










LETTER

Mesopredators in forest edges

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Abstract

Fragments and edges account for most remaining forest habitats globally. Apex predators and megaherbivores often decline in these degraded habitats while smaller generalist omnivores can persist or thrive in forest edges, especially if they can utilize nonnative resources (“cross-boundary food subsidies”). Outcomes for small-medium carnivores (mesopredators) remain unclear or idiosyncratic. We tested responses of a widespread and common forest mesopredator to edges and the composition of the adjacent nonforested areas using 91 camera trapping surveys in Southeast Asia. Leopard cats (*Prionailurus bengalensis* and *Prionailurus javanensis*) showed a hump-shaped relationship with forest cover and a positive association with oil palm plantations, but they did not increase near other types of nonnative land cover. Leopard cats' success in edges appears due to their hunting abundant rodent prey inside oil palm plantations, providing natural pest management for farmers. Abundant leopard cats also hunt and suppress native small vertebrates, which may trigger negative ecological cascades and suppress biodiversity in forest edges.

KEYWORDS

camera trapping, carnivore, deforestation, felid, leopard cat, mesopredator release, oil palm, pest control, *Prionailurus bengalensis*, wildlife conservation

INTRODUCTION

Land use change incurs direct effects (i.e., less habitat) and indirect effects (i.e., fragmented and edge habitats) on the wildlife in remaining natural habitats (Haddad et al., 2015). For example, fragmentation is associated with altered biodiversity, species interactions, and ecosystem function at the local, regional, and global scale (Haddad et al., 2015). Forest edges—defined here as native tree

cover that abuts nonforested and human-disturbed areas such as clearcuts or agriculture—abound where there is fragmentation and even at the borders of large protected areas. Wildlife communities in forest edges are influenced by the altered biophysical habitat conditions and hunting (Benítez-López et al., 2017), but not always in consistent or predictable ways. For example, forest megafauna show a variety of responses to edges (Amir, Moore, et al., 2022; Carr et al., 2023) while interior forest specialists

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consistently decline (Presley et al., 2019) and ecotone-specialists and generalists increase (Filgueiras et al., 2021; Moore et al., 2022). Edge responses remain unknown for the vast majority of wildlife species.

Wildlife can benefit from edges via favorable abiotic conditions (e.g., microclimate) and biotic conditions (e.g., more open understory or different plant species composition) that suit their ecology (Filgueiras et al., 2021; Luskin & Potts, 2011). Forest edges can also improve foraging conditions (e.g., availability of preferred natural foods or hunting conditions; Honda et al., 2023) and edges near humans and agriculture provide opportunities for crop raiding, garbage scavenging, or other cross-boundary food subsidies (Luskin, Brashares, et al., 2017; Oro et al., 2013). Finally, the loss of large herbivores and apex predators from fragments and hunting of game species in forest edges could also benefit smaller animals by reducing predation and competition (e.g., the mesopredator release hypothesis; Benítez-López et al. 2017). However, wildlife that proliferates in forest edges can negatively impact more sensitive plant and animal species. For example, mesopredators cause heightened bird nest predation (Prugh et al., 2009), and negative impacts on people such as zoonotic disease risks (Gibb et al., 2020; Luskin et al., 2023) and livestock and crop damage (Luskin et al., 2014; Taylor et al., 2016). Therefore, a key question in contemporary applied ecology and conservation is quantifying wildlife responses to edges (Moore et al., 2022).

Many mesopredators are habitat generalists that tolerate edge conditions and experience release from competition and persecution where larger carnivores decline (Newsome et al., 2015). Medium-sized carnivorous mesopredators can be further supported in edges where they access food subsidies via depredating small domestic animals like goats and chickens (Newsome et al., 2015). However, the responses of smaller mesopredators to edges are often species- and context-dependent (Crooks, 2002). For example, in South America, two small felids, the oncilla (*Leopardus tigrinus*) and margay (*L. wiedii*), show increases in habitat use in some disturbed habitats (de Oliveira et al., 2010) and declines in others (Nagy-Reis et al., 2017). Edge responses remain unknown for most mesopredators, limiting inferences on wildlife ecology and conservation and humans.

