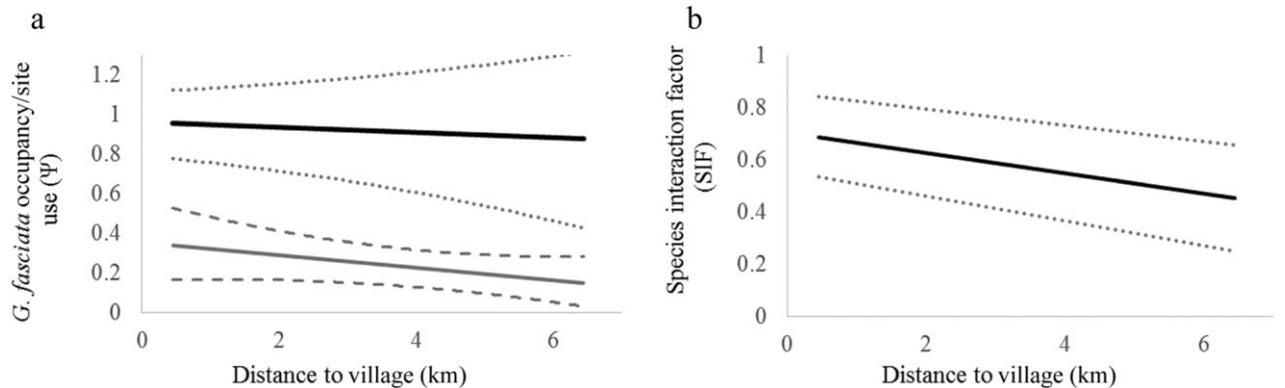


Figure 4 Level of co-occurrence between the native broad-stripe vontsira *Galidictis fasciata* and exotic dog *Canis familiaris*, including (a) the probability of occupancy (i.e. site use) (Ψ) for *Gs. fasciata* with (gray line) and without (black line) *Ca. familiaris* as a function of distance to village (km) and (b) the species interaction factor (SIF) revealing evidence of spatial segregation of *Gs. fasciata* and *Ca. familiaris* as distance to village increases. SIF of 1.0 denotes independent occurrence, while SIF < 1.0 indicates lack of co-occurrence. Gray dashed lines show the 95% confidence intervals. Photographic sampling of carnivores occurred across the Masoala-Makira landscape from 2008 to 2013.

that native carnivores are less likely to co-occur with exotics within patchy forest nearest villages (Figs 2–4). Finally, we found that co-detection probabilities were independent ($rNE = rNe$) for the majority of our native–exotic carnivore pairings (Table 1). However, we did find that *E. goudotii*, whose detection was positively influenced by bird activity, was more difficult to detect when *Ca. familiaris* was present. Conversely, *Cr. ferox*, whose detection increased with increasing patchiness, had an increase in detection when *Felis* sp. was present (Table 1).

Discussion

The negative impacts of exotic carnivores (especially *Ca. familiaris*) as competitors, predators and disease vectors on native wildlife have been documented in a variety of habitats worldwide (Gompper, 2013; Hughes & Macdonald,

2013), thus drawing attention to this factor as a major threat to native species worldwide. However, we still lack sufficient knowledge of the spatial interactions between these exotic carnivores and co-occurring native wildlife, particularly across rainforest habitat. Additionally, little is currently known about the poorly studied carnivores of Madagascar. Our study contributes to the body of knowledge on native–exotic carnivore interactions, and to the general knowledge of Malagasy carnivores, by providing the first investigation of the spatial co-occurrence among multiple co-occurring native and exotic carnivores, including identifying important variables explaining these relationships. We provide strong evidence of the negative influence of exotic carnivores on native ones across the landscape. The presence of exotic carnivores resulted in decreased site use of native carnivores, providing evidence of the replacement of native species by exotic species across the landscape. Further, these

