


Using camera traps to investigate spatial co-occurrence between exotic predators and native prey species: a case study from northeastern Madagascar

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Abstract

The presence of exotic predators in ecosystems across the world is a leading driver of native species' declines. Exotic predators largely influence native species through predation and harassment, which may cause native species to avoid them spatially. We used a camera trap dataset from seven sites in Madagascar's largest protected area complex to investigate spatial co-occurrence patterns between three exotic predators (free-ranging domestic dogs *Canis familiaris* and cats *Felis silvestris*, and small Indian civet *Viverricula indica*) and native ground-dwelling forest birds ($n = 5$) and small mammals ($n = 4$). We created 216 two-species occupancy models for 27 exotic predator-native species pairings to examine how habitat, exotic predator presence or both, influenced each native species' occupancy and/or detection. We found that native bird and small mammal occupancy and/or detection were strongly related to an exotic predator's presence 52% of the time (i.e. 14 of 27 exotic predator-native species pairings). Six of the 14 species pairings (i.e. 43%) had non-independent co-occurrence patterns, four of which were habitat-mediated. The effect of exotic predator presence on native species' detection was largely negative, depressing native species' detection in seven out of 12 instances (i.e. 58% of the time). The small Indian civet and free-ranging cats each strongly influenced the occupancy and/or detection of six species for a combined impact on seven native species, while domestic dogs strongly influenced two species. By including habitat covariates in two-species occupancy models, we gained deeper insight into the effect exotic predator presence has on native species' distribution. We also note that the strong effect of exotic predator presence on our ability to detect native species can hinder the ability of researchers to provide accurate parameter estimates. We recommend future research into the synergistic effects that habitat degradation and exotic species presence has on native species.

Introduction

Quantifying and reducing the impacts of exotic species on native ecosystems are globally important conservation goals (Turner, 1996; Glen, Pech & Byrom, 2013b; Jeschke *et al.*, 2014). Exotic predators in particular can be 'back-seat drivers' of ecosystem change (Bauer, 2012) through a number of direct and indirect mechanisms. They prey on native species (Butler, 2004; Medina & Nogales, 2008; Young *et al.*, 2011), spread diseases (Butler, 2004; Lacerda, Tomas & Marinho-Filho, 2009; Hughes & Macdonald, 2013), and/or compete for resources (Vanak & Gompfer, 2009, 2010; Paschoal *et al.*, 2012). The presence of exotic predators can cause native

species to alter their activity patterns (Gerber, Karpanty & Randrianantenaina, 2012a; Farris *et al.*, 2015a; Zapata-Ríos & Branch, 2016), influence reproduction (Massaro *et al.*, 2008), change the nature of, or negatively affect trophic interactions (Roemer, Donlan & Courchamp, 2002; Nogales *et al.*, 2014), and interact synergistically with other anthropogenic pressures to exacerbate declines (Doherty *et al.*, 2015). Due to their outsized influence on native ecological communities, quantifying the impacts of exotic predators on native wildlife is of vital importance (Glen & Dickman, 2005; Glen *et al.*, 2013a; Ballari, Kuebbing & Nunez, 2016).

As predation is often the biggest threat exotic predators pose to native species (Medina *et al.*, 2011; Silva-Rodríguez &

Sieving, 2012; Hughes & Macdonald, 2013), we expect to see evidence of spatial avoidance of predators by prey either because of behavioral mechanisms related to fear (Weckel, Giuliano & Silver, 2006; Bischof *et al.*, 2014) or actual depressed population numbers of prey caused by direct predation. Recently, the development of two-species occupancy models has allowed researchers to use detection/non-detection data to examine the relationships between co-occurring species' distributions and detections (MacKenzie *et al.*, 2005). Further developments have allowed the inclusion of habitat variables in these models (Richmond, Hines & Beissinger, 2010) to better examine species co-occurrence patterns without ignoring the influence of habitat (Lazenby & Dickman, 2013; Robinson, Bustos & Roemer, 2014; Peoples & Frimpong, 2016). By analyzing detection/non-detection data using two-species occupancy models, researchers can quantify the potential impacts of exotic predators on native species in an efficient, non-invasive way (Lazenby & Dickman, 2013; Robinson *et al.*, 2014).

