Forest carnivores living on the edge with invasive predators

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Abstract

The proliferation of forest edges and invasive predators have been identified as two primary threats to carnivore populations globally. These threats often occur in unison, facilitated by anthropogenic activities (e.g., fragmentation), and together may pose a greater influence than when they occur separately. Targeted conservation actions for forest carnivores, including Madagascar carnivores, have been hindered by a failure to understand the relative contributions of these factors in driving species declines. To fill this gap, we conducted an extensive camera survey along the edge of intact, continuous protected rainforests in eastern Madagascar to evaluate the extent invasive predators and forest edge separately and in combination affect native carnivore space use. We hypothesized that structural vegetation changes at the forest edge interact with invasive predator trap success and occurrence to reduce native carnivore space use near the forest edge and separately have less influence than when combined. In contrast to findings in fragmented and degraded forests of Madagascar, we found hard forest edge and invasive predators alone do not indiscriminately reduce native carnivore space use in continuous intact forest. Instead, we found free-roaming dogs and cats interact with their surrounding environment (i.e., forest edge) in unique ways that shape species response differently than within interior forest. At the forest edge, vegetational changes of increasing shrub cover and the occurrence of dogs reduce space use of three of four native carnivores. However, we found greater effects of proximity to villages, especially with high invasive predator activity (free-roaming cats). Ultimately, native carnivores showed variable sensitivities to pressures we examined, providing support for species-specific management actions to maximize conservation outcomes. We encourage future studies to consider evaluating the magnitude of separate and combined threats to carnivores. In doing so, conservationists can better identify when threats can be managed in isolation and when they require simultaneous mitigation.

Introduction

The independent and synergistic effects of forest edge and invasive intraguild competitors threaten forest dependent carnivores globally. Forest edges have increased around the world due to rampant forest fragmentation from intensified human activity, principally increased resource extraction and forest conversion for agricultural and human expansion (Haddad et al., 2015). Free-roaming (owned or feral) dogs (Canis familiaris) and cats (Felis spp.) are the world's most abundant and widespread invasive, intraguild competitors (Woodroffe & Ginsberg, 1998; Gompper, 2014). Forest edge and invasive predators can independently influence community and population dynamics, or in unison result in additive or interactive effects (Didham et al., 2007; Doherty et al., 2015). Identifying the relative impacts of each is essential for developing targeted actions at or near forest edges to maximize conservation outcomes for threatened species at the peripheries of protected forests.

Hard forest edge is characterized by an abrupt transition in landscape from forest to non-forest (Taubert et al., 2018). Forests converted from interior to edge undergo sudden or gradual alterations in abiotic and biotic conditions along a gradient from distance to edge. Changes in microclimate

(e.g. humidity, air temperature; Magnago *et al.*, 2015) and vegetation structure (e.g. shrub cover, canopy cover, canopy height; Didham & Lawton, 1999) often occur, which can reduce habitat suitability for species across trophic levels (Betts *et al.*, 2019). Edge effects become apparent when species space use or density changes, or a community shift occurs at forest peripheries (Laurance & Yensen, 1991). Edge effects are thus identifiable by measurable changes in populations or communities near the forest edge relative to the interior forest (Harper *et al.*, 2005). With global forest fragmentation leading to 50% of the remaining forest cover to be within 500 m of an edge (Pfeifer *et al.*, 2017), edge effects could be a significant driver of change for forest dependent carnivore populations.

Native forest dependent carnivores are disproportionately negatively impacted by forest conversion from human activities relative to other taxonomic groups (Woodroffe & Ginsberg, 1998). Increased forest edge can reduce carnivore survival (Balme, Slotow, & Hunter, 2010), population density (Revilla, Palomares, & Delibes, 2001), space use (Kuehl & Clark, 2002), and increase their risk to human persecution (Woodroffe & Ginsberg, 1998). As an added threat, invasive predators, dogs and cats, are generally more active near forest edges and often coincide with anthropogenic activity centers (e.g., human settlements, roads; Farris *et al.*, 2015a; Paschoal *et al.*, 2018). Yet, free-ranging dogs and cats may also occupy interior forest, either accompanying humans or traveling alone (Farris *et al.*, 2015b, 2015c; Paschoal *et al.*, 2016). Dogs and cats threaten native carnivores through increased competition, direct predation, fear-mediated behavioral effects, and disease transmission (Medina *et al.*, 2011; Gompper, 2014). Dogs and cats interacting with native carnivores have been shown to reduce native carnivore fitness from harassment (Young *et al.*, 2011), increase mortality from intraguild killings (Silva-Rodriguez, Ortega-Solis, & Jimenez, 2010), alter space use (Revilla, Palomares, & Delibes, 2001; Vanak & Gompper, 2010), and influence temporal activity (Gerber, Karpanty, & Randrianantenaina, 2012a). However, native carnivores have variable sensitivity to abiotic and biotic changes, with some species better able to adapt to altered habitats (Kiffner, Stoner, & Caro, 2013; Pfeifer *et al.*, 2017). For example, in Argentina, Pampas fox, *Pseudolopex gymnocercus* show high adaptability and Geoffroy's cat, *Leopardus geoffroyi*, low adaptability to anthropogenic changes, with responses mediated by ecological and behavioral attributes (Caruso *et al.*, 2016).

Carnivore response to the proliferation of forest edges and presence of invasive dogs and cats may differ from when pressures are found independently. In these cases, pressures that overlap in space or time can result in a synergistic (interactive) effect, which is greater than the sum of their independent (additive) effect (Doherty *et al.*, 2015). For example, if forest logging and invasive predator presence each reduce native carnivore occurrence by 10% in isolation, then together should result in an additive 20% reduction. However, if a 40% reduction is found instead, overlapping disturbances are resulting in a synergistic effect.

Multiple threats are common near forest edges with strong potential to interact with invasive predators. Preferred areas of invasive species sometimes overlap with preferred areas for native carnivores. For example, habitat features including vegetation structure, proximity to anthropogenic centers, and prevalence of trails influence invasive predator behavior and alter invasive-native interactions. In forested areas, dogs are known to select bare ground, trails, and roads for movement and avoid dense vegetation (Sepúlveda *et al.*, 2015). Cats have been shown to increase their use of areas with high shrub cover, where prey availability is higher (Recio *et al.*, 2014). As a result, native carnivores face direct (predation) and indirect (prey-mediated) effects from dogs and cats when using a wide-range of habitat types across their range, namely high shrub forest edge habitat. The effect dogs and cats may have on native carnivores could also be dependent on the magnitude of invasive predator presence in the environment, with higher density or activity resulting in more intense pressure (Ribeiro *et al.*, 2019).

Invasive predator influence on habitat use of native species is well documented and has raised concerns in both wildlife management and conservation fields (Hughes & Macdonald, 2013; Doherty *et al.*, 2016, 2017). For species of conservation concern, different management strategies may be warranted depending on whether changes in habitat near a forest edge and the presence of invasive predators influence species independently, additively, or synergistically. However, evaluation of the extent to which their influence is additive or interactive with structural changes to forests near the edge is still much needed particularly in biodiversity hotspots threatened by rapid habitat degradation (Kier *et al.*, 2009; Vanak & Gompper, 2010).

We investigate the relative effects of forest edge and invasive predators in a biodiversity hotspot on the largely under-studied, endemic family Eupleridae. Forest edge effects and introduced free-roaming dogs and cats are two primary threats to all endemic carnivores of Madagascar (IUCN, 2023). Forest fragmentation, degradation, dogs, cats, or a combination have been shown to influence carnivore space use and temporal activity (Wampole, Farris, & Gerber, 2021). However, these disturbances have not been evaluated independently and in combination within a single study to assess whether pressures act additively or synergistically to negatively impact species; nor has the amount of activity of invasive predators been investigated to examine how it influences the magnitude of these effects, if any.

Euplerid conservation can be better guided by understanding the relative effects of habitat degradation from forest edge and invasive predators (Gerber, Karpanty, & Randrianantenaina, 2012b; Murphy *et al.*, 2018). For example, if patterns observed in fragmented forest are consistent, and forest edge and invasive predators interact to negatively influence euplerids, intact contiguous forest landscapes may only buffer species from threats at distances far from the forest edge and require simultaneous mitigation of co-occurring pressures. However, if patterns are independent and pressures additive, then continuous forest may buffer species from pressures near forest edges and conservation can target co-occurring pressures independently.

We hypothesized that (1) native carnivore space use is influenced by both invasive predators and changes in habitat (specifically vegetation structure) from hard forest edge effects; (2) in combination, invasive predators and forest edges interact, causing a greater negative effect synergistically than their combined additive effects; and (3) native carnivore space use could be influenced by the presence/absence of invasive predators or the amount of invasive predator activity. We evaluated our hypothesis by estimating the magnitude (e.g., effect size) of separate single pressures from invasive predators and forest edges and their combined effects (additive or interactive) using an occupancy modeling framework (MacKenzie *et al.*, 2018). We used single-season, single-species models (MacKenzie *et al.*, 2002) to test the effect of invasive predator activity (trap success) and forest edge variables; and a multi-species co-occurrence model (Rota *et al.*, 2016) to test effect of invasive predator co-occurrence (presence/absence) and forest edge variables on native carnivore space use.

