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Abstract Predator–primate interactions are understudied, yet predators have been shown to influence primate behavior, population dynamics, and spatial distribution. An understanding of these interactions is important for the successful management and conservation of these species. Novel approaches are needed to understand better the spatial relationships between predators and primates across changing landscapes. We combined photographic surveys of predators and humans with line-transect sampling of lemurs across contiguous and fragmented forests in Madagascar to 1) compare relative activity; 2) estimate probability of occupancy and detection; 3) estimate predator–primate and local people–primate co-occurrence; and 4) assess variables influencing these parameters across contiguous and fragmented forests. In fragmented (compared to contiguous) forest sites endemic predator and lemur activity were lower whereas introduced predator and local people activity were higher. Our two-species interaction occupancy models revealed a higher number of interactions among species across contiguous forest where predator and lemur occupancy were highest. Mouse lemurs show evidence of "avoidance" (SIF < 1.0) with all predator species (endemic and introduced) in contiguous forest whereas white-fronted brown lemurs show "attraction" (SIF > 1.0) with feral cats and local people in contiguous forest. Feral cats demonstrated the highest number of interactions with lemurs, despite their distribution being limited to only contiguous forest. Distance to forest edge and distance to nearby villages were important in predicting predator occupancy and detection. These results highlight the growing threat to endemic predators and lemurs as habitat loss and fragmentation increase throughout Madagascar. We demonstrate the effectiveness of

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a novel combination of techniques to investigate how predator species impact primate species across a gradient of forest fragmentation.

Keywords Exotic/introduced carnivore · Fossa · Interaction occupancy model · Lemur · Multispecies occupancy · Predator–prey dynamics

Introduction

The ongoing patterns in forest loss and fragmentation throughout primate habitat worldwide makes it especially urgent to understand the spatial interactions of predators and primates and how the altering of landscapes impacts these interactions. Forest loss and fragmentation negatively impact a host of primate species in various regions of the world (Arroyo-Rodríguez and Dias 2010; Boyle and Smith 2010; Estrada *et al.* 2012; Ganzhorn *et al.* 2003; Gilbert 2003; Harcourt and Doherty 2005; Johns and Skorupa 1987; Kankam and Sicotte 2013; Onderdonk and Chapman 2000; Schwitzer *et al.* 2011; Yanuar and Chivers 2010). In addition, habitat loss and fragmentation further intensify extinction risk for numerous primate species via ecological factors such as environmental stochasticity and catastrophic events (Lande 1998). As a result, an understanding of how native and introduced predators impact primate populations in disturbed and fragmented forests is critical for conservation and management of these populations. This also includes an understanding of how human (nonresearcher; hereafter "local people") presence impacts primate populations across these forest types.

Local people presence and/or activity may pose a significant threat to primate populations resulting from disturbance, forest loss, poaching, or other anthropogenic pressures (Blom *et al.* 2004; Golden 2009; Goudie 2013; Griffiths and van Schaik 1993; Yamagiwa 2003). As predators and primates are increasingly forced into isolated fragments of forest, natural or exacerbated predation rates by predators may negatively impact primate populations that are simultaneously being limited by declining habitat quality and human encroachment. For example, predation by fossa (*Cryptoprocta ferox*), Madagascar's largest carnivore, lead to the extirpation of sifakas (*Propithecus diadema*) from disturbed, fragmented forest sites in Madagascar and the consumption of primates by fossa (relative to other prey) increases in forest fragments (Irwin *et al.* 2009). Although research exists on the impacts of habitat loss and fragmentation on both predators and primates worldwide, an attempt to link predator and primate interactions across fragmented and contiguous forests is still lacking.

Predator–primate interactions remain understudied, particularly as they relate to forest loss and fragmentation, as a result of the challenges associated with investigating these relationships. Predation influences primate behavior, population dynamics, spatial distribution, and group size (Colquhoun 2006; Goodman 2003; Hart 2007; Hill and Lee 1998; Irwin *et al.* 2009; Isbell 1994; Karpanty 2006; Miller 2002; Miller and Treves 2007; Shultz *et al.* 2004; Terborgh and Janson 1986; Willems and Hill 2009; Zuberbühler and Jenny 2002). In addition to the direct effects of predators on primate survival, it is equally important to quantify the indirect, nonlethal interactions, and/or risk effects associated with antipredator behavior as these interactions may also be significant to primate populations (Creel 2011; Lima 1998). Investigation of these nonlethal interactions and antipredator behaviors, as well as lethal interactions and direct mortality, is challenging and often relies on indirect investigation, such as chance sightings of predation attempts or events, vocalization, or playback studies [nonlethal interactions] (Karpanty and Wright 2007; Rahlfs and Fichtel 2010; Schel and Zuberbühler 2012), as well as diet analysis of predator scat and investigation of prey remains [lethal interactions] (Braczkowski *et al.* 2012; Burnham *et al.* 2013; Hart 2007; Henschel *et al.* 2011; Isbell 1994; Jooste *et al.* 2013). Indeed, much of our knowledge on predator–primate dynamics has resulted from such indirect investigations and, while these studies remain important in understanding predator–primate interactions, novel approaches are needed to better understand the spatial relationships and variation in those relations, between predators and primates across changing landscapes. The combination of camera trapping and line-transect sampling presents a unique approach to investigate these interactions to further our knowledge of how predator–primate dynamics are impacted by forest loss and fragmentation.

Our aim was to provide valuable insight on the spatial interactions or co-occurrence, i.e., random assemblages vs. species attraction/avoidance, among predators, local people, and lemurs, as well as the variables influencing these relationships. To achieve this goal our objectives were to 1) compare the relative activity and/or trap success of predators and lemurs between contiguous and fragmented forest sites; 2) determine the landscape and habitat variables impacting predator and lemur occupancy and detection across the landscape; 3) quantify the distributional relationship (co-occurrence) between predator–lemur and local people–lemur occupancy in contiguous and fragmented forest sites; and 4) assess the level of convergence among variables impacting predator–lemur and local people–lemur occupancy, detection, and co-occurrence. To achieve our objectives, we quantified the spatial distribution and occupancy of predators, local people, and lemurs in both contiguous and fragmented forests across the Masoala–Makira landscape in northeastern Madagascar, and assessed patterns of co-occurrence (interactions) between local people and lemurs, as well as predators and their potential lemur prey. We predicted to find decreased activity (trap success) for endemic carnivores and lemurs in fragmented forest and increased activity for introduced predators in fragmented forest. Further, we predicted to find negative relationships with endemic predator and lemur occupancy and various anthropogenic variables, e.g., distance to village, distance to edge, percent matrix. Finally, we expected to find more negative interactions (SIF < 1.0) between introduced predator–lemur and local people–lemur in fragmented forest where available habitat is diminished and patchy.