Our goal was to use detection/non-detection data collected from seven camera trap surveys conducted in the largest protected area complex in Madagascar to infer the presence of potential predator-prey relationships between three exotic predators—free-ranging domestic dogs (*Canis familiaris*) and cats (*Felis silvestris*), and the small Indian civet (*Viverricula indica*)—and a suite of native ground-dwelling forest bird ($n = 5$) and small mammal ($n = 4$) species (Supporting Information Fig. S1). While there have been studies on how exotic predators are influencing native carnivores and lemurs (Brockman *et al.*, 2008; Gerber, Karpanty & Randrianantenaina, 2012b; Gerber *et al.*, 2012a; Moresco *et al.*, 2012; Farris *et al.*, 2015a,c), there has been little research on how exotic predators influence other threatened taxa on the island. Using two-species occupancy models, we evaluated 27 exotic predator-native species pairings to test whether (1) habitat only; (2) exotic predator presence only; or (3) habitat plus exotic

predator presence influenced native species' occupancy and detection probabilities. We also posit that the presence of a non-independent spatial co-occurrence pattern [i.e. species interaction factor (SIF) not equal to one; see Table 1 for parameter definitions] between an exotic predator and a native species could potentially imply the presence of a predator-prey relationship, although our data cannot ascertain whether that relationship is one of fear-driven spatial avoidance, direct predation or both.

Materials and methods

Study area and camera trapping surveys

From 2008 to 2011, we conducted camera trap surveys at 148 camera locations across seven sites in the Makira and Masoala protected area complex to monitor native carnivore populations (Fig. 1 and Supporting Information Table S1). Located in northeastern Madagascar, the Masoala-Makira complex is the largest contiguous area of protected forest in Madagascar (5197 km², excluding community-managed buffer areas). This protected forest region is home to six native and three exotic (free-ranging domestic dogs and cats, and small Indian civet) carnivores (Farris *et al.*, 2015b), 85 bird species (Thorstrom & Watson, 1997), and over 30 small mammal species (Soarimalala & Goodman, 2011).

We surveyed three sites within Makira Natural Park, one site bordering Makira, and three sites bordering Masoala National Park ($n = 7$). We ranked our sites based on habitat degradation, resulting in two intact (S01 and S02), three intermediately degraded (S03, S04 and S05) and two degraded sites (S06 and S07; see Farris *et al.*, 2015b). Habitat degradation was assessed using a number of characteristics, such as total amount of edge, the percentage of primary rainforest and the amount of core forest (Farris *et al.*, 2015b). Camera trapping

Table 1 Eight single-season, two-species occupancy models run in program PRESENCE to analyze landscape co-occurrence patterns of 27 exotic predator-native species pairings

Co-occurrence model ^{a,b}	Hypotheses tested	Estimate SIF ^a ?
$\psi_E, \psi_{NE} = \psi_{Ne}, \rho_N = r_N$	Neither habitat nor exotic predator presence influences native species' occupancy/detection	No
$\psi_E, \psi_{NE} = \psi_{Ne}, \rho_N, r_N$	Only exotic predator presence influences native species' detection	No
$\psi_E, \psi_{NE}, \psi_{Ne}, \rho_N = r_N$	Only exotic predator presence influences native species' occupancy	Yes
$\psi_E, \psi_{NE}, \psi_{Ne}, \rho_N, r_N$	Only exotic predator presence influences native species' occupancy/detection	Yes
$\psi_E(H), \psi_{NE}(H) = \psi_{Ne}(H), \rho_N(H) = r_N(H)$	Only habitat influences native species' occupancy/detection	No
$\psi_E(H), \psi_{NE}(H) = \psi_{Ne}(H), \rho_N(H), r_N(H)$	Habitat-mediated influence of exotic predator presence on native species' detection	No
$\psi_E(H), \psi_{NE}(H), \psi_{Ne}(H), \rho_N(H) = r_N(H)$	Habitat-mediated influence of exotic predator presence on native species' occupancy	Yes
$\psi_E(H), \psi_{NE}(H), \psi_{Ne}(H), \rho_N(H), r_N(H)$	Habitat-mediated exotic predator presence influence on native species' occupancy/detection	Yes

Data was collected during camera trapping surveys of seven sites (total camera sites = 148) in northeastern Madagascar (2008–2011).

^a $\psi_E/\psi_{NE}/\psi_{Ne}$ – the occupancy probability of (a) an exotic predator when a native species is absent; (b) a native species when an exotic predator is present; and (c) a native species when an exotic predator is absent. ρ_N/r_N – the detection probability of a native species when (a) an exotic predator is absent and (b) when an exotic predator is present. SIF – species interaction factor; estimates >1 suggest co-occurrence greater than would be at random, <1 suggest co-occurrence less than would be at random, and = 1 suggest co-occurrence equal to what would be at random.

^b(H) – Includes top habitat covariates that explained occupancy/detection for the exotic carnivore and native species from previous studies (Farris *et al.*, 2015b; Murphy *et al.*, 2017a,b) were included. See Supporting Information Table S2 for a list.