Materials & methods

Study site

We conducted field surveys during the cool-dry season (June–October 2019) within and bordering Mantadia National Park in the eastern humid rainforest of Alaotra-Mangoro Region, Madagascar. Mantadia is approximately 100 km^2 and is one of the last remaining large expanses of intact rainforest in Madagascar. Forests outside of the park boundaries have experienced intense logging, tavy (slash and burn agriculture), and mining, resulting in small remnants of highly fragmented, and degraded forest stands (McConnell, Sweeney, & Mulley, 2004). Our study covered roughly a 50 km^2 area near the western edge of Mantadia (Fig. 1). The southern edge of our study area contained hard forest edge, delineated by a heavily used national park road. Villages adjacent to the road are surrounded by agricultural fields and contain cats and dogs. The northern edge of Mantadia abuts intact continuous forest that intersects community protected forest (Torotofotsy) with outlying small settlements and footpaths to large village communities outside the park boundary to the west. Madagascar's family Eupleridae is comprised of 7 endemic small bodied (0.4–8.6 kg) carnivores that are largely understudied within a threatened forest region of Madagascar (Brooke *et al.*, 2014; DiMinin *et al.*, 2016; Tilman *et al.*, 2017; Torres-Romero & Giordano, 2022). Five of the 7 species of native, endemic carnivore's distributional ranges include Mantadia and were expected to be observed during our survey (IUCN, 2023): *Cryptoprocta ferox* (fosa), *Fossa fossana* (spotted fanaloka), *Eupleres goudotii* (eastern falanouc), *Galidictis fasciata* (broad-striped vontsira), and *Galidia elegans* (ring-tailed vontsira).

Camera trap survey and image processing

We established 78 sites operating from 28 to 111 days (mean = 88.77) on existing trail systems spanning from the hard forest edge to the interior forest. Sites were placed apart at a distance greater than most target species home ranges (mean = 482.2 m, SD = 101 m) and consistent with previous camera studies in Madagascar (Wampole, Farris, & Gerber, 2021). At each site, we placed one remote trail camera (Browning- Strike Force Pro XD) 20–30 cm off the ground and cleared vegetation from the camera focal area to decrease the likelihood of false triggers. Cameras were set to take 3 sequential photographs without delay when triggered and operate continuously throughout the 24-h period. We processed images using the software Digikam (www. digikam.org) to identify species photographic detections. We created site detection histories for each species using camtrapR (v2.0.2, Niedballa *et al.*, 2016) in the R programing language (R Core Team, 2020). We considered a 30-min time difference between photographs of the same species at the same site to be an independent detection event (Gerber, Karpanty, & Randrianantenaina, 2012b) and set encounter occasion length as a 1-day interval; as such, detection probability is estimated at the scale of a 24-h period.

Edge effect covariates

We evaluated forest edge effects, characterized by changes in vegetation structure with increased distance from a hard forest edge, by quantifying vegetation metrics at two spatial scales: site (SL, 50 m radius) and landscape (LL, 1000 m radius). We quantified site level metrics to capture fine-scale vegetation characteristics, while landscape-level captured coarse vegetation structure. We then tested for a linear effect across distance to hard forest edge to quantify alternative explanatory variables of vegetational forest edge effects used in subsequent occupancy modeling.

We estimated fine-scale vegetation structure (SL) using the point intercept method (Canfield, 1941) following protocols by Gerber, Karpanty, & Randrianantenaina (2012a,b). Starting at the location of the camera trap, we measured vegetation presence every 2 m along a 50 m transect in 3 cardinal directions: N, SE, SW (corresponding to 0, 120, 240°). We recorded the presence of down/dead- (≥15 cm DBH), ground- (0–0.5 m), and shrub- (0.5–5 m) cover, as well as low- (0–5 m), mid- (5–15 m), and high- (≥15 m) canopy cover; percent cover was calculated for each vegetation class at each camera site as the number of presence points/total sampling points × 100.

We estimated coarse vegetation structure (LL) from Landsat 4–5 imagery, 30 × 30 m resolution (usgs.gov, acquired October 10, 2018) following protocols by Freitas, Mello, & Cruz (2005). We defined three dominant landscape vegetation cover classes (1) *high canopy* − mature forest, (2) *low canopy* − secondary forest, and (3) *non-canopy* − not forested, shrub, groundcover, or bare-ground. Vegetation classes were verified using ground truths and SL data. We established a 1000 m radius buffer around each camera site and calculated percent cover for each vegetation class using the R package landscapemetrics (v.1 .4.4; Hesselbarth *et al.*, 2019).

To assess secondary predictor variables of possible forest edge effects to which native species could respond, we fit
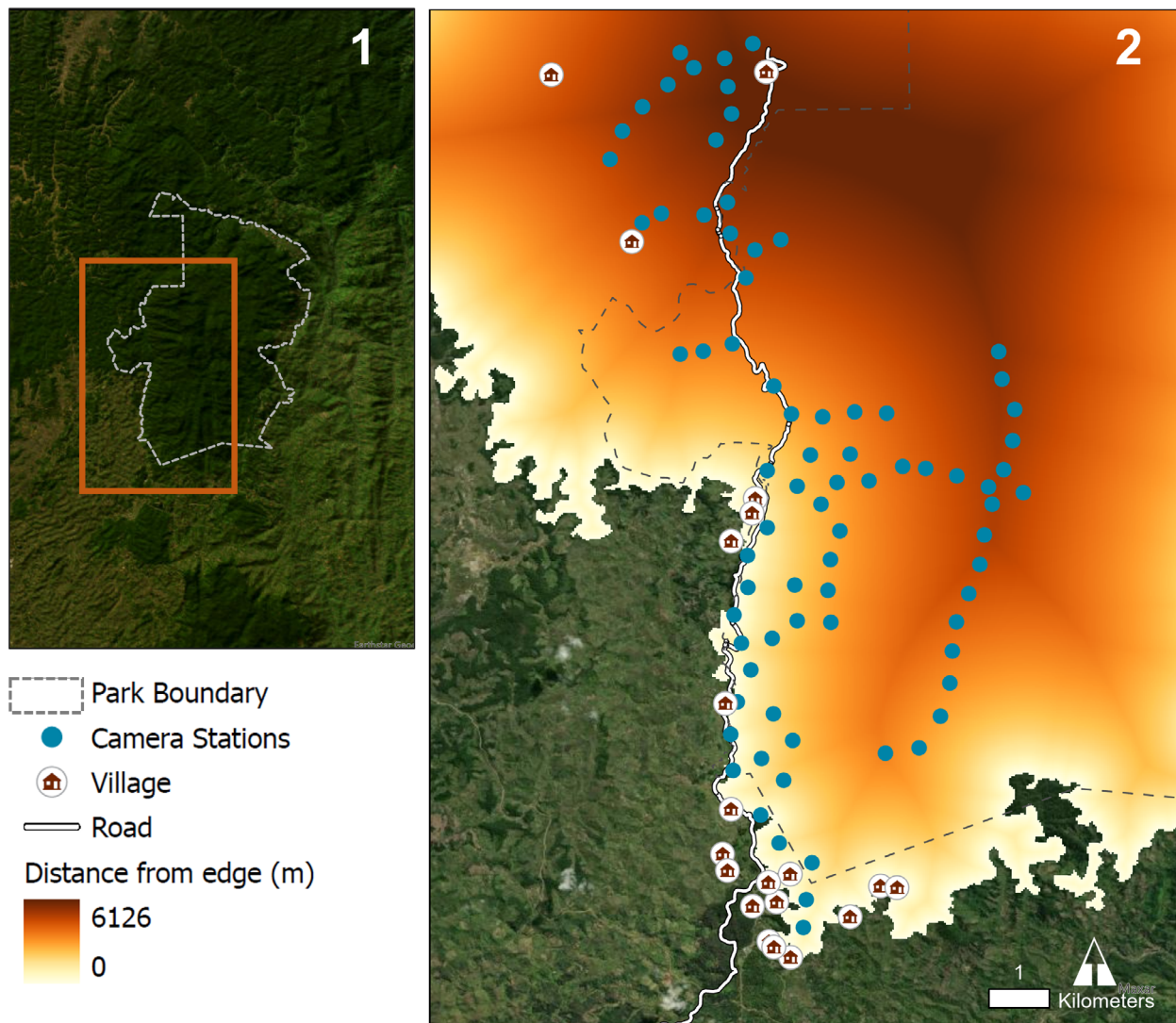
Figure 1 (1) We established our survey area on the south-eastern edge of intact contiguous eastern rainforest of Mantadia National Park (orange box). (2) Camera traps were placed along existing human or game trails with increased distance from the forest edge and variable distance from villages.

linear regression models using SL and LL vegetation metrics with the Euclidean distance from a hard forest edge (hereafter titled *forest edge*; Appendix S1). We defined a hard forest edge using our landscape level vegetation classification data, drawing a polyline along the intersection of contiguous canopy and non-canopy vegetation classifications and calculated the distance from each camera site to the polyline using Arc-GIS (10.6.1; ESRI, 2011). Vegetation metrics with a statistically significant independent linear relationship to the Euclidean distance from a hard forest edge were included as an edge effect in subsequent occupancy models. We found three structural vegetation metrics that met our criteria and captured possible vegetational edge effects: *shrub* (SL, $\beta = -0.418$, $P = 0.01$), *non-canopy* (LL; $\beta = -0.394$, $P < 0.01$), and *high canopy* (LL; $\beta = 0.306$, $P < 0.01$). We

also considered the Euclidean distance to hard forest edge (*forest edge*) as a potential variable in the occupancy models, which represents unexplained variation in habitat as distance from the edge increases. We therefore considered four alternative vegetational covariates for forest edge effects- *shrub*, *non-canopy*, *high canopy*, and *forest edge* in our analysis.