Methods

Study Site

We surveyed predators and lemurs using photographic surveys and line transects in two contiguous and two fragmented forest study sites across the Masoala–Makira landscape (Fig. 1) from August 2010 to November 2012, including three surveys of one of our contiguous forest sites (Table I). Six species of endemic predators (Eupleridae), 3 species of introduced predators, and 22 species of lemurs are known to occur across the Masoala–Makira landscape (Table II) (Farris *et al.* 2012; Goodman 2012; Garbutt 2007) . Madagascar's endemic predators have generalist diets (Goodman 2012; Garbutt 2007); however, we focus on the following endemic and introduced predators (Goodman 2003): fossa (*Cryptoprocta ferox*), ring-tail vontsira (*Galidia elegans*), domestic dog (*Canis familiaris*), and feral cats (*Felis silvestris catus*). In addition, local people activity and disturbance is prevalent across this region, including the poaching of predators and lemurs (Golden 2009). To understand how human activity/presence is impacting primate populations we included photographic capture events of local people (all local people activity given we could not distinguish between poachers and nonpoachers) in our analyses.

The two contiguous (C) forest study sites, Anjanaharibe (AJB-C) and Mangabe (MGB-C), were located inside the Makira Natural Park (NP), which is a combination of a 3724-km^2 park and 3510-km^2 community-managed buffer zone. Makira NP protects the largest remaining tract of contiguous rain forest in Madagascar and is thought to contain the highest levels of biodiversity in Madagascar (Holmes 2007; Kremen 2003). The AJB-C and MGB-C study sites consist of intact, primary rain forest with varying degrees of degraded, secondary rain forest present near the forest edge (Fig. 1). MGB-C is bisected by a heavily traveled local people trail that connects the western and eastern portions of Makira NP. For our fragmented (F) forest sites, the Farankarina site (FRK-F) is located inside the Farankarina forest reserve, a 16.5 km^2 reserve and is separated by at least 5 km from intact forest (Fig. 1). This site consists of primary, undisturbed

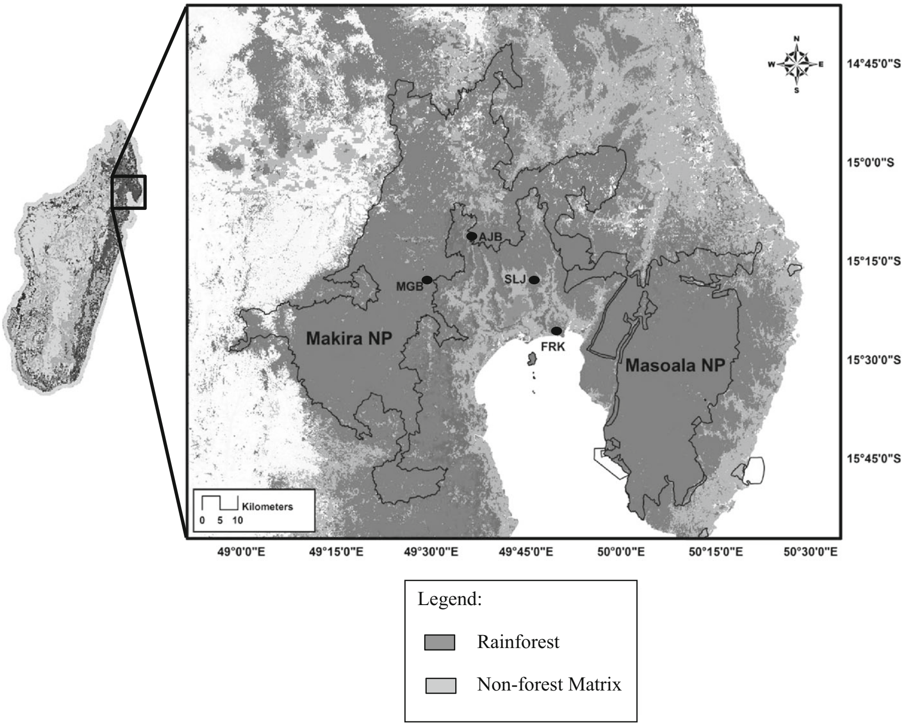

Fig. 1 Map of study sites across the Makira Natural Park highlighting the location of Masoala National Park, Makira Natural Park, as well as the two contiguous study sites: Anjanaharibe (AJB) and Mangabe (MGB) and the two fragmented study sites: Lohan'sahanjinja (SLJ) and Farakarina (FRK).

Table I Sampling details and survey effort for photographic and lemur surveys performed across the Masoala–Makira landscape in NE Madagascar, including elevation range and distance to nearest village from edge of study site

Study site	Forest type	Survey dates	No. of camera stations	Trap nights	Elevation (m)	Distance to nearest village (km)
Anjanaharibe (1AJB)	Contiguous (C)	Sept.–Nov., 2010	25	1257	350–690	2.8
Anjanaharibe (2AJB)	Contiguous (C)	Aug.–Oct., 2011	24	1383	350–690	2.8
Anjanaharibe (3AJB)	Contiguous (C)	Aug.–Oct., 2012	24	1536	350–690	2.8
Mangabe (MGB)	Contiguous (C)	March–May, 2011	24	1509	324–786	4.8
Lohan'sanjinja (SLJ)	Fragmented (F)	Dec.–Feb., 2010	24	1570	93–507	1.5
Farankarina (FRK)	Fragmented (F)	June–Aug., 2011	23	1462	21–886	2.1

Trap nights = 24-h period in which at least one of the two cameras at a given camera station is not malfunctioning × number of camera stations in study site.

rain forest in the southern portion of the protected area (~15 km^2) and highly degraded forest with extensive forest loss in the northern portion and extending beyond the protected area (~23.5 km^2). Our final site, Lohan'sanjinja, (SLJ-F) was located 9.3 km from the nearest protected area and no community management system existed for this site. This site consists of a narrow strip of highly degraded forest (~1.3 km wide) with extensive forest loss and a collection of forest patches connecting it to intact forest in the north (Fig. 1).