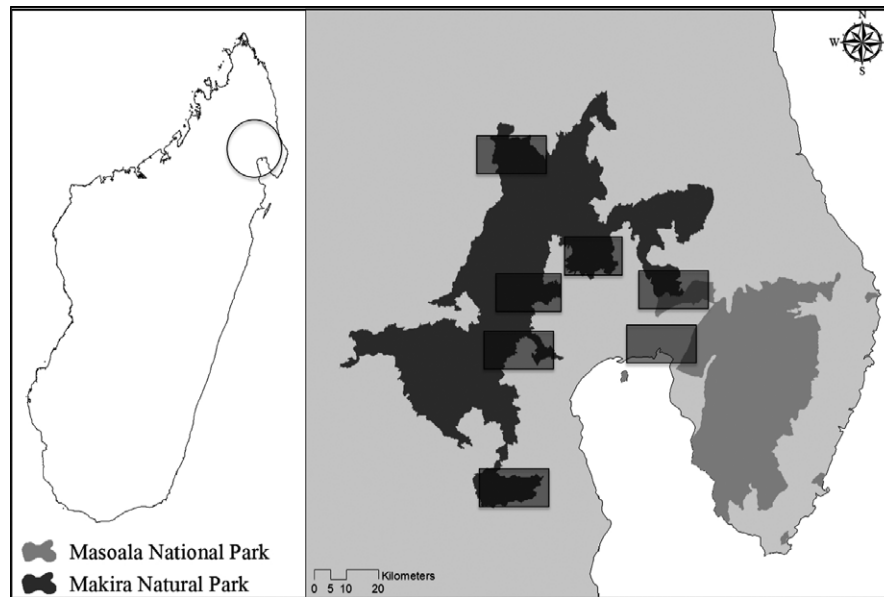


Figure 1 The Makira and Masoala protected area complex and surrounding land in northeastern Madagascar is the largest contiguous forest in Madagascar (5197 km², excluding community-managed buffer areas). Seven sites in the areas outlined by the boxes were photographically surveyed with camera traps from 2008 to 2011 (total camera sites = 148). Due to sensitivity of the data collected in several of these same areas on hunting by local people as part of a related project, we are unable to provide the exact locations of survey grids.

surveys consisted of 18–24 unbaited camera stations spaced 400–600 m apart. Each station had two camera traps operating 24 h day⁻¹, positioned 20–30 cm off the ground on opposite sides of wildlife (0.0–0.5 m) or human (>0.5 m) trails. The height was chosen due to the small body sizes of the target carnivores, but it was effective for capturing ground-dwelling, forest birds (Murphy *et al.*, 2017a) and small mammals (Murphy *et al.*, 2017b). We checked stations every 5 to 10 days for maintenance purposes. We alternated pairings of our cameras—DeerCam (DC300), Reconyx (PC85 and HC500), Moultrie (D50 and D55), Cuddeback IR, and HCO Scoutguard SG565FV—at each station to reduce any detection biases among brands of camera used in this study.

We obtained enough detection data from camera traps to analyze spatial relationships between the three exotic predators and five species of ground-dwelling and understory forest birds—Madagascar crested ibis (*Lophotibis cristata*), red-breasted coua (*Coua serriana*), scaly ground-roller (*Geobiastes squamiger*), Madagascar wood-rail (*Mentocrex kioloides*) and Madagascar magpie-robin (*Copsychus albospectularis*)—and four genera/species of small mammals—greater hedgehog tenrec (*Setifer setosus*), common tenrec (*Tenrec ecaudatus*), tufted-tailed rats (*Eliurus* spp.) and red forest rats (*Nesomys* spp.; Table 2 and Supporting Information Fig. S1; Murphy *et al.*, 2017a,b). We created capture histories for the nine native species and three exotic predators, where we recorded whether a species was detected (i.e. ‘1’ or present) or undetected (i.e. ‘0’ or absent) for each trap night (i.e. 24-h period) at each camera station. We then collapsed these capture histories, to improve model convergence, so that each encounter occasion was equal to nine trap nights.

Landscape co-occurrence models and hypotheses

We analyzed species’ landscape (i.e. across all our camera locations) co-occurrence patterns using single-season, two-species occupancy models in Program PRESENCE (version 10.9; Hines, 2006). We used the conditional two-species occupancy model, which allows for inclusion of habitat variables in addition to effects of other species’ presence on occupancy and detection of subordinate species (Richmond *et al.*, 2010). We did not use Rota *et al.* (2016)’s multispecies occupancy model, as that model assumes symmetric interactions, and our intent was to determine the effect of exotic predators on native species. For habitat-only and exotic predator-habitat models, we included habitat covariates for the exotic predators and the native species from previous studies (Supporting Information Table S2; Farris *et al.*, 2015b; Murphy *et al.*, 2017a,b) that were shown to strongly influence each species’ distribution and detection (i.e. 95% confidence intervals for explanatory variables that did not include 0). Three native species—scaly ground-roller, common tenrec, and tufted-tailed rat—did not have any habitat covariates that strongly influenced their occupancy in our prior analyses, so we only included the exotic predator’s top habitat covariate in those models. To avoid model convergence issues, we did not include free-ranging cat trap success (fsts) or small Indian civet trap success (vits) in models where the exotic predator was the free-ranging cat or small Indian civet, respectively. This only influenced four species pairings (Supporting Information Table S2).