Invasive predator model inclusion specification

For the single-species occupancy model, we included *dog* and *cat* trap success − the number of independent photographic capture events of a target species divided by the number of trap nights, as variables modeling native species occurrence (ψ) and detection probability (P). We use trap

success as an index of invasive predator activity at a site. We did so to consider how a small amount of site activity by invasive predators may not influence native species space use, while a lot of activity might reduce native species detection or occurrence. For the multi-species co-occurrence model, invasive predator presence/absence was a conditional state to model native carnivore occupancy (ψ). This assumes that native carnivores respond to the presence of an invasive predator similarly at any degree of trap success greater than zero. The co-occurrence model thus considers how native and invasive co-occurrence may reduce native carnivore occupancy regardless if an invasive predator is active at a site once a month or present daily.

Secondary metrics

Finally, we established two secondary metrics that were independent of our primary hypotheses (i.e. native carnivore space use is influenced by both invasive predators and changes in habitat from hard forest edge effects) but could be important predictors of carnivore space use (Table 1). We included the Euclidean distance to village (*village*) and human trap success (*human*, calculated as the sum of independent detection events per site, scaled by the number of nights the site was sampled). Each is assumed as a possible disturbance that could influence carnivore space use, such as site avoidance from a fear mediated response to noise or hunting pressure, or alternatively an attractant to a site for access to food (Didham *et al.*, 2007; Caruso *et al.*, 2016).

Occupancy models

Single-species model

We examined the influence of invasive predator trap success and forest edge effects by constructing a set of 12 candidate global models (8 additive, 4 interactive) evaluating our primary hypotheses and 4 additional global models evaluated our secondary hypotheses (Appendix S2). We first created 8 global models that modeled ψ as an additive effect of invasive predator and forest edge variables. We paired each invasive predator variable (*dog*, *cat*) with each forest edge variable (*shrub*, *non-canopy*, *high canopy*, *forest edge*) separately by global model, as forest edge variables represent competing hypotheses about types of structural edge effects. We then created 4 global models that modeled ψ as an interaction between invasive predators and forest edge variables on native carnivores, by combining *shrub* and *forest edge* separately with each invasive predator (*dog*, *cat*). We had no a priori knowledge to justify inclusion of interaction terms between invasive predators and canopy cover variables (*non-canopy*, *high canopy*) for Madagascar carnivores; thus, we excluded these combinations from consideration. The result was a set of candidate models of plausible interactions of vegetation structure and invasive predators on carnivore space use supported by the literature (Table 1). Finally, we generated 4 candidate global models, representing secondary hypotheses − that native carnivore occupancy was influenced

by proximity to a village and not explained by forest edge effect variables; we therefore modeled ψ as an additive and interactive effect of *village* and invasive predators (*dog*, *cat*). For all global models, we modeled p by *forest edge* with each invasive predator (*dog*, *cat*), and included secondary variables, *human* and *village*, to account for variation in p unrelated to our hypotheses and have been supported in previous studies (Farris *et al.*, 2017a). Structural vegetation characteristics were not considered to reduce the number of possible models and because *forest edge* was expected to be more relevant.

We generated all possible combinations of each global model while holding forest edge variables constant (*shrub*, *non-canopy*, *high canopy*, *forest edge*) to ensure only relevant models were generated. We did so using the "dredge" function in the R package MuMIN (v.1.43.17; Bartoń *et al.*, 2020). Our complete model set of 960 models included all possible combinations of singular, additive, and interactive influences of hypothesized forest edge effects and each invasive predator on native carnivore occupancy. Due to the small sample size for the broad-striped vontsira, we removed interaction terms and restricted models to include no more than two variables on ψ or p in any given model ($n = 114$ models). Prior to model fitting, all covariates were log transformed then scaled and centered, reducing the effects of outliers, improving model convergence, and providing meaningful comparison between estimated coefficients. Covariates included in a single model were tested for multicollinearity. For all variables included in a single model correlation coefficients were below 0.60. We compared models using Akaike Information Criterion corrected for small sample size (AICc; Burnham & Anderson, 2002). All analyses were done in the R programming language, and models were fit using the package unmarked (v. 1.0.0; Fiske & Chandler, 2011).

We quantified the strength of variables that represent absolute importance of forest edge and invasive predator influence using model averaged coefficients that provide a weighted effect size (Galipaud, Gillingham, & Dechaume-Moncharmont, 2017). We standardized covariates and summarized coefficient size by small (0.1–0.5), medium (0.5–1.0), and large (>1.00) effects. For comparative purposes, we also report the sum of Akaike weights (*sw*) by variable as additional support of coefficient relative importance, following standard practice (Appendix S3; Burnham & Anderson, 2002) despite current debate concerning its utility (Galipaud, Gillingham, & Dechaume-Moncharmont, 2017). Finally, we assessed the effects of invasive predators and forest edge variables using model averaged predictions, accounting for model selection uncertainty (Burnham & Anderson, 2002).

Multispecies co-occurrence model

We evaluated the influence of invasive predator co-occurrence on native carnivore space use, independently and in combination with potential forest edge variables. For each native carnivore, we considered the influence of two species co-occurrence (native carnivores and − dogs only (native +

Table 1 Covariate descriptions and literature support for use in occupancy models investigating native Madagascar carnivore space use for 2019 camera survey of Mantadia National Park, Madagascar

Hypothesis	Covariate	Description	References	Model Parameter
Forest edge	*forest edge*	Euclidean distance from each site to nearest forest edge boundary	Farris et al. (2017a,b), Ross et al. (2020)	ψ, p
	Shrub	Percent shrub at site, measured by point intercept	Farris et al. (2015b,c, 2017a,b), Stanton Jr et al. (2018)[a]	ψ
	non-canopy	Percent non-canopy landscape at 1000 m buffer from categorized Landsat imagery	Whitworth et al. (2019)[b]	ψ
	high canopy	Percent high canopy landscape at 1000 m buffer from categorized Landsat imagery	Whitworth et al. (2019)[b]	ψ
Invasive predator	*Dog*	Trap success	Farris et al. (2017a,b), Merson et al. (2019)	ψ, p
	Cat	Trap success	Farris et al. (2015c), Gerber, Karpanty, & Randrianantenaina (2012b)	ψ, p
Secondary	*Human*	Trap success	Farris et al. (2017a)	ψ, p
	Village	Euclidean distance from each site to nearest village	Farris et al. (2017a)	ψ, p
Interaction	*shrub*cat*	Interaction of percent shrub at site and cat trap success	Farris et al. (2015b,c), Recio et al. (2014)[b]	ψ
	shrub*dog	Interaction of percent shrub at site and dog trap success	Sepúlveda et al. (2015)	ψ
	forest edge*cat	Interaction of distance to forest edge and cat trap success	Farris et al. (2017b), Merson et al., (2019), Ross et al. (2020)	ψ
	forest edge*dog	Interaction of distance to forest edge and dog trap success	Farris et al. (2015c), Merson et al. (2019)	ψ
	village*cat	Interaction of distance to village and cat trap success	Farris et al. (2017a,b), Gerber, Karpanty, & Randrianantenaina (2012b), Paschoal et al. (2018)[b]	ψ
	village*dog	Interaction of distance to village edge and dog trap success	Farris et al. (2015b), Farris et al. (2016)	ψ

The hypothesis column indicates categories of candidate variable types tested with each corresponding covariate on occurrence probability (ψ) and/or detection probability (P) as indicated by model parameter column.

[a] Global meta-analysis.