Southeast Asia suffers high rates of forest loss, edge creation, and biodiversity declines (Brodie et al., 2023; Wilcove et al., 2013). With over 70% of Southeast Asia's remaining forest lying within 1 km of an edge (Haddad et al., 2015), understanding how wildlife communities change in edges is crucial in the region. Preliminary work suggests dramatic shifts in wildlife community composition in Asian forest edges, with a decline of apex predators (Luskin, Albert, et al., 2017) and particularly high abundances of crop-raiding omnivores (e.g., pigs and macaques), which in turn disturb plant communities (Luskin, Brashares, et al., 2017; Luskin et al., 2019, 2021). High densities of other small mammals have also been reported from forest edges in the region (Moore et al., 2022), potentially providing an abundant food source for adaptable carnivorous mesopredators (Holzner et al., 2019). In comparison to larger charismatic species and compared to other regions globally, Southeast Asian mesopredators have received relatively little research attention.

Practitioner points

- The rise of native mesopredators in forest edges provides pest control ecosystem services by regulating rodent proliferation in cultivated lands and natural forest edges, benefiting people and conservation.
- Native mesopredators can be managed by farmers (e.g., oil palm plantation managers) through the retention of natural forest patches and the selective cultivation of preferred microhabitats (e.g., shade trees and understory vegetation).
- Abundant mesopredators may impose unnaturally high predation pressure on small native vertebrate species and undermine conservation in forest edges.
- The trade-offs associated with mesopredators in forest edges can be elucidated through mesopredator diet studies spanning different habitats.

We assessed the responses of Southeast Asia's most widespread mesopredator to forest edges, the leopard cat (*Prionailurus bengalensis* and *Prionailurus javanensis*). Leopard cats are common and broadly distributed, but their ecology and behavior remain poorly understood, primarily due to their cryptic nocturnal and semiarboreal behavior. This challenge has been partially overcome with advances in camera trap technology (Zainalabidin et al., 2020). Leopard cats have been reported in disturbed forests and edges (Chua et al., 2016; Mohamed et al., 2013; Rajaratnam et al., 2007) and have been observed in and around oil palm plantations and other tree crops where they hunt rodents (Chua et al., 2016; Rajaratnam et al., 2007; Wood & Liau, 1984). A key question is whether leopard cats merely persist near forest edges and oil palm plantations or if they increase in these degraded areas (Hood et al., 2019). Leopard cat responses to forest degradation and the availability of nonforest resources could fundamentally differ across spatial scales as they adjust their movements and home range sizes (Hansen et al., 2020; Thornton et al., 2011). For example, high total forest cover in the landscape can support viable populations while movement and habitat use within a landscape is driven by localized conditions (e.g., specific sites most suitable for hunting, safely resting, or breeding; Hood et al., 2019). Thus, we tested our hypotheses using a multiscale approach, examining the drivers of leopard cat relative abundance using occurrence datasets and covariates that described regional, landscape, and local conditions.

We synthesized camera trapping from across Southeast Asia to examine leopard cat habitat associations. Leopard cats generally require some intact forests to hunt, rest, or breed (Ross et al., 2015) and thus our hypotheses and sampling focus on conditions in forests while they may occasionally utilize other non-forest habitats for foraging or dispersing. We tested four competing hypotheses about

leopard cat habitat associations and functional relationship to forest edges:

1. Leopard cats have a nonsignificant relationship with forest cover (“persistence hypothesis”)
2. Leopard cats have a negative relationship with forest cover (“edge preference hypothesis”)
3. Leopard cats have a hump-shaped relationship with forest cover (“intermediate disturbance hypothesis”)
4. Leopard cats have a positive relationship with forest edges *only* when there is also oil palm, since they are known to hunt rodents in oil palm plantations (“cross-boundary food subsidy hypothesis”).