We used eight models to estimate parameters (Table 1) for the 27 exotic predator-native species pairings. We first created a null model with no habitat covariates where ψ_{NE} (occupancy of

Table 2 Number of detections for the three exotic predators and nine native species for which we analyzed landscape co-occurrence patterns

Species	Total # of detections
Free-ranging domestic dog (<i>Canis familiaris</i>)	868
Free-ranging cat (<i>Felis silvestris</i>)	53
Small Indian civet (<i>Viverricula indica</i>)	41
Madagascar crested ibis (<i>Lophotibis cristata</i>)	107
Madagascar magpie-robin (<i>Copsychus albospecularis</i>)	284
Madagascar wood-rail (<i>Mentocrex kioloides</i>)	221
Scaly ground-roller (<i>Geobiastes squamiger</i>)	227
Red-breasted coua (<i>Coua serriana</i>)	671
Common tenrec (<i>Tenrec ecaudatus</i>)	46
Greater hedgehog tenrec (<i>Setifer setosus</i>)	145
Tufted-tailed rats (<i>Eliurus</i> spp.)	240
Red forest rats (<i>Nesomys</i> spp.)	229

Data analyzed came from camera trapping surveys of seven sites (total camera sites = 148) in northeastern Madagascar (2008–2011). For images of the nine native species, please see Supporting Information Fig. S1.

native when exotic was present) was equal to ψ_{Ne} (occupancy of native when exotic was absent), and r_N (detection of native when exotic was present) was equal to p_N (detection of native when exotic was absent), meaning that neither habitat nor exotic predator presence influenced native species' occupancy and detection (Table 1). We then created a model similar to the null that included habitat covariates (suggesting that only habitat had an influence on native species occupancy and detection). In both of the above cases, the measure of species co-occurrence, or SIF, would be equal to 1.0 indicating independence. We then created three models, varying in whether only exotic predator presence influenced native species' occupancy, detection or both (Table 1). Finally, we created three models where exotic predator presence and habitat could potentially influence native species' occupancy, detection or both (Table 1). In the final two cases, SIF would not be constrained to 1.0.

We hypothesized that if exotic predators had the strongest influence on native species' occupancy and detection, models including only exotic predator presence would be the top models. Alternatively, if only habitat influenced native species' occupancy and detection, top models would be habitat-only. If the influence of exotic predators was mediated by habitat (i.e. both exotic predators and habitat influenced native occupancy and detection), top models would include a combination of the two types of parameters.

If exotic species had a negative influence on native species, we expected that native species' occupancy at sites co-occupied by exotic predators (ψ_{NE}), and detection at sites occupied by exotics (r_N), would be lower than native species' occupancy and detection at sites where exotic predators were absent (ψ_{Ne} and p_N , respectively; Silva-Rodríguez & Sieving, 2012; Zapata-Ríos & Branch, 2016). We hypothesized that if exotics negatively influenced natives, the species would co-occur (as estimated by the SIF) less often with exotic predators than could be expected at random (SIF < 1 and 95% confidence intervals do not overlap 1).

We ranked models using Akaike Information Criterion (AIC; Akaike, 1973) and considered models with $\Delta AIC \leq 2.0$ as competing models. We extracted our parameter estimates from the top model and considered estimates to be different if their 95% confidence intervals did not overlap each other. Because our camera station spacing (400–600 m apart) is not likely large enough to fully encompass any of the exotic predators' estimated home range, we define exotic predator occupancy probability as 'local site use' as in (Farris *et al.*, 2015c). Finally, we assumed that the co-occurrence patterns between exotic predators and native species were temporally and geographically stable across the 3 years (2008–2011) it took to survey the seven study sites.

Results

For 23 of the 27 species pairs, competitive models included exotic predator presence and habitat; for the remaining four species pairs, competitive models only included habitat variables (Supporting Information Table S2). Of the 23 species pairs with exotic predator presence + habitat top models, exotic predator presence influenced either native species' occupancy ($n = 3$), detection ($n = 14$) or both ($n = 6$; Supporting Information Table S2). The majority, 52%, or 14 of these 27 species pairs had a top model indicating strong influence (i.e. non-overlapping 95% confidence intervals between respective parameters) of presence of exotic predator on native species occupancy or SIF ($n = 2$), detection ($n = 8$) or both ($n = 4$; Table 3). Free-ranging cats and small Indian civets each strongly influenced six native species for a total of seven unique species (four native birds and three native small mammals; Table 3). Domestic dogs strongly influenced two native small mammals (red forest rat and common tenrec).