[b] Outside Madagascar but within tropical rainforest eco-regions.

dog), − cats only (native + cat), − dogs and cats (native + dog + cat) and three species co-occurrence (native carnivore, dogs and cats; native*dog*cat). We also included an independent model, which excluded any influence of species interactions (Appendix S1). Following Rota et al. (2016), we modeled species co-occurrence as natural parameters (f), quantified as the log odds of species occupancy. For example, when considering 2 species (dog and fosa) co-occurrence varying by *shrub*, we specify f's as ratios of combinations of fosa only occupancy probability (ψ_{10}), dog only (ψ_{01}), dog and fosa (ψ_{11}), and no occurrence (ψ_{00}), which are linked to covariates as a linear model as

$$f_1 = \log\left(\frac{\psi_{10}}{\psi_{00}}\right) = \alpha_0 + \alpha_1 \text{shrub}$$

$$f_2 = \log\left(\frac{\psi_{01}}{\psi_{00}}\right) = \beta_0 + \beta_1 \text{shrub}$$

$$f_{12} = \log\left(\frac{\psi_{11}\psi_{01}}{\psi_{10}\psi_{01}}\right) = \gamma_0 + \gamma_1 \text{shrub}$$

where α_0, β_0, and γ_0 are intercepts and α_1, β_1, and γ_1 are slope parameters associated with *shrub*. From the natural parameters, we can derive a conditional probability using the inverse-logit link to examine variation in fosa occupancy, conditional on the occurrence of dogs across varying measures of shrub as

$$P(\text{fosa} \mid \text{dog}) = \text{logit}^{-1}((\alpha_0 + \gamma_0) + (\alpha_1 + \gamma_1) \times \text{shrub}).$$

For each native species, we modeled natural parameters of marginal occurrence (occurrence without species interactions, e.g., f_1 and f_2), using variables found to have medium (0.5–1.0) or large (>1.00) absolute importance from our single-species model results. We modeled covariates on species interactions (e.g., f_{12}) based on important predictor variables from previous studies (Wampole, Gerber, Farris 2021) and considered here (*shrub*, *forest edge*, *village*; Table 1). We created 17 candidate models, for fosa, fanaloka, and falanouc, which included marginal, pairwise, and three-species co-occurrence models. These models represented our specific hypotheses in the ways in which native carnivore space use

could be influenced by invasive predator co-occurrence separately or in combination with forest edge variables (*forest edge*, *shrub*) and our secondary hypothesis *village*. Due to data sparsity for the broad-striped vontsira, we fit only pairwise co-occurrence models, resulting in six candidate models. We compared models using AICc and evaluated top model coefficients to determine relative support for the separate and combined influences of invasive predator co-occurrence and hypothesized forest edge effects. Models were fit using the package unmarked (Fiske & Chandler, 2011).

Results

Survey

We sampled for 9396 trap nights ($n = 78$ sites) and captured 1341 independent detections of target species. Fanaloka were the most frequently detected species ($n = 538$), followed by falanouc ($n = 276$), dogs ($n = 248$), fosa ($n = 161$), cats ($n = 76$), broad-striped vontsira ($n = 29$) and ring-tailed vontsira ($n = 13$). We detected native carnivores at different frequencies, separately and in combination with invasive predators near and far from a forest edge, providing appropriate combinations to test our hypotheses (Appendix S4). However, ring-tailed vontsira were excluded from our analysis due to insufficient sample size (naïve occupancy = 0.08).

Single species occupancy model

We did not find that native species occupancy was significantly changed (medium or large effect) by an interaction between invasive predator trap success and forest edge variables (Fig. 2a). We instead found small interactive effects of dogs in high shrub, and cats further from forest edge for 2 species. Fanaloka occupancy was lower at sites with higher dog trap success and percent shrub cover. Fosa occupancy was slightly increased at sites with cats further from the forest edge. However, we found support for a large positive independent effect of *forest edge* on fosa occupancy (Fig. 3a). Except for the fosa, we found no evidence that forest edge variables separately influenced carnivore occupancy. We also found no substantial evidence that invasive predator trap success independently influenced native carnivore occupancy. *Dog* alone had a small positive effect on fanaloka occupancy, with larger effects from the interaction of *cats* and *village*. We also found a medium positive interactive effect of *cat* and *village* for falanouc and fanaloka (Fig. 3b, c), and a small positive independent effect of *village* on broad-striped occupancy (Fig. 2).

We found native carnivore detection varied in sensitivity, both direction and magnitude to investigated pressures (Fig. 2b). Native carnivore detection showed significant changes in response to cats, dogs, forest edge, villages, and humans (Fig. 4). *Cat* had a medium positive effect on falanouc alone, with no effect on detection for any other native carnivore (Fig. 2). *Dog* had a large negative effect on falanouc and a small negative effect on fosa detection. *Forest*
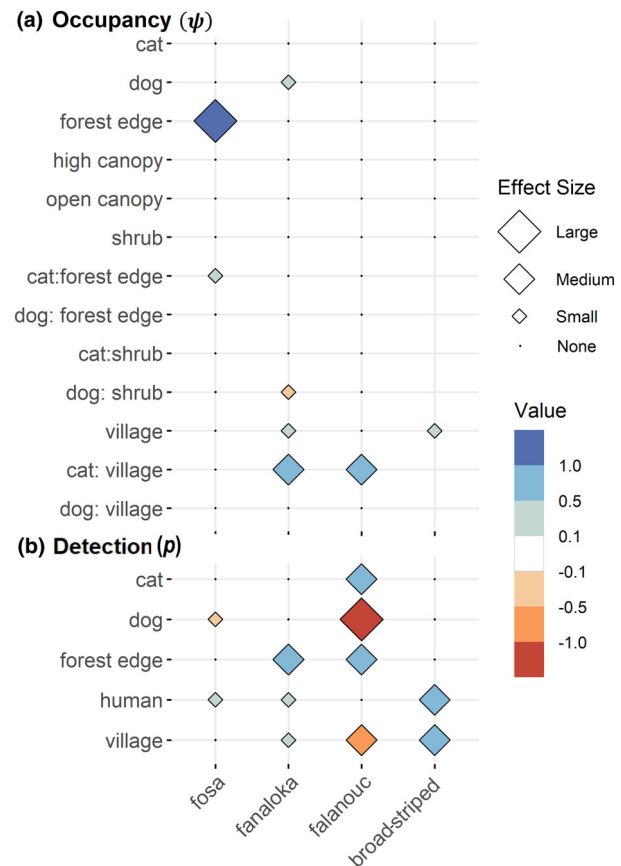

Figure 2 Model averaged coefficient effect sizes for separate and combined pressures on (a) native carnivore (indicated at the bottom) occurrence (ψ) and (b) Detection probability (P). Colors indicate the categorical effect size and value indicates the coefficient estimate. Single variables (e.g., cat) indicate a main effect that is not conditional on another variable, while combined variables (e.g., cat:forest edge) indicate an interaction effect. Larger weighted effect sizes indicate more support for the interaction or single variable; equal size effects between interactions and single variables indicate uncertainty to which is more supported.

edge had a medium positive effect on fanaloka and falanouc detection. *Village* had a medium negative effect on falanouc detection, a small positive effect on fanaloka, and a medium positive effect on broad-striped vontsira detection. Finally, *human* had a small positive effect on fosa and fanaloka, and a medium positive effect on broad-striped vontsira (Fig. 2b.
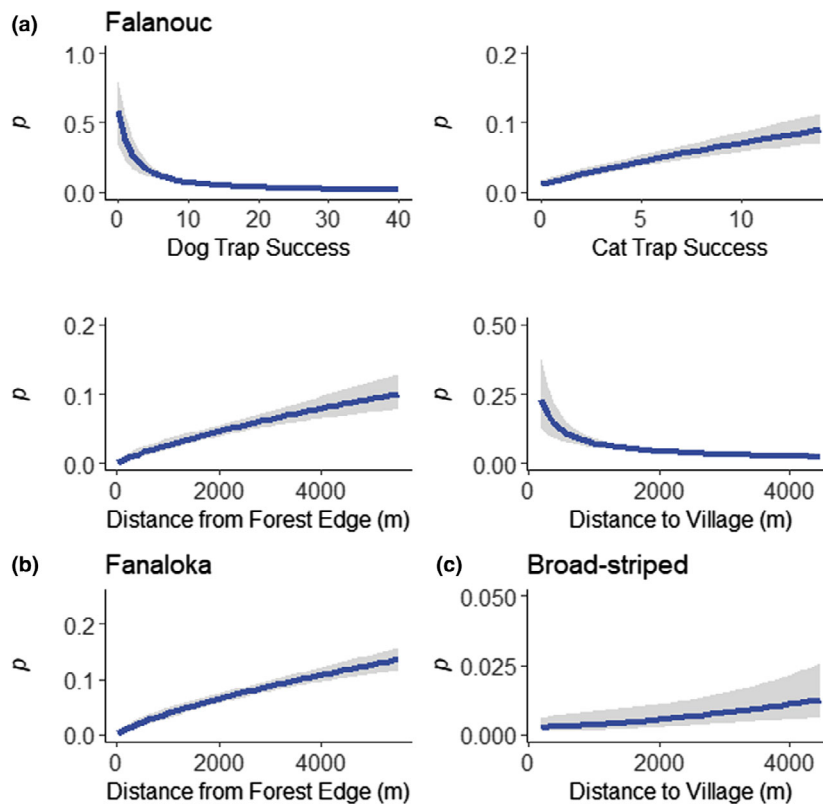
Multispecies occupancy model

Support for the relative separate and combined effects of forest edge effects and invasive predator co-occurrence was variable among species (Table 2). We found no clear support (independent co-occurrence model was most supported) that fosa occupancy is explained by co-occurrence with invasive predators (Fig. 5a). The second top model supported dogs and *shrub* in combination interact to reduce fosa occupancy
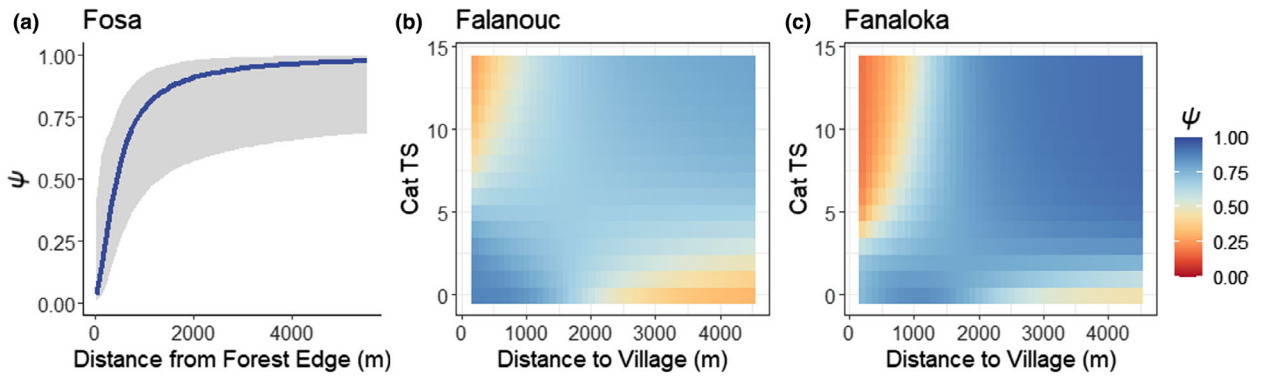
Figure 3 Single-season, single species model averaged predictions for medium-large effects on native carnivore occupancy (ψ). Fosa occupancy probability (ψ) increased with distance from a forest edge (a). Falaounc (b) and fanaloka (c) occupancy probability was influenced by an interaction of cat trap success (Cat TS) and distance from a village.