Field Methods

Predator Surveys At all four study sites we established a camera-trapping grid consisting of 23–25 camera stations spaced *ca.* 500 m apart to photographically sample wildlife (Table I). We used both digital (Moultrie D40, Reconyx PC85 and Cuddeback IR) and film-loaded camera-traps (DeerCam DC300) which were operational 24 h/d and positioned *ca.* 20–30 cm off the ground. We placed two cameras on opposing sides of existing human trails (0.5–2.0 m wide) and game trails (<0.5 m wide). We checked cameras every 5–10 d to change batteries, memory cards, and/or film and to ensure proper functioning due to the high levels of rain and humidity. We took every effort to minimize the time spent at each camera station during camera checks so as to reduce our impact on wildlife detection. Cameras were operational for a mean number of 67 d (±SE 0.87) per survey and we used no bait or lure at camera stations to attract wildlife.

Lemur Surveys We established three, 2 km long lemur transects at each of the four study sites. These transects were located along the existing human and game trails used for our photographic surveys of predators. At each study site we surveyed lemur transects five or six times diurnally, between 07:00 and 11:00 h, and five or six times

Table II Total number of observations (line-transect sampling) and/or captures (photographic surveys) of endemic predators, introduced predators, and lemurs during our surveys from August 2010 to November 2012 across the Masoala–Makira landscape, NE Madagascar

Scientific name	Common name	Total observations/captures
Endemic predators		
Cryptoprocta ferox	**Fossa**	244
Fossa fossana	Malagasy civet	486
Eupleres goudotii	Falanouc	141
Galidia elegans	**Ring-tail vontsira**	112
Galidictis fasciata	Broad-striped vontsira	53
Salanoia concolor	Brown-tail vontsira	44
Introduced predators		
Viverricula indica	Indian civet	44
Canis familiaris	**Domestic dog**	1195
Felis silvestris familiaris	**Feral cat**	62
Lemurs		
Eulemur albifrons	**White-fronted brown lemur**	57
Eulemur rubriventer	Red-bellied lemur	1
Hapalemur griseus	Eastern lesser bamboo lemur	P[a]
Varecia rubra	Red-ruffed lemur	3
Varecia variegate	White-ruffed lemur	2
Propithecus candidus	Silky sifaka	1
Indri indri	Indri	25
Microcebus rufus	**Eastern mouse lemur**	67
Avahi laniger	**Eastern wooly lemur**	101
Cheirogaleus major	Greater dwarf lemur	13
Phaner furcifer	Forked-marked lemur	P[a]
Daubentonia madagascariensis	Aye-aye	P[a]

Species included in analyses for this article are in bold.

[a] Species was present and observed but not detected during line-transect sampling.

nocturnally, between 18:30 and 0:00 h. For all lemur observations we recorded species, date, time, number in group, distance to center of group, height, detection cue, behavior, and weather conditions.

Landscape and Habitat Sampling To understand how landscape and habitat metrics impact predator–primate occupancy, detection, and co-occurrence we used Landsat satellite imagery (2006 and 2009) with habitat classifications and masking provided by the Wildlife Conservation Society, Madagascar Program to measure the distance of each camera station to the nearest forest edge and to the nearest village. To sample vegetation at each camera station we walked a 50 m transect in three directions (0, 120, and 240°) starting at the camera station and classified the canopy height and percent cover every 10 m at each transect. At 25 m and 50 m on each transect we used the point-quarter method (Pollard 1971) to measure tree density and basal area, recording diameter at breast height (DBH) for any stem/tree >5 cm diameter. Finally, at 20 m and 40 m we measured understory cover at three levels (0–0.5 m, 0.5–1.0 m, and 1.0–2.0 m) by placing a 2-m pole on the ground at 1-m intervals and recording presence (1) for vegetation touching the pole and absence (0) when no vegetation was touching. Understory sampling was conducted on a 20-m transect running perpendicular to the established 50-m habitat transect (Davis *et al.* 2011).

Analyses

Predator Trap Success and Lemur Activity For comparison of carnivore and lemur activity, occupancy, and co-occurrence we used the combination of camera-traps (carnivores) and line-transect sampling (lemurs), which is a well-documented means of comparison (Barea-Azcón *et al.* 2007; LaFleur *et al.* 2013; Silveira *et al.* 2003; Trolle *et al.* 2008), particularly given our continuous and consistent sampling effort throughout the course of the entire survey period. We defined a single "capture event" for predators as all photographs of a distinct individual of particular species within a 30-min time period. This 30-min sampling period aims to remove temporal dependence between consecutive photographs and has become a standard in camera trap surveys (Di Bitetti *et al.* 2006). For predators and local people we used capture events to construct daily detection histories consisting of 0's (not detected) and 1's (detected) for each species at each camera station. To provide a measure of relative activity for each predator species, we calculated trap success (TS) by dividing the number of capture events by total number of trap nights, minus malfunctions, multiplied by 100. We defined a trap night as a 24-h period in which at least one of the two cameras at a given camera station was functioning properly. For lemurs we defined a "capture event" as all observations of a given species occurring within 25 m of one another for a particular survey. This 25-m spacing was used to ensure groups were not double counted and to ensure spatial independence for captures of solitary lemur species. Any lemur capture occurring within 250 m of the camera station (based on the 500-m spacing between camera stations) was considered a detection (1) for that particular camera site. For each study site we used lemur transect surveys to construct detection histories (0's and 1's) for each lemur species. To compare lemur activity across camera sites and study sites, we divided the number of lemur captures by number of transect surveys for each study site.

Single-Season, Single-Species Occupancy Occupancy estimation provides an estimate of species occurrence across a study area using detection/non-detection data from various survey techniques while accounting for spatial variation and variation in detection probabilities (Bailey *et al.* 2004; Thompson 2004; Gerber *et al.* 2014; this special issue). The collection of detections (1's) and nondetections (0's) over a given survey generates a detection history for the target species, which is used to estimate two population parameters: occupancy and detection probability (MacKenzie 2006). This technique provides a better estimate of the proportion of an area occupied by the target species than using presence–absence only data (detection not incorporated). In addition, this modeling approach allows for the inclusion of covariates to determine how numerous variables influence occupancy and/or detection of the target species.

To investigate how predator, local people, and lemur occupancy and detection vary across the landscape we combined detection histories across all four study sites (AJB-C, MGB-C, FRK-F, SLJ-F) and analyzed single-season, single-species occupancy models with covariates in program PRESENCE (Hines 2006). We used only one survey of the AJB study site (1AJB-C 2010 survey) to estimate single-season, single-species lemur and predator occupancy given that covariate values were identical, not independent, across all three surveys of this site. To estimate occupancy for lemurs we constructed a detection history using camera stations that overlapped with lemur transects, which provided 11–13 camera stations per study site and 48 sites overall. To estimate occupancy for predators we constructed a detection history using the location of all individual camera stations, which provided 20–25 camera stations per study site and 95 sites overall. Detection histories for both predators and lemurs were collapsed down to 6-d intervals (encounter occasions) to improve maximum likelihood convergence. We used the following variables as covariates in our models: distance to forest edge, distance to nearest village, canopy height, percent canopy cover, tree density, basal area, understory cover, and the trap success of local people, domestic dogs, feral cats, fossa, and ring-tail vontsira. To improve maximum likelihood convergence with covariates and ensure covariates were on the same scale, we *Z*-scored all variables with values >2.0.