negative relationships are linked to anthropogenic disturbance and/or human presence (increased patchiness and distance to nearest village). Our ongoing research shows that native carnivores have moderate probabilities of occupancy within degraded, fragmented forest and that exotic carnivores are widespread across the landscape, including higher occupancy than half of the native carnivore species, even in contiguous, non-degraded forest (Farris, 2014). These results suggest that our findings are not simply habitat-mediated relationships, but rather that native carnivores avoid or are excluded from sites where *Ca. familiaris* and *V. indica* are present. These findings provide confirmation of our hypothesis that native carnivores would exhibit limited co-occurrence with exotic carnivores in contiguous, non-degraded forest where prey activity is highest and exotic carnivore and human activity were lowest (Farris, 2014). This study highlights the threat to the persistence of native carnivores across both degraded and non-degraded forests as exotic carnivores continue to increase across Madagascar. Similar findings on the effect of exotic carnivores, namely *Ca. familiaris* and their role as competitors, predators and disease vectors, on native carnivores are highlighted in extensive reviews by Young *et al.* (2011) and Vanak *et al.* (2013). Our results for *Ca. familiaris* display their ability to influence the spatial distribution of native carnivores, adding to the existing body of knowledge. Specifically, we add evidence of competitive dynamics between *Ca. familiaris* and native carnivores with smaller-bodied native carnivores, altering their spatial distribution where *Ca. familiaris* is present, as noted by Vanak *et al.* (2013).

Studies investigating the effect of exotic carnivores on native carnivores, especially with multiple co-occurring exotic carnivores, are rare (Catling & Burt, 1995; Greenville *et al.*, 2014). The negative effects of exotics on natives may increase when multiple exotic carnivores are present. For example, site use of *E. goudotii* diminishes greatly in the presence of both *V. indica* and *Ca. familiaris*. If a strong negative species interaction factor exists between *V. indica* and *Ca. familiaris*, resulting in *V. indica* using forested areas in which *Ca. familiaris* are not present, as was observed for similar exotic carnivores by Krauze-Gryz *et al.* (2012), the negative effects on *E. goudotii* may increase greatly when both exotic carnivores are present. While additional co-occurrence modeling among exotic carnivores themselves (perhaps using an alternative occupancy parameterization) may provide insight into these relationships and their influence on native species, our research on exotic carnivore single-species occupancy shows no relationships among exotic carnivores (Farris *et al.*, 2014, in press). Additional research on co-occurring exotic carnivores will increase our understanding of these relationships and bolster our efforts to curtail the expansion of these exotic predators and lessen their effects on the ecosystems they invade.

Understanding how presence of one species influences detection of another is an additional benefit to this modeling approach. Bailey *et al.* (2009) noted that it is possible for one species to alter the detection of a target species and, in turn,

influence their probability of occupancy across the landscape. We found similar results as *E. goudotii* was detected less often in the presence of *Ca. familiaris* ($rNE < rNe$). The increasing difficulty in detecting *E. goudotii* when *Ca. familiaris* is present may provide important insight into this relationship, including behavioral responses of *E. goudotii* across this landscape. We suggest that *E. goudotii* are more likely to avoid the use of trails in areas where *Ca. familiaris* activity is high. The importance of co-detection should not be overlooked when estimating co-occurrence or investigating species relationships in similar studies.

The approach used in this study, introduced by Peoples (2015), provides insight into the influence of habitat on co-occurrence relationships. While five of our exotic–native carnivore pairings exhibited independent relationships where occurrence was simply habitat-mediated [$\psi BA = \psi Ba$ (Habitat); SIF = 1.0], seven of the carnivore pairings showed the opposite, strong co-occurrence relationships (SIF \neq 1.0) with interactions influenced by changes in habitat or landscape variables. This has strong management implications. For example, an effective approach to reduce potential interactions such as competition and/or predation events between *Ca. familiaris* and the native *S. concolor* and *E. goudotii* is to ensure that we protect non-patchy, contiguous forest located at least 5 km from the nearest village. Additional studies investigating exotic–native carnivore relationships have found similar results (Vanak & Gompper, 2010; Gerber *et al.*, 2012b; Greenville *et al.*, 2014) as highlighted by Lacerda, Tomas & Marinho-Filho (2009) who argue that *Ca. familiaris* contributes to edge effects and demonstrate that native carnivores avoid these edges where *Ca. familiaris* is active. Our results on carnivore co-occurrence, and our additional work on carnivores across this region (Farris *et al.*, 2012, 2015, in press), provide additional support for this argument that *Ca. familiaris* contribute to, and potentially exacerbate, edge effects across degraded and/or fragmented forests. We found no evidence that prey or co-occurring species activity levels explained the relationships among native and exotic carnivores across the landscape. However, our models incorporated ground-dwelling bird and small mammal trap success only and did not incorporate the complete diverse prey base for Madagascar's native carnivore community (Goodman, 2012). Additional work is needed to improve our understanding of the diet of Madagascar's native and exotic carnivores before we can adequately assess their importance in explaining co-occurrence relationships.