Figure 4 Prediction plots for medium and large effects on native carnivore detection probability (*P*) determined from model averaged coefficient from single-season, single-species occupancy model. (a) Falanouc detection was influenced by *dog*, *cat*, *forest edge*, and *village*. (b) Fanaloka detection increased with further distance from the *forest edge*. (c) Broad-striped vontsira detection was influenced by *village* and *human* (human not shown but see Fig. 2). No medium or large effects were found for the fosa.

($\beta = -0.743$, $\text{SE} = 0.362$, $P = 0.040$; Table 2; Fig. 6). We found support that fanaloka occupancy is positively associated with dogs but declines with high shrub cover ($\beta = -0.7145$, $\text{SE} = 0.314$, $P = 0.03$). However, this does not result in a meaningful decline in fanaloka occupancy (Fig. 5b). We also found model support that falanouc occupancy is largely influenced by co-occurrence with dogs in

shrub cover ($\beta = -1.008$, $\text{SE} = 0.373$, $P < 0.01$; Fig. 5c). We found no clear support for any variation in broad-striped vontsira occupancy (Fig. 5d). Across species, we saw a similar trend in response of native carnivores to dog co-occurrence within high shrub cover sites; however, the strength of species response was variable, with 3 of 4 species reducing occurrence in response (Fig. 6).

Table 2 Comparison of top models ($\Delta AIC_c < 3$) from single-season multi-species occupancy analyses from 2019 camera survey of Mantadia National Park, Madagascar

	Model	K	AIC_c	ΔAIC_c	ModelLik	AICcWt	LL	Evidence ratio
Fosa	ψ_M	13	3103.62	0.00	1.00	0.33	−1535.96	−
	ψ_C (dog:shrub)	15	3104.16	0.55	0.76	0.25	−1533.21	1.32
	ψ_C (dog)	14	3105.77	2.15	0.34	0.11	−1535.55	3.82
Fanaloka	ψ_C (dog:shrub)	17	4783.26	0.00	1.00	0.41	−2369.53	−
	ψ_C (dog)	16	4784.85	1.59	0.45	0.19	−2371.96	2.21
Falanouc	ψ_C (dog:shrub)	14	3579.80	0.00	1.00	0.54	−1772.57	−
	ψ_M	12	3582.39	2.59	0.27	0.15	−1776.80	3.65
Broad-striped vontsira	ψ_M	12	2019.47	0.00	1.00	0.44	−995.33	−
	ψ_C (dog:shrub)	14	2021.95	2.49	0.29	0.13	−993.64	3.47
	ψ_C (cat)	13	2022.30	2.83	0.24	0.11	−995.31	4.13
	ψ_C (dog)	13	2022.35	2.88	0.24	0.10	−995.33	4.23

Co-occurrence occupancy models (ψ_C) estimate the influence of invasive predators on native carnivore occupancy and independent occurrence models (ψ_M) assume no influence of invasive predators on native carnivore occupancy. ψ_C with environmental variable indicate support for an interaction between invasive predator and the environmental variable (e.g. ~dog:shrub). Evidence ratios indicate the level of support for the top model relative to the model in that row, for each species.
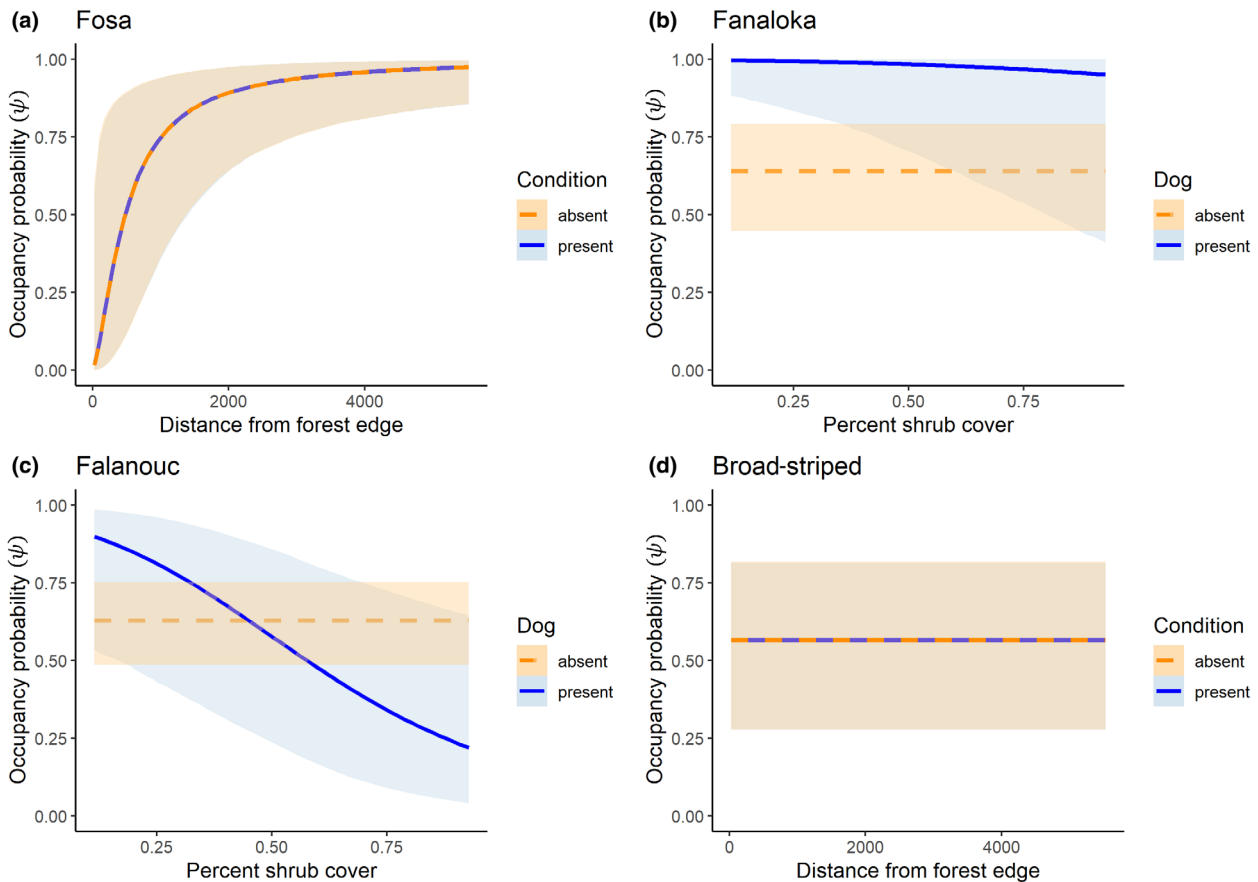
Figure 5 Conditional occupancy probability of each native carnivore with respect to invasive species presence from the top multi-species occupancy models from 2019 camera survey of Mantadia National Park, Madagascar. The condition absent (orange) or present (blue) refers to the invasive predator in the top model, with 95% confidence intervals (shaded area).
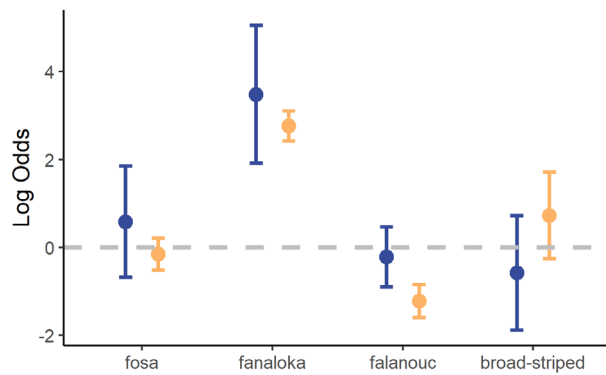
Figure 6 Comparison of the effect of dog co-occurrence at mean percent shrub cover (blue) and dog co-occurrence at one standard deviation above the mean (yellow) on native carnivore occupancy. The points (blue and yellow) represent the mean change in native carnivore occupancy on the log odds scale from the estimated marginal occupancy (gray line) along with 95% confidence intervals. Log odds above 0 indicate a higher probability of native carnivore occurrence for dogs present, and log odds below 0 indicate a lower probability, relative to a state without dogs present.