For each target species (predators, local people, and lemurs), we first generated a list of *a priori* models. To assess model fit we used a Pearson's goodness-of-fit test ($P = 0.05$) and to assess overdispersion we used a measure of c-hat. For any species investigated, if the model did not fit the observed data (based on our goodness-of-fit test and/or showed evidence of severe overdispersion, c-hat value > 3.0) occupancy was not estimated, unless otherwise noted. We used Akaike Information Criterion (AIC; Akaike 1973) to rank models and perform model selection to determine the highest ranking covariates and top ranking models, based on AIC score, and competing models based on ΔAIC < 2.0. In addition to analyzing all *a priori* models we also generated one to three *post hoc* models based on the highest ranking covariates for occupancy and detection. For each target species we reported the highest ranking model, and the estimates of occupancy and detection with standard errors.

Two-Species Co-occurrence Interaction Models: Predators-Lemurs In addition to the single-season, single-species occupancy modeling, the two-species interaction (co-occurrence) modeling approach provides a unique framework to investigate biological interactions between two species, including competitive exclusion, predator–prey interactions, and community assemblages (MacKenzie *et al.* 2004). These co-occurrence models 1) take into account imperfect detection of all target species; 2) estimate the occupancy of two or more species; and 3) determine if the presence of one species impacts the occupancy or detection of the other (MacKenzie 2006). The co-occurrence model provides nine estimable parameters (see MacKenzie *et al.* 2004) including a "species interaction factor" (SIF), a measure of interaction to determine if two target species co-occur independently (SIF = 1.0), if co-occurrence is less than it would be if independent (SIF < 1.0, "avoidance"), or if co-occurrence is greater than it would be if independent (SIF > 1.0, "attraction").

To evaluate whether the presence of a particular predator species influenced the occurrence of a particular lemur species we used a single-season, two-species interaction occupancy model (MacKenzie 2006; MacKenzie *et al.* 2004) and modeled these interactions in Program PRESENCE (Hines 2006). We combined all surveys of contiguous forest (1AJB-C, 2AJB-C, 3AJB-C, MGB-C), and all surveys of fragmented forest (SLJ-F, FRK-F) to provide a comparison of interactions across these two forest types. Given that the two-species interaction occupancy models investigate the probability of co-occurrence of two species at a given site, we could use only lemur transects that overlapped with camera stations. As a result, we used a total of 23 camera stations in fragmented forest and 72 stations in contiguous forest to estimate predator–primate co-occurrence. We investigated the interaction, based on the SIF variable, between each combination of predator and lemur species. A formal comparison of models is required to assess whether two species occur independently of one another [SIF $\neq$ 1.0] (MacKenzie 2006). To accomplish this assessment of independence we created two models for each predator–lemur species comparison: 1) a "full model" in which occupancy of species A and B, and SIF are estimated; and 2) a "reduced model" in which occupancy of A and B are estimated and SIF is fixed to 1.0 (independent). Two species were said to be independent when the difference in the ΔAIC value between these two models was >2.0 (MacKenzie 2006). Any predator–lemur comparison in which the two species were not independent (ΔAIC < 2.0) were not reported.

Ethical Note

This noninvasive research project complied with protocols approved by the Institutional Animal Care Committee of Virginia Tech and adhered to the legal requirements of Madagascar's Ministry of the Environment and Forests (permit N° 128/11 and 128/12).

Results

Our photographic and line-transect surveys documented a total of 6 endemic predators, 2 introduced predators, and 12 lemur species (Table II); however, for this article we focused solely on confirmed lemur predators (fossa, ring-tail vontsira, domestic dog, feral cat, and local people) and lemur species having adequate captures for model convergence for our two-species interaction occupancy models (white-fronted brown lemur, eastern wooly lemur, and eastern mouse lemur).

Endemic predator trap success was higher across contiguous forest while introduced predator and local people trap success was higher in fragmented forest sites (Table III). Feral cats were not detected at any fragmented forest sites but were present in all surveys of contiguous forest. For lemurs, wooly

Table III Mean trap success (SE) or relative activity of endemic predators, introduced predators, and local people (nonresearcher humans) and the number of detections per survey for each lemur species at each survey site across the Masoala–Makira landscape

Scientific name	Common name	Contiguous forest sites				Fragmented forest sites	
		1AJB-C	2AJB-C	3AJB-C	MGB-C	SLJ-F	FRK-F
Cryptoprocta ferox	Fossa	2.2 (0.7)	1.3 (0.5)	1.7 (0.5)	7.2 (1.0)	2.0 (0.7)	1.0 (0.4)
Galidia elegans	Ring-tail vontsira	1.5 (0.4)	1.0 (0.3)	0.4 (0.2)	3.8 (1.6)	0.5 (0.2)	1.1 (0.3)
Canis familiaris	Domestic dog	1.0 (0.5)	1.1 (0.6)	0.7 (0.3)	26.1 (4.5)	19.6 (7.3)	14.9 (7.4)
Felis silvestris catus	Feral cat	0.2 (0.1)	0.3 (0.1)	2.0 (0.6)	1.3 (0.5)	0.0 (0)	0.0 (0)
Homo sapiens (Local people)	Human (nonresearcher)	2.2 (0.9)	11.8 (10.6)	2.4 (1.3)	165.4 (33.2)	170.5 (57.9)	119.3 (52.3)
Avahi laniger	Eastern wooly lemur	0.62	0.67	0.39	0.40	0.43	0.72
Eulemur albifrons	White-fronted brown lemur	0.47	0.21	0.17	0.21	0.13	0.33
Microcebus rufus	Eastern mouse lemur	0.71	0.69	0.49	0.29	0.53	1.61

Trap success is calculated as total number of captures/trap nights, minus malfunctions, × 100, with a capture defined as all independent photos of a distinct individual of a species within a 30-min time period.

lemur and mouse lemur relative activity (number of captures per transect) was highest in the fragmented FRK-F site while white-fronted brown lemur activity was highest in the contiguous 1AJB-C survey (Table III).