Seven species pairs showed a strong influence of exotic predator presence on occupancy (i.e. non-overlapping 95% confidence intervals between ψ_{NE} and ψ_{Ne}) and/or SIF (i.e. 95% confidence interval that did not overlap 1), with six of these pairings mediated by habitat features (Table 3; Fig. 2). Five of these six co-occurrence patterns showed a lack of co-occurrence (i.e. SIF < 1.0; Fig. 2). Red forest rats and common tenrecs occurred less often with domestic dogs than expected at random, as Madagascar wood-rails and red forest rats with small Indian civets (i.e. SIF < 1.0; Fig. 2 and Table 3). Greater hedgehog tenrecs co-occurred less often, and scaly ground-rollers more often (i.e. SIF > 1.0), with free-ranging cats than expected at random (Fig. 2 and Table 3). Four of these five 'avoidance' co-occurrence patterns were habitat-mediated (e.g. by proportion of rainforest present at the site), as with domestic dogs and red forest rats and small Indian civets and Madagascar wood-rails (see Fig. 3a–c). Contrary to our expectations, the scaly ground-roller had a higher occupancy probability where free-ranging cats were present ($\psi_{NE} = 0.71 \pm SE 0.22$) compared to where they were absent ($\psi_{Ne} = 0.05 \pm SE 0.03$) and an SIF > 1.0, indicating they co-occur together more than expected by chance (Fig. 2, Table 3).

Twelve species pairings indicated that the exotic predator had a strong influence (i.e. non-overlapping 95% confidence

Table 3 Parameter^a estimates from landscape co-occurrence analyses of exotic predators and native species

Species pairings ^b	ψ_{NE} (SE)	ψ_{Ne} (SE)	SIF (SE)	p_N (SE)	r_N (SE)
Domestic dog – Red forest rat	0.29 (0.10)	0.70 (0.18)	<i>0.72 (0.13)</i>	<i>0.74 (0.04)</i>	<i>0.36 (0.07)</i>
Domestic dog – Common tenrec ^c	0.22 (0.08)	0.87 (0.31)	<i>0.59 (0.14)</i>		
Free-ranging cat – Scaly ground-roller ^c	<i>0.71 (0.22)</i>	<i>0.05 (0.03)</i>	<i>2.10 (0.50)</i>	<i>0.83 (0.11)</i>	<i>0.17 (0.05)</i>
Free-ranging cat – Red-breasted coua				<i>0.86 (0.05)</i>	<i>0.29 (0.05)</i>
Free-ranging cat – Madagascar magpie-robin				<i>0.40 (0.05)</i>	<i>0.15 (0.04)</i>
Free-ranging cat – Madagascar wood-rail				<i>0.42 (0.05)</i>	<i>0.06 (0.02)</i>
Free-ranging cat – Red forest rat				<i>0.26 (0.07)</i>	<i>0.74 (0.04)</i>
Free-ranging cat – Greater hedgehog tenrec	0.20 (0.09)	0.48 (0.12)	<i>0.52 (0.22)</i>		
Small Indian civet – Scaly ground-roller				<i>0.16 (0.05)</i>	<i>0.81 (0.10)</i>
Small Indian civet – Red-breasted coua				<i>0.18 (0.03)</i>	<i>0.67 (0.04)</i>
Small Indian civet – Madagascar magpie-robin				<i>0.77 (0.09)</i>	<i>0.16 (0.04)</i>
Small Indian civet – Madagascar wood-rail	0.53 (0.08)	0.97 (0.36)	<i>0.57 (0.10)</i>	<i>0.04 (0.02)</i>	<i>0.37 (0.05)</i>
Small Indian civet – Red forest rat	0.19 (0.10)	0.47 (0.09)	<i>0.36 (0.20)</i>	<i>0.48 (0.07)</i>	<i>0.95 (0.08)</i>
Small Indian civet – Tufted-tailed rat				<i>0.56 (0.11)</i>	<i>0.19 (0.06)</i>

Estimates come from single-season, two-species occupancy analyses of data collected during camera trapping surveys at seven sites (total camera sites = 148) in northeastern Madagascar (2008–2011); models were run in program PRESENCE. Estimates that are different (i.e. parameter 95% confidence intervals do not overlap) are *italicized*.

^aPlease see Table 1 for parameter definitions.

^bThe exotic predator (dominant) is listed first and the native species (subordinate) is next.

^cIndicates caution in interpreting results due to small sample sizes that lead to a lack of any habitat covariates that strongly (i.e. 95% confidence intervals overlapped 0) influenced native species' occupancy and/or detection in previous modeling efforts (see Supporting Information Table S2).