We evaluated our hypotheses at three spatial scales, which allowed for three additional hypotheses about the influence of scale in determining which factors shape mesopredator populations:

5. Climate and biogeographic factors would be most important for regional occurrence patterns (across all Southeast Asia)
6. Forest cover would be the most important at the landscape spatial scale (i.e., variation in detections among landscapes)
7. Oil palm would be most important at the local spatial scale (i.e., variation in abundance within a landscape).

To match the regional, landscape, and local spatial scale of our hypotheses, we used three separate data sets and corresponding analytical approaches. At the regional scale, we assessed the covariates and mapped the probability of presence using MaxEnt species distribution model (SDM) with presence-only data ($n = 451$ occurrences). To contribute to the species' IUCN Red List threat assessment, we also update their “extent of occurrence” within remaining forest cover and in protected areas. At the intermediate spatial scale, we assessed variation *among landscapes* based on the detection rates reported in published camera trapping ($n = 91$ studies from 42 landscapes). At the local scale, we assessed variation *within landscapes* based on predicted abundance from hierarchical modeling (drawing on detection histories from 20 camera trapping surveys at 10 landscapes).

METHODS

Study area and species description

We focused our study on tropical rainforests and mixed-evergreen forests, including most of Myanmar, Thailand, Cambodia, Lao PDR, Peninsular Malaysia, and Indonesia (Sumatra, Borneo, and Java). Recent molecular studies suggest leopard cats on the mainland (*P. bengalensis*) and Sunda islands (*P. javanensis*) are two distinct species (Kitchener et al., 2017). However, we analyzed them together due to their similarities in ecology and physical traits. Leopard cats weigh 1–5 kg in Southeast Asia (Castelló, 2020; Sunquist & Sunquist, 2014) and are generally considered nocturnal or crepuscular (Azlan & Sharma, 2006; Chen et al., 2016; Grassman, 2000; Mohamed et al., 2013; Smith et al.,

2010). Their diet mainly consists of rodents, especially in the Muridae family, but also includes birds, insects, and other small animals (Bashir et al., 2014; Chuang, 2012; Kamler et al., 2020; Rajaratnam et al., 2007; Shehzad et al., 2012; Sunquist & Sunquist, 2017).

Approach to multiscale habitat associations

We assessed habitat associations at three spatial scales utilizing three different statistical approaches. For our regional-scale analysis, we used MaxEnt SDM with presence-only localities. We refer to SDM as regional analysis since SDMs are ideal for establishing biogeographic habitat associations. We included abiotic variables (elevation and rainfall) and habitat covariates such as forest cover and oil palm that specifically address our hypotheses. We built SDMs and compared the importance of explanatory layers using MaxEnt and the jackknife analysis (all at 1 km resolution) (Chamberlain et al., 2022).

For our landscape-scale analysis, we examined *among-landscape* variation in detections from published camera surveys using generalized linear mixed models (GLMMs). We included covariates describing the area within a 20 km radius of the centroid of each of our focal landscapes using zonal statistics (% of each landcover type within a defined radius).

For our local-scale analyses, we examined *within-landscape* relative abundance using detection histories from new camera trapping, analyzed with a Royal–Nichols (RN) hierarchical abundance model (Royle & Nichols, 2003). We derived covariates describing the area within a 1 km radius of each camera using zonal statistics.

We consider the effect of edges on leopard cats using an index inversely proportional to the percentage of forest cover (Haddad et al., 2015). We also used the Human Footprint Index (Venter et al., 2016), which is a globally consistent GIS layer incorporating human population and infrastructure (scaled from 0 to 100) and the Forest Landscape Integrity Index (Grantham et al., 2020; hereafter just “forest integrity”), which is a globally consistent GIS layer that scores forest condition based on both observed degradation (e.g., logging) and inferred degradation (e.g., edges and habitat connectivity; scaled from 0 to 10). Within occupied landscapes, broad abiotic factors are less likely to drive abundance so we did not include rainfall in our GLMMs or RN models.