Understory cover had the greatest impact (both positive and negative depending on the species) on the majority of our endemic and introduced predator occupancy and detection probabilities (Table IV). Distance to village and distance to forest edge were important variables for occupancy and survey period (time) was important for detection. We found strong positive associations between local people and domestic dog occupancy. Local people show the most wide-ranging occurrence across the landscape ($\widehat{\Psi} = 0.82 \pm \mathrm{SE}0.06$) while feral cats show the lowest occurrence ($\widehat{\Psi} = 0.30 \pm \mathrm{SE}0.08$) for introduced predators (Table IV). Canopy height had the greatest influence on mouse lemur occupancy (Table IV), whereas local people trap success and fossa trap success had the greatest impact on wooly lemur occupancy and detection (respectively). Both wooly lemur ($\widehat{\Psi} = 0.90 \pm \mathrm{SE}0.09$) and mouse lemur ($\widehat{\Psi} = 0.53 \pm \mathrm{SE}0.14$) had high occupancy across the landscape (Table IV). We were unable to provide estimates of white-fronted brown lemur occupancy and detection as a result of the limited number of captures for this lemur species.

Table IV Top single-season, single-species occupancy model results (model likelihood > 0.125) for each target species across the Masoala–Makira landscape, including estimates for occupancy (Ψ) and probability of detection (*p*) with standard error

Species	Model	AIC	AIC wgt	*k*	–2 Log likelihood	Ψ (SE)[a]	*p* (SE)[a]
Fossa	Ψ (.)[1], p (Under) [2]	762.35	0.25	3	756.35	0.63 (0.06)	0.18 (0.02)
	Ψ (Locals)[3], p (Under)	762.74	0.21	4	754.74	0.63 (0.08)	0.18 (0.02)
	Ψ (.), p (Village)[4]	763.05	0.18	3	757.05	0.67 (0.07)	0.16 (0.02)
Ring-tail vontsira[b]	Ψ (Under), p (Dog)[5]	459.11	0.64	4	451.11	0.58 (0.10)	0.10 (0.02)
	Ψ (Under), p (.)	462.19	0.14	3	456.19	0.56 (0.11)	0.11 (0.02)
Domestic dog	Ψ (Under), p (Time)[6]	1063.81	0.14	15	1033.81	0.64 (0.06)	0.37 (0.06)
Feral cat	Ψ (Under), p (Time)	312.46	0.97	15	282.46	0.30 (0.08)	0.12 (0.05)
Human (Locals)	Ψ (Dog), p (Under, Time)	1139.11	0.99	16	1107.11	0.82 (0.06)	0.41 (0.05)
Wooly lemur	Ψ (Locals), p (Fossa)[7]	292.28	0.17	4	284.28	0.90 (0.09)	0.20 (0.03)
	Ψ (.), p (Fossa)	292.34	0.16	3	286.34	0.90 (0.10)	0.20 (0.04)
Mouse lemur	Ψ (Can ht.) [8], p (.)	188.79	0.10	3	182.79	0.53 (0.14)	0.32 (0.06)

[1] (.) = constant rate of occupancy and/or detection; [2] Under = understory cover; [3] Locals = human; local people (nonresearcher) trap success; [4] Village = distance to nearest village; [5] Dog = *Canis familaris* trap success; [6] Time = survey specific rate of occupancy and/or detection; [7] Fossa = Fossa trap success; [8] Can ht. = Canopy height; [9] Edge = distance to forest edge.

[a] Average occupancy and detection reported based on mean covariate value for models without constant detection.

[b] No *a priori* model fit observed data based on GOF test; thus the highest ranking model was chosen after removal of models that did not fit the data.

As a result of the limited number of lemur surveys in relation to photographic surveys of predator species, lemur captures were low, which led to difficulty in convergence of co-occurrence models when estimating detection probabilities. To address this problem we used single-season, single-species occupancy and estimated the detection rate of each predator and lemur species in both contiguous and fragmented forest. For any predator–lemur comparison in which captures were too low to estimate detection probabilities for our co-occurrence models (n = 8) we fixed the detection rate in our two-species interaction occupancy models for these predator–lemur species combinations that allowed our interaction models to converge and provide estimates of the species interaction factor (SIF) between species. Using these "fixed" detection rates should have minimal impact on the final SIF and occupancy estimates as they simply provide an estimate of detection based on the capture history of this species resulting from a less complex modeling framework (single season, single species modeling) and these "fixed" detection rates were similar (±0.03) to estimated detection from other species combinations where models did converge.

Species interaction models indicate a strong contrast in predator–primate co-occurrence in contiguous vs. fragmented forest sites. In particular, we found a