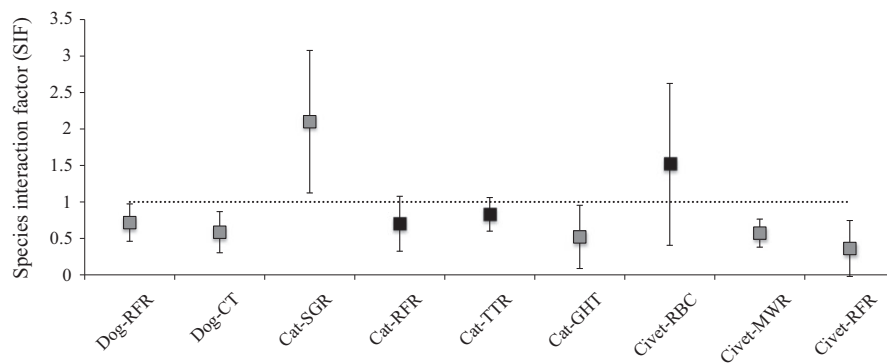


Figure 2 Species interaction factor (SIF) estimates from landscape co-occurrence analyses run in program PRESENCE from camera trapping data collected during surveys of seven sites (total camera sites = 148) in northeastern Madagascar (2008–2011); bars indicate 95% confidence intervals (CIs). If 95% CIs on SIF estimates include 1, this suggests the probability that two species co-occur across the landscape is equal to expectations at random. SIF < 1 suggests that the probability the two species co-occur is lower than would be expected at random, while SIF > 1 suggests that the probability the two species co-occur is greater than would be expected at random. Native species abbreviations are: CT, common tenrec; GHT, greater hedgehog tenrec; MWR, Madagascar wood-rail; RBC, red-breasted coua; RFR, red forest rat; SGR, scaly ground-roller; TTR, tufted-tailed rat.

intervals between p_N and r_N ; Table 3) on native species' detection and seven of these relationships were negative ($p_N > r_N$; Table 3) as predicted. Unexpectedly, five exotic predator-native species pairings were positive (free-ranging cat-red forest rat, and the small Indian civet with the following: scaly ground-roller, Madagascar wood-rail, red-breasted coua, and red forest rat) and estimated the native species' detection as higher where the exotic predator was present than where it was absent ($p_N < r_N$; Fig. 4). Out of the 12 species pairs, 11 had the influence of exotic predator presence on detection mediated by habitat (see Fig. 5).

Discussion

Despite analyzing our data at a relatively coarse level due to collapsing data so that one survey occasion equaled nine trap nights, we found that the presence of exotic predators had a strong influence on native species' parameters in 14 out of 27 species pairs (52%). Often, researchers use two-species occupancy models to examine co-occurrence patterns without including habitat features that are known to influence species' distributions. To do so is to risk confounding the effect of habitat with the effect of another species' presence on a

species' distribution (Robinson *et al.*, 2014; Farris *et al.*, 2015c). Six species pairings showed non-independent co-occurrence patterns ($SIF \neq 1.0$), with five providing evidence for the native species co-occurring less often with the exotic predator than expected at random. Out of these six, four were habitat-mediated. Our findings that scaly ground-roller and common tenrec distributions are influenced by free-ranging cats and domestic dogs, respectively, should be interpreted cautiously as we cannot determine if we are confounding a habitat effect with an exotic predator effect on these two native species' distributions. While it is a local custom to hunt common tenrecs with domestic dogs (Golden, 2009), it is also possible

that this co-occurrence pattern (and that between free-ranging cats and scaly ground-rollers) can be explained by some unmeasured habitat feature.

The four habitat-mediated co-occurrence patterns suggested a synergistic relationship between habitat degradation and exotic predator presence. The SIFs between red forest rats and both domestic dogs and small Indian civets declined considerably (indicating increasing lack of co-occurrence) the closer they were to the forest edge and as the proportion of rainforest at the sites declined. This pattern suggests that as disturbance in primary rainforest increases, so does the influence of these two exotic predators on either red forest rat habitat use, abundance