Presence-only data collation for regional habitat associations

We collated leopard cat presences from citizen scientists, museum collections, and published literature. We first searched the Global Biodiversity Information Facility (GBIF) repository for presence-only observations which includes museum collections and citizen-science data (Chamberlain et al., 2022). We supplemented this with the Borneo Carnivore Database (Rustam et al., 2016), a collection of presence-only observations of carnivores on Borneo. We also include records from published and new camera trapping (described below). We disregarded

observations over 20 years old and those without geo-referenced information. There have been substantial landcover changes in the past two decades and thus some forest observations could now appear as located in nonforest habitat in the more recently derived spatial layers used in the MaxEnt analysis, and this would bias results towards showing preferences for nonforest habitats.

MaxEnt SDM for regional habitat associations

We built a SDM using MaxEnt, a presence-only machine learning algorithm that is used to predict species occurrence over broad areas (version 3.4.4). We included rainfall, forest integrity, elevation, human footprint, forest cover, and oil palm cover as predictors in the model. We evaluated model performance using receiver operating characteristic (ROC) analysis, setting aside 15% of the data. We report the jackknife training gain test results to show the relative contribution of each predictor variable to the model. Using the model output, we mapped the predicted habitat suitability across the leopard cat range.

Leopard cat breeding success and long-term fitness have generally been associated with forests (Ross et al., 2015) and where nonforest habitats are present, appear to only use these habitats to forage at night (Chen et al., 2016; Choi et al., 2012; Grassman, 2000; Silmi et al., 2021). We therefore also show the MaxEnt SDM output clipped to within forested areas only. We extracted leopard cats' Southeast Asian range using the 2015 IUCN Red List EOO shapefile and updated the regional "extent of occurrence" (EOO) with the area of remaining forest cover as of 2015 (Miettinen et al., 2016). We calculated the protected area within leopard cats' Southeast Asian range using the IUCN World Database on Protected Areas (UNEP-WCMC and IUCN, 2021).

Collating camera trap detections for landscape-level habitat associations

We compiled leopard cat counts from published camera trap studies by searching Web of Science for: camera trap* AND Asia* or Thai* or Malaysia* or Indonesia* or Singapore* or Borneo* or Cambodia* or Vietnam* or Lao* or Myanmar* or Burm* or Sumatra* or Borneo*. We selected studies written in English and reporting sampling effort (number of cameras, and deployment length or total trap nights), and number of independent detections (requiring a 30–60-min interval between detections of the same species, referred to as "independence period"). We examined the references listed in key papers to identify and include further sources. We discarded camera trapping studies that did not use the standard approach in the region of unbaited cameras placed on wildlife trails on trees 0.2–0.4 m above the ground (Rovero & Ahumada, 2017). This deployment approach maximizes the detection of the majority of terrestrial and semi-terrestrial species over 1 kg (Rovero & Ahumada, 2017). We recorded the location (landscape name and coordinates), number of independent detections, and sampling effort (trap nights) for each study. We did not have access

to camera-level detection histories so each study was grouped into one 1256 km² sampling unit. We grouped multiple studies from the same landscape per year by summing detections and effort among the studies and averaging the covariate values. We defined a landscape as a national park or forest fragment such that the centroids of independent landscapes were at least 40 km apart.