Discussion

Previous studies within fragmented and heavily degraded forest of Madagascar painted a bleak picture for native carnivores' long-term persistence due to strong negative effects of habitat degradation from increasing forest edge and invasive predator presence (Wampole, Farris, & Gerber, 2021). We sought to understand how these two major threats to native carnivores alone and in combination affect carnivore space use within continuous protected forest of Madagascar. By doing so, we aimed to evaluate whether patterns observed in fragmented forests are indicators of the effects on native carnivores within one of the last remaining large, protected forests complex of Madagascar.

We found that forests edge alone is not a significant threat to euplerids when continuous forest is available. Of the four investigated carnivores, fosa had the only significant response to forest edge alone. Fosa avoided use of sites near the forest edge but were otherwise little affected by all other investigated threats. Interestingly, this contrasts previous findings where fosa occupancy remained constant across gradients of disturbance (Murphy *et al.*, 2018) and utilize areas surrounding villages and agricultural areas as corridors to movement between forest patches (Wyza *et al.*, 2020). Within our study, *forest edge* was a clear delineation between expansive- forested and unforested landscape (Fig. 1). Fosa are the largest and furthest ranging carnivore and often suffer high persecution due to perceived or actual depredation events on livestock (Merson *et al.*, 2019). Within continuous forest, fosa appear to be avoiding high-risk edge habitat, where movement between forest patches is not needed, unlike fragmented systems. Congruent with previous recommendations, our findings support that large intact protected areas provide critical habitat for maintaining fosa

populations (Gerber, Karpanty, & Randrianantenaina, 2012b). Otherwise, no large impacts were observed due to changes in vegetation structure near the forest edge alone.

Invasive predators alone also did not lead to significant negative effects contrasting findings in highly degraded and fragmented systems where invasive predators are prolific and result in significant reductions in native carnivore space use at forest edges and within interior forest (Wampole, Farris, & Gerber, 2021). Similar native-invasive associations were found between continuous and fragmented systems for fanaloka-dog, falanouc-cat, and fosa-dog (Farris *et al.*, 2015c). However, we found these associations were specific to certain forest edge conditions and did not influence native carnivore space use within interior forest. Importantly, how invasive predators were quantified influenced the degree of impact we observed on natives. Different but complementary results emerged by evaluating two scales of invasive predator pressure activity (trap success) and co-occurrence (presence/absence). For example, we found in continuous forest, fanaloka and falanouc only responded to the cats when their activity was high near villages. Likewise, falanouc occupied areas less when they co-occur with dogs, regardless of their activity level, only within high shrub forest edge. These findings suggest, free-roaming dogs and cats may themselves be considered an edge effect and interact with their surrounding environment (i.e. forest edge) in unique ways that shape species response differently than within interior forest (Lacerda, Tomas, & Marinho-Filho, 2009).

A review by Sévêque *et al.* (2020) found changes in carnivores resource partitioning (spatial, temporal, or trophic niche) are dependent on the type of human disturbance and how the landscape or availability of resources are affected. Differences between our findings and those of previous studies (Wampole, Gerber, Farris, 2021) support that the landscape in which dogs and cats interact with native carnivores matters. We found habitat degradation in fragmented forests with higher proportions of forest edge facilitated greater negative effects of invasive predators on native carnivores of Madagascar. However, continuous forest appears to buffer natives from strong negative effects under most conditions. Unfortunately, Madagascar has lost >50% of its natural forest cover, with only 66% of remaining forest classified as interior forest (Morelli *et al.*, 2020). Despite over 150 protected forests, few of these protected areas are within continuous intact forests, and most are experiencing increased fragmentation and encroachment from land conversion to agriculture to support increasing population growth. This has resulted in larger and more numerous human settlements abutting protected forest boundaries (IUCN, 2023).

We found human settlements (*village*) drove changes in carnivore space use more than examined vegetational forest edge effects. Villages are anthropogenic centers with high human activity, surrounding agriculture, frequent *tavy* (slash/burn agricultural practice), often contain free-ranging poultry, and free-roaming dogs and cats. Villages within our study were located at the forest edge and within interior forests (Fig. 1). We found two native carnivores (fanaloka, falanouc)

under conditions of low-moderate cat activity increased occupancy, or activity near villages. If euplerids are increasing proximity to villages to capitalize on alternative resources facilitated by human settlements, they could be more vulnerable to hunting or persecution (Golden, 2009), retaliatory killing if they target livestock (Merson *et al.*, 2019), and negative interactions with dogs/cats (Farris *et al.*, 2022). We found that carnivores did show reduced occupancy when high cat activity occurred near villages and divergent relationships with dogs (Fig. 6). Euplerids are small body carnivores, similar or smaller in size to the average domestic cat. Cats may present a risk as a competitor, while dogs as a predator or harasser, and if so would explain some of the variation in responses we observed. Although research on the impact of cats and dogs on Eupleridae is ongoing (Rivera *et al.*, 2022), studying the impact of villages is critical to understanding changes in Eupleridae ecology and the future of their conservation (Kshirsagar *et al.*, 2020).

Conservation implications

Our study found, fanaloka (*Fossa fossana*) and falanouc (*Eupleres goudotti*) emerged as one of most responsive species to examined pressures. Evaluating additive and interactive effects with consideration to invasive predator activity and co-occurrence led to greater understanding of the negative effects of invasive predators and forest edge effects on species space use. In our study, a singular approach would have misguided our understanding of the effects of invasive predator on native carnivores, highlighting the importance of evaluating both when considering interspecific effects. This will ultimately help guide conservation and help focus future work. We use the falanouc below as an example:

The falanouc is a unique species, featuring a long-protrusive pointed rostrum and thought to specialize on earth worms and insects (Goodman, 2022). However, their ecology is little known and previous research has found limited evidence to what influences their space use, beyond a negative correlation with degraded habitat in fragmented systems (Wampole, Farris, & Gerber, 2021). In our study, we had more detections of falanouc than any other previous surveys (Wampole, Farris, & Gerber, 2021) and found evidence of dynamic interactions with investigated pressures altering species space use. Based on our findings, falanouc may be at higher risk of negative interactions with dogs if both select for movement along established trails and avoid use of dense shrub. We also found falanouc occupancy and activity (*i.e.* detection) is higher near villages, with occupancy influenced by the amount of cat activity. Falanouc tolerated some degree of cat activity but appeared to alter spatio-temporal patterns in response to cats. Spatial–temporal changes include behaviorally mediated responses, such as reducing movement, avoiding trails or open spaces (e.g., where we place cameras) or choosing to not occupy a site (Farris *et al.*, 2020). We ultimately found evidence of both changes in falanouc activity and occupancy. Selection for areas near villages occurred conditional on limited pressure from invasives and indicated use of an alternative resource facilitated

by proximity to a village. Villages support large agricultural areas and may support greater or alternative prey availability from agricultural spillover (Rand, Tylianakis, & Tscharntke, 2006). Notably, important links between prey trap success (bird and small mammals), invasive predators, and native carnivores (falanouc, fanaloka) near villages have also been observed in fragmented forests (Farris *et al.*, 2015c). Together these findings suggest conservation efforts can have the greatest positive effect for falanouc by reducing cat activity near villages and focusing on excluding dogs from forest edge containing high shrub cover.

Conservation policy/practices that establish buffer zones (such as minimum of 500 m) between communities and protected forest edges for sustainable resource use would be impactful to mitigating pressures on species at park boundaries. To improve conditions for native carnivores, buffer zones would need to minimize changes in forest vegetation structure and use by invasive predators (dog presence/cat activity). Invasive predators could be minimized either through reducing free-roaming behavior of dogs and cats or decreasing abundance near villages. Free spay and neuter clinics are offered to communities surrounding protected areas in Madagascar and can help reduce propagule pressure from free-roaming dogs and cats if local communities/individual are willing to participate (see maddoginitiative.com). Ultimately, establishment of sustainable buffer zones for invasive predators would require support and joint partnerships from community leaders and park authorities to create equitable policy and program implementation (Budhathoki, 2004).

Conclusions

Global environmental change has introduced multiple and interacting pressures on species and challenges researchers with determining the primary drivers of declines (Didham *et al.*, 2007). We found that conservation actions should prioritize reducing pressures where they are jointly occurring, and of less concern is where they occur separately. Ultimately, a species' life history and ecology will influence the degree of plasticity and resilience to a given threat(s). Interspecific variation was evident in both the magnitude and direction of native carnivore responses to pressures and support the necessity of setting species-specific management actions. Our study highlights the importance of evaluating the extent to which interactions among pressures are occurring and considering the larger landscape in which threats are occurring (i.e. fragmented or continuous forest systems) in studies aimed at assessing species risk under multiple threats. Future multi-season research could be conducted to test how invasive predators' activity influences long-term native carnivore occupancy. However, it is clear that continued protection of large, intact continuous forest is essential for endemic carnivores of Madagascar.