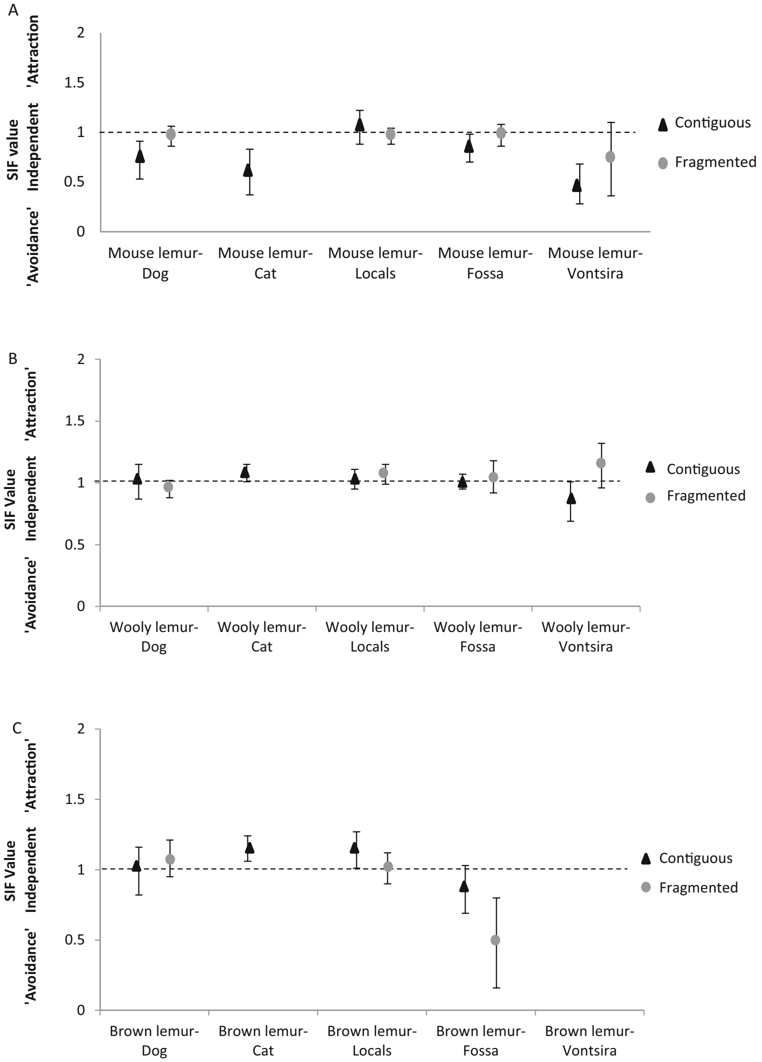

Fig. 2 Species interaction factor (SIF), or the level of co-occurrence between species (where SIF = 1.0 is independent; dashed line), in contiguous and fragmented forest between **(A)** mouse lemur (*Microcebus rufus*) and predators; **(B)** white-fronted brown lemur (*Eulemur albifrons*) and predators; and **(C)** wooly lemur (*Avahi laniger*) and predators resulting from photographic surveys and line transects from August 2010 to November 2012 across the Masoala–Makira landscape, Madagascar.

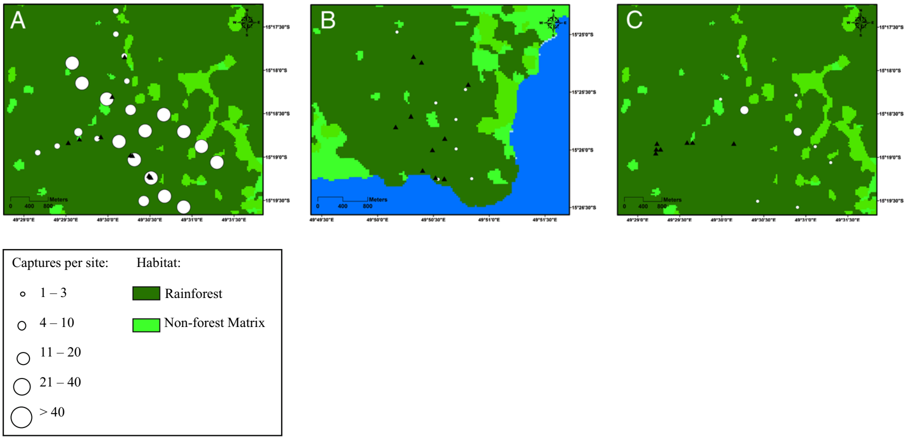

Fig. 3 Capture locations for **(A)** locals (white circles) and *Eulemur albifrons* (black triangles) highlighting the species "attraction" [SIF = 1.14 (0.13)] at the Mangabe study site (MGB) in contiguous forest; **(B)** *Cryptoprocta ferox* (white circles) and *Eulemur albifrons* (black triangles) highlighting the species "avoidance" [SIF = 0.48 (0.32)] at the Farankarina study site (FRK) in contiguous forest; and **(C)** *Galidia elegans* (white circles) and *Microcebus rufus* (black triangles) highlighting the species "avoidance" [SIF = 0.48 (0.20)] at the MGB study site in contiguous forest.

higher number of species interactions ($N = 8$) in contiguous forest where both predator and lemur occupancy were higher (Fig. 2; Appendix I). Mouse lemurs show evidence of "avoidance" (SIF < 1.0; Fig. 3C) of all predator species across contiguous forest (Fig. 2; Appendix I). White-fronted brown lemurs show evidence of "avoidance" with fossa (Fig. 3) in both contiguous and fragmented forest (Fig. 2; Appendix I). Further, this cathermal lemur species also shows evidence of 'attraction' (SIF > 1.0; Fig. 3) with both feral cats and local people in contiguous forest (Fig. 2; Appendix I). Feral cats demonstrated the greatest number of interactions with lemurs for all predator species, despite their distribution being limited to contiguous forest (Fig. 2; Appendix I).

In contiguous forest feral cats show an interaction with each lemur species (though weak in the case of wooly lemurs). Local people show an interaction with only white-fronted brown lemurs while domestic dogs show an interaction with only mouse lemurs (Fig. 2; Appendix I).

Discussion

Change in Relative Activity or Trap Success: Contiguous to Fragmented Forest

Our analyses highlight the differences in activity and distribution of endemic and introduced predators, as well as local people between contiguous and fragmented forests. Fragmented forest had considerably higher trap success for local people and domestic dogs; however, we found no captures of feral cats across our two fragmented sites. Interestingly, recent studies by Gerber (2011) and Gerber *et al.* (2012) from the southeastern Ranomafana NP differ from results presented here. Gerber *et al.* (2012) found a strong increase in feral cat occupancy in fragmented forest where we found feral cats only in contiguous forest. The difference in feral cat captures between these two studies may be related to differences in management strategies between these two areas, the sampling method used by Gerber *et al*. (2012), which included the use of bait, or even the hunting and consumption of feral cats by local people in our region (C. Golden, *pers. commun*.). Whereas capture rates and distribution of feral cats differed between the two sites, occupancy estimates of domestic dogs and local people were similar between the two studies.

For lemurs the difference in activity between contiguous and fragmented forest is less striking. The high activity of lemur species at the fragmented FRK-F site, however, likely results from the presence of primary rain forest cover in the southern protected part of the FRK-F reserve as lemur observations for this portion of the site were considerably higher. In addition, this study incorporates only the three most common lemur species observed. We found a strong decrease in total lemur species richness from contiguous to fragmented forest, including an absence of all diurnal species (excluding white-fronted brown lemurs) in all fragmented forest sites surveyed (Farris, *unpubl. data*). This outcome is alarming given the ongoing patterns of forest loss and fragmentation throughout Madagascar.

Single-Season, Single-Species Occupancy Across the Landscape

Our low numbers of captures, primarily for lemurs, prevented the comparison of contiguous and fragmented forests using occupancy estimation with covariates; however, our single-season, single-species occupancy and detection estimates across all sites provide insight into how predators and lemurs are impacted by changes across the landscape. The extremely high occupancy for both local people and domestic dogs within forests across the landscape is an alarming sign and demands the attention of conservationists and managers across this region. The strong positive association between local people and dogs is expected given the use of domestic dogs by local people to perform various tasks such as herding and hunting. The relatively high occupancy of fossa across the landscape is similar to recent research conducted by Gerber (2011) and Gerber *et al*. 2012) in southeastern Madagascar on carnivores, and is perhaps not surprising given the large areas across which this species roams.