GLMMs for assessing landscape-level habitat associations

To test our hypotheses about how forest cover and oil palm influence leopard cat relative abundance, we used GLMMs to assess variation in leopard cat detections among camera trap studies from different landscapes. Regressing the continuous relative abundance index (RAI or photos per 100 trap nights) showed poor model fit due to minor levels of zero inflation and overdispersion. Therefore, we used independent counts as the response variable, which is compatible with more accommodating distributions, and in our case, the negative binomial outperformed zero-inflated Poisson (Dunn et al., 2022). We included a fixed continuous term to control for study effort (measured in trap nights)—instead of including effort as a linear offset—to use model selection to assess the right functional relationship (e.g., to include effort as linear, logged, or square root). We included a random categorical term for the landscape because some landscapes were surveyed in multiple years. We note that this regression approach does not account for variation in detection probability and does not reflect absolute or true abundance (Sollmann et al., 2013). Therefore, in this analysis, we are implicitly assuming that detection probability among our rainforest camera traps does not vary and acknowledge this may introduce measurement error. We also acknowledge that there is unexplained variation in detectability owing to slight differences in equipment, deployment, and data curation methodologies. This measurement error reduces the likelihood of detecting true relationships should they exist (type II error or "false-negative").

The landscape-level analysis tests how the relative proportion of forest and land use (e.g., oil palm) influence leopard cat abundance in the landscape (detections summed across all cameras used in a study), while the local-scale analysis focuses on the influence of edges with new cameras specifically placed near and far from edges (described in the following sections) on leopard cat habitat use. The importance of landscape-scale effects (e.g., forest area, isolation) and the type of nonforest habitat of surrounding natural areas have been shown for numerous mammals in numerous settings (Prugh et al., 2008).

We included forest and disturbance covariates to test our hypotheses, which we derived from GIS layers covering the circular area within a 20 km radius (1256 km²) around the centroid of each study landscape. We used a 20-km radius to accommodate large camera trapping grids and low precision of locating the exact centroid in some studies. Covariate distributions are presented in the Supporting Information (Figure S1). We tested for linear and nonlinear effects for covariable, the latter by adding quadratic terms. We also constructed

additive and interactive models for each uncorrelated pair of variables (Pearson's coefficient < 0.50). We implemented conditional Akaike information criteria (cAIC) for model selection. We considered models within two cAIC units of the top model as competing. We inspected the estimated β coefficients from the top model(s) and if the 95% CI for the β coefficient crossed 0, we did not consider the variable informative. We ran our models using the package *lme4* in R (version 4.0.4).

Detection histories for hierarchical models (new camera trapping)

We conducted 20 new camera trapping sessions in 10 arrays in tropical forests in Thailand, Peninsular Malaysia, Sumatra, Borneo, and Singapore between December 2013 and June 2020. We deployed 18–78 passive infrared Bushnell and Reconyx camera traps across sampling areas ranging from 10 to 813 km² (Figure 2). We standardized deployment methods across arrays (see Supporting Information, Table S1 for forest characteristics, description of study sites, camera deployments, and data preparation). Cameras were spaced >500 m apart in large forests (>50 km²) and 100–500 m apart in smaller fragments, such as in Singapore. We attached cameras to trees 0.3 m above ground along hiking trails or natural wildlife trails and deployed cameras for 60–90 days. This short deployment period inhibited testing for variation in detections within years (e.g., seasonality). We considered detections of the same species independent if they occurred at least 30 min apart.

Hierarchical abundance models to assess local-scale habitat associations

We assessed the effect of habitat variables on leopard cat relative abundance at the local scale (within landscapes) using single-season, single-species hierarchical abundance