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Author contributions

EW, ZF, and BG conceived the ideas and designed methodology; EW and PR collected the data; EW analyzed the data; EW led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

References

Balme, G.A., Slotow, R.O.B. & Hunter, L.T.B. (2010). Edge effects and the impact of non protected areas in carnivore conservation: leopards in the Phinda–Mkhuze Complex, South Africa. *Anim. Conserv.* **13**, 315–323.

Bartoń, K. (2020). MuMIn: Multi-model inference. R package version v.1.43.17.

Betts, M.G., Wolf, C., Pfeifer, M., Banks-Leite, C., Arroyo-Rodríguez, V., Ribeiro, D.B., Jos, B. et al. (2019). Extinction filters mediate the global effects of habitat fragmentation on animals. *Science* **366**, 1236–1239.

Brooke, Z.M., Bielby, J., Nambiar, K. & Carbone, C. (2014). Correlates of research effort in carnivores: body size, range size and diet matter. *PloS One* **9**, e93195.

Budhathoki, P. (2004). Linking communities with conservation in developing countries: buffer zone management initiatives in Nepal. *Oryx* **38**, 334–341.

Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference: a practical information-theoretic approach*, 2nd edn. New York: Springer.

Canfield, R.H. (1941). Application of the line interception method in sampling range vegetation. *Journal of Forestry* **39**, 388–394.

Caruso, N., Lucherini, M., Fortin, D. & Casanave, E.B. (2016). Species-specific responses of carnivores to human-induced landscape changes in Central Argentina. *PloS One* **11**, e0150488.

Di Minin, E., Slotow, R., Hunter, L.T., Montesino Pouzols, F., Toivonen, T., Verburg, P.H., Leader-Williams, N., Petracca, L. & Moilanen, A. (2016). Global priorities for national carnivore conservation under land use change. *Scientific reports* **6**(1), 23814.

Didham, R., Tylianakis, J., Gemmell, N., Rand, T. & Ewers, R. (2007). Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol. Evol.* **22**, 489–496.

Didham, R.K. & Lawton, J.H. (1999). Edge structure determines the magnitude of changes in microclimate and vegetation structure in tropical forest fragments. *Biotropica* **31**, 17–30.

Doherty, T.S., Dickman, C.R., Glen, A.S., Newsome, T.M., Nimmo, D.G., Ritchie, E.G., Vanak, A.T. & Wirsing, A.J. (2017). The global impacts of domestic dogs on threatened vertebrates. *Biol. Conserv.* **210**, 56–59.

Doherty, T.S., Dickman, C.R., Nimmo, D.G. & Ritchie, E.G. (2015). Multiple threats, or multiplying the threats? Interactions between invasive predators and other ecological disturbances. *Biol. Conserv.* **190**, 60–68.

Doherty, T.S., Glen, A.S., Nimmo, D.G., Ritchie, E.G. & Dickman, C.R. (2016). Invasive predators and global biodiversity loss. *Proc. Natl. Acad. Sci. USA* **113**, 11261–11265.

ESRI. (2011). *ArcGIS desktop: release 10*. Redlands: Environmental Systems Research Institute.

Farris, Z.J., Boone, H.M., Karpanty, S., Murphy, A., Ratelolahy, F., Andrianjakarivelo, V. & Kelly, M.J. (2016). Feral cats and the fitoaty: first population assessment of the black forest cat in Madagascar's rainforests. *J. Mammal.* **97**, 518–525.

Farris, Z.J., Gerber, B.D., Karpanty, S., Murphy, A., Andrianjakarivelo, V., Ratelolahy, F. & Kelly, M.J. (2015a). When carnivores roam: temporal patterns and overlap among Madagascar's native and exotic carnivores: activity patterns of Madagascar's carnivore community. *J. Zool.* **296**, 45–57.

Farris, Z.J., Gerber, B.D., Karpanty, S., Murphy, A., Wampole, E., Ratelolahy, F. & Kelly, M.J. (2020). Exploring and interpreting spatiotemporal interactions between native and invasive carnivores across a gradient of rainforest degradation. *Biol. Invasions* **22**, 2033–2047.

Farris, Z.J., Gerber, B.D., Karpanty, S., Ratelolahy, F., Andrianjakarivelo, V. & Kelly, M.J. (2022). Spatio-temporal overlap between a native and an exotic carnivore in Madagascar: evidence of spatial exclusion. *Small Carnivores: Evolution, Ecology, Behaviour, and Conservation*, **1**, 259–274.

Farris, Z.J., Gerber, B.D., Valenta, K., Rafaliarison, R., Razafimahaimodison, J.C., Larney, E., Rajaonarivelo, T., Randriana, Z., Wright, P.C. & Chapman, C.A. (2017b). Threats to a rainforest carnivore community: a multi-year assessment of occupancy and co-occurrence in Madagascar. *Biol. Conserv.* **210**, 116–124.

Farris, Z.J., Golden, C.D., Karpanty, S., Murphy, A., Stauffer, D., Ratelolahy, F., Andrianjakarivelo, V., Holmes, C.M. & Kelly, M.J. (2015c). Hunting, exotic carnivores, and habitat loss: anthropogenic effects on a native carnivore community, Madagascar. *PLoS One* **10**, e0136456.

Farris, Z.J., Kelly, M.J., Karpanty, S., Murphy, A., Ratelolahy, F., Andrianjakarivelo, V. & Holmes, C. (2017a). The times they are a changin': multi-year surveys reveal exotics replace native carnivores at a Madagascar rainforest site. *Biol. Conserv.* **206**, 320–328.

Farris, Z.J., Kelly, M.J., Karpanty, S. & Ratelolahy, F. (2015*b*). Patterns of space co-occurrence among native and exotic carnivores in North-Eastern Madagascar. *Anim. Conserv.* **19**, 189–198.

Fiske, I. & Chandler, R. (2011). Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *J. Stat. Softw.* **43**, 1–23.

Freitas, S.R., Mello, M.C. & Cruz, C.B. (2005). Relationships between forest structure and vegetation indices in Atlantic rainforest. *For. Ecol. Manage.* **218**, 353–362.

Galipaud, M., Gillingham, M.A.F. & Dechaume-Moncharmont, F. (2017). A farewell to the sum of Akaike weights: the benefits of alternative metrics for variable importance estimations in model selection. *Methods Ecol. Evol.* **8**, 1668–1678.

Gerber, B.D., Karpanty, S.M. & Randrianantenaina, J. (2012*a*). Activity patterns of carnivores in the rain forests of Madagascar: implications for species coexistence. *J. Mammal.* **93**, 667–676.

Gerber, B.D., Karpanty, S.M. & Randrianantenaina, J. (2012*b*). The impact of forest logging and fragmentation on carnivore species composition, density and occupancy in Madagascar's rainforests. *Oryx* **46**, 414–422.

Golden, C.D. (2009). Bushmeat hunting and use in the Makira Forest, North-Eastern Madagascar: a conservation and livelihoods issue. *Oryx* **43**, 386–392.

Gompper, M.E. (2014). *Free-roaming dogs and wildlife conservation (Ed)*. Oxford: Oxford University Press.

Goodman, S.M. (2022). *The new natural history of Madagascar.* Oxford, England: Princeton University Press.

Haddad, N.M., Brudvig, L.A., Clobert, J., Davies, K.F., Gonzalez, A., Holt, R.D., Lovejoy, T.E., Sexton, J.O., Austin, M.P., Collins, C.D., Cook, W.M., Damschen, E.I., Ewers, R.M., Foster, B.L., Jenkins, C.N., King, A.J., Laurance, W.F., Levey, D.J., Margules, C.R. & Townshend, J.R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci. Adv.* **1**, e1500052.

Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. & Esseen, P.A. (2005). Edge influence on Forest structure and composition in fragmented landscapes. *Conserv. Biol.* **19**, 768–782.

Hesselbarth, M.H.K., Sciaini, M., With, K.A., Wiegand, K. & Nowosad, J. (2019). Landscapemetrics: an open-source R tool to calculate landscape metrics Version 1.4.4. *Ecography* **42**, 1648–1657.

Hughes, J. & Macdonald, D.W. (2013). A review of the interactions between free-roaming domestic dogs and wildlife. *Biol. Conserv.* **157**, 341–351.

IUCN. (2023). The IUCN Red List of Threatened Species. http://www.iucnredlist.org/

Kier, G., Kreft, H., Lee, T.M., Jetz, W., Ibisch, P.L., Nowicki, C., Mutke, J. & Barthlott, W. (2009). A global assessment of endemism and species richness across Island and mainland regions. *Proc. Natl. Acad. Sci. USA* **106**, 9322–9327.

Kiffner, C., Stoner, C. & Caro, T. (2013). Edge effects and large mammal distributions in a national park. *Anim. Conserv.* **16**, 97–107.

Kshirsagar, A.R., Applebaum, J.W., Randriana, Z., Rajaonarivelo, T., Rafaliarison, R.R., Farris, Z.J. & Valenta, K. (2020). Human-dog relationships across communities surrounding ranomafana and Andasibe-Mantadia National Parks, Madagascar. *J. Ethnobiol.* **40**, 483–498.