The role of understory cover in predator occupancy and detection appears to be widespread and may be important for predicting predator occupancy across the landscape. The importance of distance to forest edge and to village for both endemic and introduced predator occupancy also draws attention to the ongoing trends in fragmentation, edge effects, and human encroachment and their impacts on endemic and introduced wildlife species across eastern rain forest habitat. For example, the strong inverse relationship between distance to village and fossa occupancy may stem from the killing of fossa by farmers (Kotschwar et al. 2014) across the Masoala–Makira region due to the depredation of livestock by fossa (Farris, *pers. obs*. and communication with local people). In fact, we suspect this mortality resulting from hunting is likely one of the biggest conservation concerns for fossa in this region of Madagascar.

For lemurs the high occupancy estimates and similarly high relative activity of both wooly lemurs and mouse lemurs in fragmented forest appears to be indicative of their widespread presence across eastern rainforest habitat (Garbutt 2007). Further, mouse lemurs increased in detection nearer forest edge whereas wooly lemurs show a positive relationship with local people activity. These results support the prediction that wooly lemurs and mouse lemurs may be more common in disturbed, secondary forest compared to primary forest (Ganzhorn 1988, 1995). The inability to provide estimates of occupancy for white-fronted brown lemurs resulted from low capture rates in both contiguous and fragmented forest sites. Longer transects and more repeat surveys may be required to estimate occupancy for this, and other larger bodied, gregarious lemur species.

Two-species Co-occurrence Interaction Models: Contiguous and Fragmented Forests

The negative relationship between mouse lemurs and all predators in contiguous forest may result from predator avoidance behavior by this small nocturnal lemur, as individuals of this genus are preyed upon by fossa, ring-tail vontsira, and domestic dog (Goodman 2003). Feral cats prey on multiple lemur species (Goodman 2003) and endemic rodents (Farris, *pers. obs*.) and are believed to be an important mouse lemur predator. Mouse lemurs are wide-ranging and common throughout eastern rain forest habitat (Garbutt 2007); however, our surveys found their distribution to be limited, particularly in contiguous forest (Fig. 2A–C), and our low sample size may have led to the "avoidance" results with the more wide-ranging predators. Alternatively, this "avoidance" result may be habitat mediated because mouse lemur occupancy was positively related to canopy height whereas predators were positively influenced by understory cover, and these two habitat variables were negatively correlated with each other. Higher sample sizes would enable us to incorporate habitat covariates into the co-occurrence models to understand better the interplay between habitat and co-detection in influencing species interactions (Bailey *et al.* 2009; Waddle *et al.* 2010).

Both fossa and ring-tail vontsira are confirmed lemur predators (Goodman 2003) and our two-species interaction models demonstrate evidence of multiple lemur species "avoiding" these two endemic predator species. Moreover, these negative relationships occur in both contiguous and fragmented forests. In particular, both white-fronted brown lemur and mouse lemur show "avoidance" with fossa. In recent years attention has been placed on the diet of fossa, particularly as it relates to their hunting of lemurs, as they have been shown to prey upon numerous lemur species (Goodman 2003), have significant impact on lemur population dynamics (Irwin *et al.* 2009), and have been suggested to be a lemur specialist (Wright *et al.* 1997). We found no interactions with any predator–lemur or local people–lemur across fragmented forest; however, the high level of occupancy and widespread distribution of local people and domestic dog across the entire camera grid in fragmented forest (see local people distribution in Fig. 3) may underlie the lack of pattern in co-occurrence. High occupancy of domestic dog and local people across fragmented forests, as well as the increased patchiness and limited habitat availability, are likely creating more encounters between these species. The impact on lemurs from these potential increased encounters across fragmented forest remains unknown, but we assume domestic dog and local people encounters will be damaging for all three lemur species (Daszak *et al.* 2000;

Golden 2009; Koster 2008; Lenth *et al.* 2008). Surveys by our team of other highly fragmented sites with exceptionally high trap rates of local people and domestic dog have shown very low numbers and/or a complete absence of all lemur species (Farris, *unpubl. data*). Further, the training of domestic dogs by local people to hunt various wildlife species, including lemurs, is common for this region (anecdotal accounts and personal observation) and this is likely contributing to the diminished species richness we have observed across fragmented forests. Additional research on the use of domestic dogs by local people to hunt wildlife is needed to fully understand the pressure this places on lemur populations across this region. To our knowledge, this is the first attempt to model domestic dog and lemur interactions in Madagascar, or any domestic dog–primate interactions in any region of the world.

The lack of feral cat captures in fragmented forest in this study likely translates to minimal impact on lemur species; however, it does not diminish their influence on lemur species in contiguous forest. Despite their limited range feral cats exhibited an interaction with all three lemur species in contiguous forest. In fact, our co-occurrence models indicate a strong “avoidance” between feral cats and mouse lemurs in contiguous forest, despite both species having narrow distributions and low capture rates in these forest sites. During our surveys we obtained photographic evidence of feral cats killing endemic rodents; however, we know of no available information on the rate of take or capture efficiency of various lemur species in the diet of either feral cats or the more abundant and wide ranging domestic dog. A complete diet analysis of these two introduced predators and a better understanding of the factors associated with their occupancy are needed to assess the impact of these predators on endemic wildlife, particularly lemurs, throughout Madagascar.

Our work highlights a novel approach in combining camera trapping and line transects for investigating predator–lemur interactions; however, our data collection was designed specifically for the goal of estimating predator population parameters (which requires a large number of trap nights). We recommend future studies investigating predator–primate dynamics place greater effort on increasing the number of primate line-transect surveys across the site to improve convergence in occupancy and detection estimation. Further, if camera resources are limited such that expanding the grid size using two cameras per site is not possible, then using only a single camera per camera station and expanding both the extent of the camera grids and line transects will allow for the estimation of occupancy and detection over a broader area and include more covariate data for analyses. Using existing trails for camera placement is important to obtain adequate captures of carnivores (Dillon and Kelly 2007; Maffei *et al.* 2004); however, the location of highly accessible and heavily traveled trails may bias results for some target species, such as at our MGB-C site. Further, this high level of domestic dog and local people activity at the MGB-C site may have also impacted lemur observations as line transects were placed along existing trails to overlap with photographic sampling data. As a result, the placement of cameras and line transects is a vital part of study design for similar studies using these methods. We recommend increased sampling to include more "sites" to simultaneously model habitat variables with the two-species interaction model framework.

The importance of and potential uses of these novel, noninvasive techniques to the field of primatology are wide ranging. The techniques presented in this article allow for the investigation of multipredator species' impact on primate behavior and/or dynamics across numerous habitat types. Further, these noninvasive techniques can also assist researchers and managers in identifying factors (native and introduced) that are influencing the occupancy and detection of numerous rare, endangered, and/or elusive primate species. Finally, combining these methods with other noninvasive methods, such as scat analysis including molecular scatology (Symondson 2002), may provide a more reliable, robust investigation of predator–primate dynamics with significantly less researcher cost and effort, as well as less stress and/or harm to wildlife.