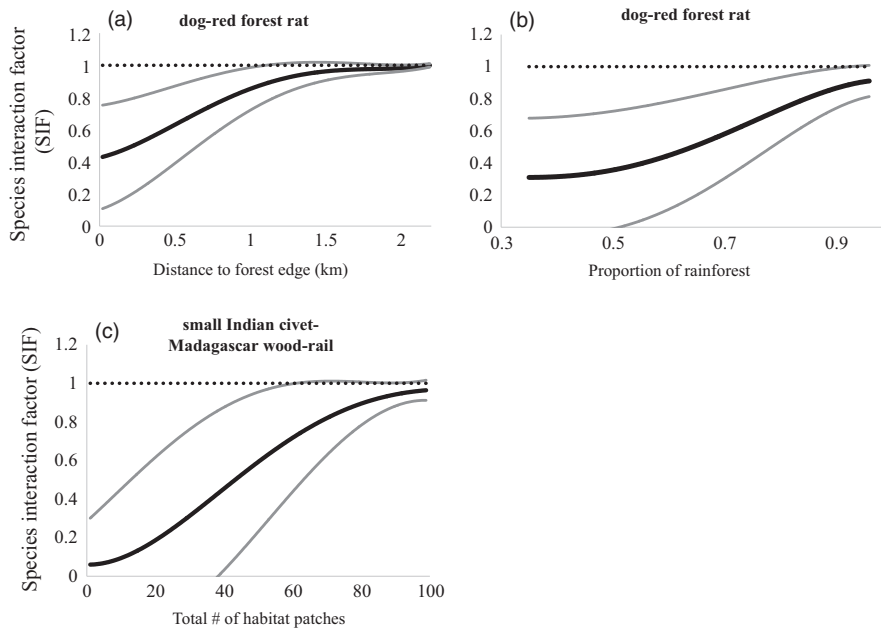


Figure 3 Visual representations of how landscape co-occurrence (SIF) between domestic dogs and red forest rats change based on the (a) distance to forest edge (km) and (b) the proportion of rainforest present at the site and how SIF changes between (c) small Indian civets and Madagascar wood-rails based on the total number of habitat patches at the site, with higher numbers of patches indicating a patchier environment. Gray lines indicate 95% confidence intervals.

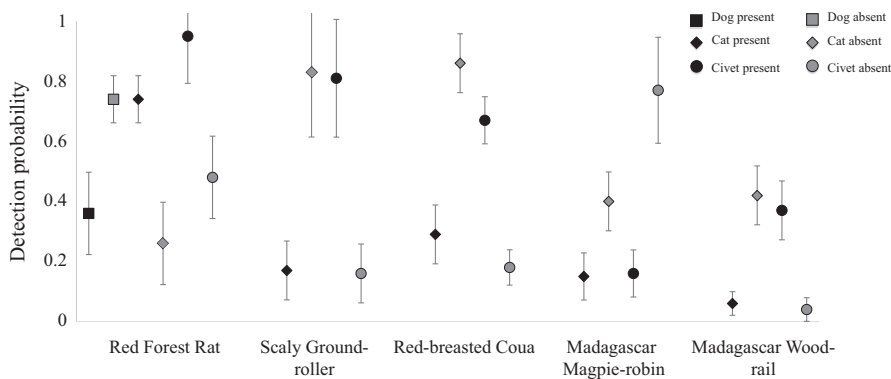


Figure 4 Differences in detection probabilities for five native species depending on the presence (black; p_N) or absence (gray; $p_{\bar{N}}$) of three exotic predators. Error bars indicated 95% confidence intervals.

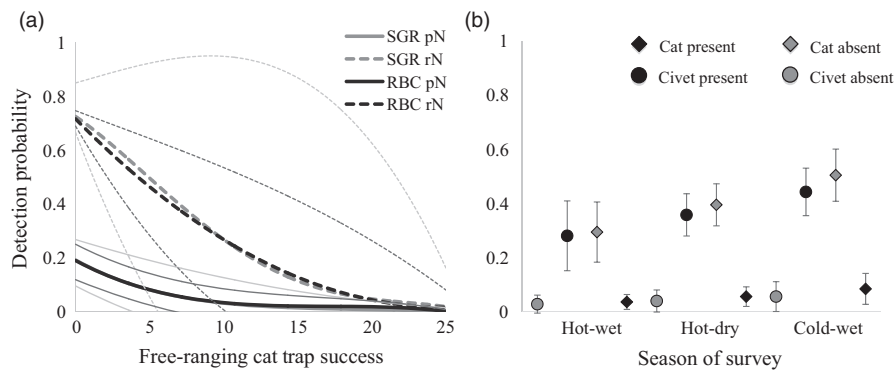


Figure 5 Visual representations of how detection probabilities of (a) of scaly ground-rollers* (SGR) and red-breasted couas (RBC) changes depending on the presence (r_N) or absence (p_N) of small Indian civet (SCI) across a gradient of free-ranging cat (FC) trap success and (b) how Madagascar wood-rail (MWR) detection probabilities change across the seasons depending on the presence or absence of small Indian civets and free-ranging cats. Gray lines indicate 95% confidence intervals. *SGR p_N in solid gray is approximately equal to RBC p_N in solid black.