Kuehl, A.K. & Clark, W.R. (2002). Predator activity related to landscape features in northern Iowa. *J. Wildl. Manag.* **66**, 1224–1234.

Lacerda, A.C., Tomas, W.M. & Marinho-Filho, J. (2009). Domestic dogs as an edge effect in the Brasília National Park, Brazil: interactions with native mammals. *Anim. Conserv.* **12**, 477–487.

Laurance, W.F. & Yensen, E. (1991). Predicting the impacts of edge effects in fragmented habitats. *Biol. Conserv.* **55**, 77–92.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology* **83**, 2248–2255.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L. & Hines, J.E. (2018). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*, 2nd edn. San Diego: Elsevier.

Magnago, L.F.S., Rocha, M.F., Meyer, L., Martins, S.V. & Meira-Neto, J.A.A. (2015). Microclimatic conditions at forest edges have significant impacts on vegetation structure in large Atlantic forest fragments. *Biodivers. Conserv.* **24**, 2305–2318.

McConnell, W.J., Sweeney, S.P. & Mulley, B. (2004). Physical and social access to land: spatio-temporal patterns of agricultural expansion in Madagascar. *Agr Ecosyst Environ* **101**, 171–184.

Medina, F.M., Bonnaud, E., Vidal, E., Tershy, B.R., Zavaleta, E.S., Josh Donlan, C., Keitt, B.S., Corre, M., Horwath, S.V. & Nogales, M. (2011). A global review of the impacts of invasive cats on Island endangered vertebrates. *Glob. Chang. Biol.* **17**, 3503–3510.

Merson, S.D., Dollar, L.J., Tan, C.K.W. & Macdonald, D.W. (2019). Effects of habitat alteration and disturbance by humans and exotic species on fosa *Cryptoprocta ferox* occupancy in Madagascar's deciduous forests. *Oryx* **54**, 828–836.

Morelli, T.L., Smith, A.B., Mancini, A.N., Balko, E.A., Borgerson, C., Dolch, R. & Baden, A.L. (2020). The fate of Madagascar's rainforest habitat. *Nat. Clim. Change* **10**, 89–96.

Murphy, A., Gerber, B.D., Farris, Z.J., Karpanty, S., Ratelolahy, F. & Kelly, M.J. (2018). Making the most of sparse data to estimate density of a rare and threatened

species: a case study with the fosa, a little-studied Malagasy carnivore. *Anim. Conserv.* **21**, 496–504.

Niedballa, J., Sollmann, R., Courtiol, A. & Wilting, A. (2016). camtrapR: an R package for efficient camera trap data management. *Methods Ecol. Evol.* **7**, 1457–1462.

Paschoal, A.M., Massara, R.L., Bailey, L.L., Doherty, P.F., Jr., Santos, P.M., Paglia, A.P. & Chiarello, A.G. (2018). Anthropogenic disturbances drive domestic dog use of Atlantic Forest protected areas. *Trop. Conserv. Sci.* **11**, 1940082918789833.

Paschoal, A.M., Massara, R.L., Bailey, L.L., Kendall, W.L., Doherty, P.F., Jr., Hirsch, A. & Paglia, A.P. (2016). Use of Atlantic Forest protected areas by free-ranging dogs: estimating abundance and persistence of use. *Ecosphere* **7**, e01480.

Pfeifer, M., Lefebvre, V., Peres, C.A., Banks-Leite, C., Wearn, O.R., Marsh, C.J., Butchart, S.H.M., Arroyo-Rodríguez, V., Barlow, J., Cerezo, A., Cisneros, L., D'Cruze, N., Faria, D., Hadley, A., Harris, S.M., Klingbeil, B.T., Kormann, U., Lens, L., Medina-Rangel, G.F. & Ewers, R.M. (2017). Creation of forest edges has a global impact on forest vertebrates. *Nature* **551**, 187–191.

R Core Team. (2020). *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. http://www.R-project.org/

Rand, T.A., Tylianakis, J.M. & Tscharntke, T. (2006). Spillover edge effects: the dispersal of agriculturally subsidized insect natural enemies into adjacent natural habitats. *Ecol. Lett.* **9**, 603–614.

Recio, M.R., Mathieu, R., Virgós, E. & Seddon, P.J. (2014). Quantifying fine-scale resource selection by introduced feral cats to complement management decision-making in ecologically sensitive areas. *Biol. Invasions* **16**, 1915–1927.

Revilla, E., Palomares, F. & Delibes, M. (2001). Edge-core effects and the effectiveness of traditional reserves in conservation: Eurasian badgers in Doñana National Park. *Conserv. Biol.* **15**, 148–158.

Ribeiro, F.S., Nichols, E., Morato, R.G., Metzger, J.P. & Pardini, R. (2019). Disturbance or propagule pressure? Unravelling the drivers and mapping the intensity of invasion of free-ranging dogs across the Atlantic forest hotspot. *Divers. Distrib.* **25**, 191–204.

Rivera, K., Fidino, M., Farris, Z.J., Magle, S.B., Murphy, A. & Gerber, B.D. (2022). Rethinking habitat occupancy modeling and the role of diel activity in an anthropogenic world. *Am. Nat.* **200**, 556–570.

Ross, P.H., Patel, E., Ferguson, B., Ravelijaona, R.N., Raoloniana, G.I., Wampole, E. & Farris, Z.J. (2020). Assessment of the threatened carnivore community in the recently expanded rainforest protected area Anjanaharibe-Sud Special Reserve, Madagascar. *Endanger. Species Res.* **43**, 89–98.

Rota, C.T., Ferreira, M.A., Kays, R.W., Forrester, T.D., Kalies, E.L., McShea, W.J., Parsons, A.W. & Millspaugh, J.J.

(2016). A multispecies occupancy model for two or more interacting species. *Methods Ecol. Evol.* **7**, 1164–1173.

Sepúlveda, M., Pelican, K., Cross, P., Eguren, A. & Singer, R. (2015). Fine-scale movements of rural free-roaming dogs in conservation areas in the temperate rainforest of the coastal range of southern Chile. *Mammal. Biol.* **80**, 290–297.

Sévêque, A., Gentle, L.K., López-Bao, J.V., Yarnell, R.W. & Uzal, A. (2020). Human disturbance has contrasting effects on niche partitioning within carnivore communities. *Biol. Rev.* **95**, 1689–1705.

Silva-Rodriguez, E.A., Ortega-Solis, G.R. & Jimenez, J.E. (2010). Conservation and ecological implications of the use of space by chilla foxes and free-roaming dogs in a human-dominated landscape in southern Chile. *Austral Ecol.* **35**, 765–777.

Stanton, R.A., Jr., Boone, W.W., IV, Soto-Shoender, J., Fletcher, R., Jr., Blaum, N. & McCleery, R.A. (2018). Shrub encroachment and vertebrate diversity: a global meta-analysis. *Glob. Ecol. Biogeogr.* **27**, 368–379.

Taubert, F., Fischer, R., Groeneveld, J., Lehmann, S., Müller, M.S., Rödig, E., Wiegand, T. & Huth, A. (2018). Global patterns of tropical forest fragmentation. *Nature* **554**, 519–522.

Tilman, D., Clark, M., Williams, D.R., Kimmel, K., Polasky, S. & Packer, C. (2017). Future threats to biodiversity and pathways to their prevention. *Nature* **546**, 73–81.

Torres-Romero, E.J. & Giordano, A.J. (2022). Impact of the Anthropocene on the status of the world's small carnivores: a global macroecological perspective. *J. Biogeogr.* **49**(5), 916–929.

Vanak, A.T. & Gompper, M.E. (2010). Interference competition at the landscape level: the effect of free-roaming dogs on a native mesocarnivore: interference competition between dogs and foxes. *J. Appl. Ecol.* **47**, 1225–1232.

Wampole, E.M., Farris, Z.J. & Gerber, B.D. (2021). A synthesis of life-history traits, functional traits, and consequences of anthropogenic pressures on Madagascar's threatened carnivores, Eupleridae. *Mamm. Rev.* **51**(3), 402–419.

Whitworth, A., Beirne, C., Pillco Huarcaya, R., Whittaker, L., Serrano Rojas, S.J., Tobler, M.W. & MacLeod, R. (2019). Human disturbance impacts on rainforest mammals are most notable in the canopy, especially for larger-bodied species. *Divers. Distrib.* **25**, 1166–1178.

Woodroffe, R. & Ginsberg, J.R. (1998). Edge effects and the extinction of populations inside protected areas. *Science* **280**, 2126–2128.

Wyza, E., Dollar, L., Rahajanirina, L.P., Popescu, V. & Stevens, N.J. (2020). Space dynamics and activity patterns of the fosa *Cryptoprocta ferox* in Ankarafantsika National Park, Madagascar: carnivores navigating a human-influenced landscape. *Oryx* **54**, 837–846.

Young, J.K., Olson, K.A., Reading, R.P., Amgalanbaatar, S. & Berger, J. (2011). Is wildlife going to the dogs? Impacts of feral and free-roaming dogs on wildlife populations. *Bioscience* **61**, 125–132.

Supporting information

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

Appendix S1. Covariate correlation tests.

Appendix S2. Single and multi-species model list.
Appendix S3. Model average coefficient table (SSOM).
Appendix S4. Detection distributions of invasive carnivores.