Finally, this research highlights the need to expand our knowledge of carnivore–primate dynamics and interactions. In particular, we need thorough density analyses across each forest type, which incorporate numerous landscape and habitat covariates, to understand better the effects of fragmentation and forest loss on carnivore and lemur species across Madagascar. Further, this research points to the need for an increased understanding of the variables influencing the presence and/or absence of domestic dogs and feral cats, both confirmed lemur predators, across eastern rain forest habitat in Madagascar. More specifically, we need additional research on the population dynamics and diet of these wide-ranging predators throughout Madagascar to understand better their impact on lemur populations, particularly in fragmented forest sites. Finally, though data exist on bushmeat use and consumption for this region (Golden 2009; Golden *et al.* 2011), human–wildlife conflict throughout Madagascar remains little studied and data on carnivore and lemur home range and daily activity patterns are critical to understanding the impact of poaching on these species. This additional research on carnivore–primate dynamics and interactions across contiguous and fragmented forests will increase our understanding of these relationships and greatly improve conservation and management efforts throughout Madagascar.

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Appendix I

Table V Best model results for single-season, two-species interaction occupancy models for each predator (A)–lemur (B) species comparison, including the occupancy (Ψ), detection (*p*), and predator–lemur species interaction factor (SIF)

Species	Forest type	Model	ΨA (SE)	ΨB (SE)	*p*A (SE)	*p*B (SE)	SIF (SE)
A B							
Dog–brown lemur	Contig.	NI and E, *p* (fixed)	0.56 (0.06)	0.56 (0.06)	0.21	0.16	0.99 (0.17)
	Frag.	NI and NE, I and NE	0.94 (0.04)	0.79 (0.12)	0.94 (0.06)	0.05 (0.10)	1.08 (0.13)
Dog–mouse lemur	Contig.	NI and NE, *p* (.)	0.48 (0.05)	0.48 (0.05)	0.18 (0.02)	0.18 (0.02)	0.72 (0.19)
	Frag.	NI and E, *p* (.)	0.87 (0.09)	0.58 (0.11)	0.17 (0.04)	0.17 (0.04)	0.96 (0.10)
Dog–wooly lemur	Contig.	NI and NE, *p* (fixed)	0.54 (0.09)	0.95 (0.04)	0.64	0.16	1.01 (0.14)
	Frag.	NI and NE, *p* (.)[6]	0.84 (0.08)	0.62 (0.10)	0.29 (0.02)	0.29 (0.02)	0.95 (0.07)
Locals–brown lemur	Contig.	NI and E, *p* (.)	0.56 (0.06)	0.56 (0.06)	0.25 (0.02)	0.25 (0.02	1.14 (0.13)
	Frag.	NI and NE, *p* (.)	0.87 (0.07)	0.35 (0.10)	0.46 (0.02)	0.46 (0.02)	1.01 (0.11)
Locals–mouse lemur	Contig.	NI and E, *p* (fixed)	0.56 (0.08)	0.40 (0.07)	0.27 (0.02)	0.27 (0.02)	1.05 (0.17)
	Frag.	NI and NE, *p* (.)	0.87 (0.07)	0.52 (0.10)	0.45 (0.02)	0.45 (0.02)	0.96 (0.08)
Locals–wooly lemur	Contig.	NI and NE, *p* (.)	0.56 (0.08)	0.81 (0.07)	0.25 (0.02)	0.25 (0.02)	1.03 (0.08)
	Frag.	NI and NE, *p* (.)	0.87 (0.07)	0.61 (0.10)	0.44 (0.02)	0.44 (0.02)	1.07 (0.08)
Cat–brown lemur	Contig.	NI and NE, *p* (.)	0.59 (0.14)	0.83 (0.15)	0.08 (0.02)	0.08 (0.02)	1.15 (0.19)
Cat–mouse lemur	Contig.	NI and E, *p* (.)	0.53 (0.08)	0.53 (0.08)	0.10 (0.02)	0.10 (0.02)	0.60 (0.23)
Cat–wooly lemur	Contig.	NI and NE, *p* (fixed)	0.48 (0.10)	0.91 (0.07)	0.19	0.16	1.08 (0.07)
Fossa–brown lemur	Contig.	NI and NE, NI and NE	0.70 (0.09)	0.67 (0.11)	0.09 (0.04)	0.07 (0.03)	0.86 (0.17)
	Frag.	NI and E, *p* (fixed)	0.65 (0.14)	0.43 (0.13)	0.13	0.13	0.48 (0.32)
	Contig.	NI and NE, *p* (.)	0.77 (0.08)	0.44 (0.08)	0.16 (0.02)	0.16 (0.02)	0.84 (0.14)

Table V (continued)

Species A B	Forest type	Model	ΨA (SE)	ΨB (SE)	*p*A (SE)	*p*B (SE)	SIF (SE)
Fossa–mouse lemur	Frag.	NI and NE, *p* (fixed)	0.88 (0.13)	0.69 (0.15)	0.12	0.36	0.97 (0.11)
Fossa–wooly lemur	Contig.	NI and E, *p* (.)	0.85 (0.06)	0.85 (0.06)	0.16 (0.01)	0.16 (0.01)	1.01 (0.06)
	Frag.	NI and NE, NI and NE	0.87 (0.13)	0.89 (0.13)	0.45 (0.11)	0.45 (0.11)	1.05 (0.13)
Vontsira–mouse lemur	Contig.	NI and E, *p* (fixed)	0.45(0.05)	0.45 (0.05)	0.09	0.21	0.48 (0.20)
	Frag.	NI and NE, NI and E	0.40 (0.13)	0.67 (0.15)	0.11 (0.04)	0.11 (0.04)	0.73 (0.37)
Vontsira–wooly lemur	Contig.	NI and NE, *p* (.)	0.48 (0.10)	0.84 (0.07)	0.13 (0.01)	0.13 (0.01)	0.85 (0.16)
	Frag.	NI and E, *p* (fixed)	0.76 (0.14)	0.76 (0.14)	0.05	0.28	1.14 (0.18)

SIF = species interaction factor; NI and E = nonindependent occurrence and equal detection; *p* (fixed) = fixed probability of detection based on detection estimated from single-season, single-species occupancy modeling; NI and NE = nonindependent occurrence and nonequal detection; I and NE = independent occurrence and equal detection; *p* (.) = constant probability of detection.

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