or both. In contrast to the red forest rat, the greater hedgehog tenrec and Madagascar wood-rail seemed to be more influenced by the presence of their respective exotic predators (free-ranging cats and small Indian civets) in undisturbed habitat compared to disturbed. As canopy height increased (an indicator of large trees and more intact forest), greater hedgehog tenrecs co-occurred less often with free-ranging cats, while as the total number of habitat patches increased (indicating more patchy and fragmented habitat), Madagascar wood-rails co-occurred more often with small Indian civets. These patterns suggest that while the effect of habitat degradation and exotic predator presence might be synergistic, how this synergistic influences native species can differ across species pairings. It is well known that habitat degradation tends to make it easier for exotic species to invade native ecosystems (e.g. Hradsky *et al.*, 2017; Paschoal *et al.*, 2018). We've recorded a higher exotic predator occupancy in more degraded sites (Farris *et al.*, 2015b), suggesting that as habitat degradation increases, native species face decreased habitat quality and increased exotic predator presence, which can amplify negative effects on native species (Brook, Sodhi & Bradshaw, 2008; Anson *et al.*, 2014; Doherty *et al.*, 2015; McDonald *et al.*, 2017). As primary rainforest becomes further degraded and exotic predators increase their presence in the region, it is entirely possible that native species populations will show intense declines.

Exotic predator presence had an overwhelmingly negative effect on native species' detection. Other studies have shown similar results (Farris *et al.*, 2015c; Wang, Allen & Wilmers, 2015). In our case, the nine native ground-dwelling forest bird/small mammal species could be potential prey due to their smaller body sizes compared to the exotic predators. Out of 12 species pairings, seven of these indicated that the exotic predator's presence decreased our ability to detect the native species, which could negatively affect researchers' efforts to comprehensively catalog native species biodiversity at other sites. We suggest that researchers intending to conduct biological surveys may need to exert more effort—whether in survey time, number of survey techniques or both—in areas where it is known

that exotic predators are present, as this influence is most certainly not limited to our study.

Currently, models have not yet been developed to examine the influence of multiple species on another's occupancy/detection (although see Rota *et al.*, 2016), but our results suggest that co-occurrence patterns between multiple exotic predators might influence native species occupancy and detection. For example, Madagascar magpie-robins had lower detection probabilities when occupying a site with free-ranging cats or small Indian civets. We were unable to include both species simultaneously to examine whether Madagascar magpie-robins would have even lower detection at sites with both exotic predators present. In addition, interactions between the exotic predators themselves could also influence the strength of the effect that exotic predators have on native species. For example, if free-ranging dogs and cats avoid each other, native species may only have to contend with one exotic predator or use areas where neither of the exotic predators is present. However, if dogs and cats can co-occur, this could increase the pressure native species face, particularly since dogs are diurnal and cats are largely nocturnal, resulting in limited ability for native species to shift activity patterns to avoid them both. As multiple-predator systems are more common than single-predator systems, it is important that researchers attempt to determine how interactions between exotic predators influence native species. This is likely to be a fruitful avenue for future research once rigorous multispecies occupancy models are available.

Conservation implications and future research

We used non-invasive camera trapping surveys and two-species occupancy models to examine co-occurrence patterns between exotic predators and a suite of native species to infer the presence of potential predator-prey relationships. This approach can be used by other researchers and/or conservation organizations, which may already have extensive camera trap data, to conduct exploratory examinations of potential interspecific interactions that can be used to narrow the focus of future ecological and/

or behavioral studies. Because two-species occupancy models only show patterns in spatial distributions, we can only infer potential behavioral explanations and note that results need further verification by more invasive diet/predation studies. Overall, we found that exotic predators made it more difficult to detect native species, and that in a majority of cases where the presence of exotic predators influenced native species' distribution, these relationships were both habitat-mediated and negative (i.e. native species and exotic predators co-occurred less often than would be expected). Our simultaneous modeling of habitat and exotic predator presence has given us new and more comprehensive insight into how exotic predators affect native species' presence across a habitat degradation gradient, and as such, allowed us to single out what might be synergistic effects between habitat degradation and exotic predator presence. However, our inability to examine how the interactions between the exotic predators influenced native species makes our picture of their effects on native species incomplete. Again, we emphasize the need for more rigorous multispecies models that are able to handle species interactions between multiple species. Across the world, the introduction of exotic predators into native ecosystems, particularly those on islands, has devastated native species. As intact habitat becomes further degraded and exotic predators continue to invade native ecosystems, it is important for researchers to attempt to determine whether synergism exists between these two disturbance processes, and how these two factors influence native species.

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Representative camera trap photographs of the five native ground-dwelling forest bird and four small mammal genera/species that were detected during camera trapping surveys of seven sites in northeastern Madagascar (2008–2011) and included in single-season, two-species occupancy models.

Table S1. Survey details for the camera trapping surveys across seven sites (total camera sites = 148) across the Makira-Masoala protected area complex, northeastern Madagascar (2008–2011) for a total of 8793 trap nights.

Table S2. Competing ($\Delta\text{AIC} \leq 2.0$) models from landscape co-occurrence analyses of camera trapping data from seven sites (total camera sites = 148) in northeastern Madagascar (2008–2011) for 27 exotic predator-native species pairings.