Recent research on Madagascar's carnivore community has revealed a decrease in native carnivores as degradation and/or exotic carnivore activity increases and negative relationships between native carnivores and a host of anthropogenic variables, including distance to edge and village, human presence and hunting/poaching rates (Farris *et al.*, 2012, in press; Gerber *et al.*, 2012b). Additionally, our long-term surveys at one site reveal considerable declines in native carnivore occupancy and large increases in *Felis* sp. occupancy over a 6-year period (Farris, unpublished data).

Our work to date on Madagascar's carnivore community points to diminishing native carnivore populations as exotic carnivore species increase. In addition, temporal analyses reveal that for the three exotic carnivores, the greatest temporal overlap occurred between *V. indica* and native carnivores (Farris *et al.*, 2015). The culmination of strong temporal overlap and the spatial co-occurrence highlighted by this study between *V. indica* and *E. goudotii*, *Fo. fossana* and *Gs. fasciata* represents an alarming conservation issue that demands attention. Additionally, in a modeling approach that combines our spatial co-occurrence results with temporal activity patterns, we found negative spatio-temporal relationships between *V. indica* and *Fo. fossana* (Farris *et al.*, 2016). This approach allows us to identify precise positions in space and time and may prove useful for aiding conservationists and managers in their efforts to develop targeted management strategies to eliminate these negative interactions.

These findings draw attention to the need for targeted management strategies to address the growing presence of exotic carnivores and reduce their interactions with native wildlife in Madagascar, and in similar habitats worldwide. In particular, we found a strong correlation between humans and *Ca. familiaris* across our survey sites (Farris, 2014) and suggest that education of local people on the negative interactions between *Ca. familiaris* and native wildlife, including encouraging local people to leave their pets at home when traveling to the forest, may greatly curtail these negative interactions. We strongly propose removal programs for *Felis* sp. across Madagascar's forests, especially across the Masoala-Makira landscape where their site use/occupancy is high and strong negative associations between *Felis* sp. and multiple native carnivore and lemur species exist (Farris, 2014; Farris *et al.*, 2014). However, trap-removal programs have proven costly and have been met with mixed results in a wide range of habitats (Winter, 2004; Foley *et al.*, 2005; Longcore, Rich & Sullivan, 2009; Campbell *et al.*, 2011). Such programs carried out over a large landscape like Masoala-Makira may not be attainable or effective. The opportunity exists to introduce a bounty program for *Felis* sp.; however, the unsustainable hunting of native carnivores and lemurs occurring across this region (Golden, 2009) further complicates the effectiveness of this approach as the increased presence of local people and/or hunting and trapping within forest habitat in response to this program may result in an increase in direct or indirect killing of native species.

As noted by Vanak *et al.* (2013), there is a lack of research on competitive dynamics between exotic carnivores, namely *Ca. familiaris*, and sympatric carnivores, including the range of species effected by these exotics. This research provides insight on a diverse group of co-occurring exotics and natives within the carnivore community and provides an effective sampling and modeling method useful to investigate these potential competitive dynamics in other habitats worldwide that suffer from multiple, sympatric introduced or exotic carnivores (Glen & Dickman, 2005). Here, we bring attention to the importance of anthropogenic landscape variables,

such as distance to village and number of patches, in explaining these negative relationships across the landscape shedding light on the connection between human encroachment into contiguous forest and increasing human–carnivore conflict. We suggest that human–carnivore conflicts, including those involving exotic carnivores, in similar habitats worldwide are likewise linked to anthropogenic variables, as has been observed in similar studies (Vanak & Gompper, 2010). Addressing human encroachment and commensal exotics species, into contiguous forests, is necessary to effectively combat the loss in biodiversity worldwide.

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Supporting information

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

Appendix S1. Station-level habitat (camera station) and landscape (500 m grid buffer) features (SE) for the seven study sites, ranked from least degraded (S01) to most degraded (S07), across the Masoala-Makira landscape (Farris, 2014).

Appendix S2. Top ranking models ($\Delta AIC < 2.0$) from our single-season, two-species occupancy models for exotic (E; dominant) and native (N; subordinate) carnivore pairings having sufficient captures for model convergence.