models described by Royle and Nichols (RN; 2003) implemented in *unmarked* (Fiske & Chandler, 2011; Gilbert et al., 2021). The RN model relates occupancy and detection probability to the number of individuals available at each site, while accounting for imperfect detection. RN models are particularly useful for describing how the relative abundance or occurrence of a species varies relative to environmental covariates (Gilbert et al., 2021). To satisfy the requirement of spatial independence of our camera traps, we resampled the data into 3.45 km² hexagonal grid cells, defined as our sampling units, and chosen to be larger than the leopard cat home range size of 1–3-km² in tropical forests and oil palm (Choi et al., 2012; Grassman, 2000; Silmi et al., 2021). We averaged the covariate values when multiple cameras fell within the same grid cell, and included sampling unit effort as a covariate in the detection formula. We used the first 90 days of captures from each grid cell and constructed a detection matrix (0 = leopard cat not detected; 1 = leopard cat detected; NA = inactive sampling unit or occasion). We included survey ID as a fixed effect in all our models to account for landscapes that were surveyed multiple times. We used AIC weight to identify the best model and considered models within 2 AIC units of the top model as competing models. We inspected the estimated β coefficients of each variable of the top model: if the 95% credible interval of the β coefficient crossed 0, we did not consider the variable informative. We differentiated generic “distance from edges” from oil palm edges by including both covariates in the model selection procedure.

RESULTS

Range and regional habitat associations

Leopard cats' IUCN Red List extent of occurrence (EOO) in Southeast Asia was 3,202,661 km², of which 1,158,584 km² (36.2%) was forested and 9.9% falls within protected and forested areas (Table 1).

TABLE 1 Leopard cat data sources and covariates.

Data type(s)	Regional	Landscape	Local	Source and/or description
GBIF presence-only	x			Global Biodiversity Information Facility (Chamberlain et al., 2022)
BCD presence-only	x			Borneo Carnivore Database (Ross et al., 2015)
Counts, presences, absences	x	x		Published camera trapping (totals per landscape)
Detection histories + all others	x	x	x	New camera trapping arrays (local)
Habitat variables				
Elevation	x			Continuous, SRTM Digital Elevation Model (Fick & Hijmans, 2017)
Rainfall	x			Continuous, mean annual rainfall (mm) (Takaku et al., 2018)
Forest cover	x	x	x	Continuous, percent forest cover (Miettinen et al., 2016)
Forest Integrity	x	x	x	Continuous (0–10), Forest Integrity Index (Grantham et al., 2020)
Oil palm	x	x	x	Continuous, % industrial plantations (Venter et al., 2016)
Human footprint	x	x	x	Continuous, Human Footprint Index (Venter et al., 2016)
Distance to edge			x	Continuous, distance to forest edge

Note: Regional analyses used MaxEnt SDM with presence-only data. Landscape-level analyses used GLMMs with independent detections as the response variable. Local-scale variation in relative abundance was estimated with RN hierarchical modeling using camera-level detection histories.

We gathered 451 geo-referenced occurrence records with 380 from GBIF, 127 from the Borneo Carnivore database, 71 from published studies (excluding 20 studies without detections), and 19 from new camera trapping sessions. There was good coverage across the tropical rainforest areas except for Myanmar, northern Lao PDR and Vietnam (Figure 1a). The MaxEnt SDM performance was effective at explaining the probability of occurrences (AUC for the ROC curve on test data = 0.79; Peterson et al., 2011). The variables containing the highest amount of information when used in isolation were rainfall, elevation, and forest integrity (Figure 1b). The relationships between the probability of presence and these top covariates were a positive hump-shaped effect of rainfall (peak presence at 2000 mm), a negative effect of elevation, and a positive hump-shaped effect from forest cover (Figure 2). There was an appearance of high probability of presence across the region when considering areas outside of forests where leopard cats forage at night, reflecting temporary nonforest habitat suitability for the species (Chen et al., 2016; Choi et al., 2012; Grassman, 2000; Silmi et al., 2021; Figure 1). Our interest here is in leopard cat ecology in natural forests where they act as mesopredators and are a part of the food web, and most research suggests their long-term fitness and breeding success is dependent on forests (Ross et al., 2015). Therefore, we also present results after applying a forest cover mask (Figure 1d) to refine the MaxEnt probability of

presence in remaining forests. This map shows relatively few “highly suitable” habitats centered on the lowlands in eastern Borneo, central Peninsular Malaysia, and Cambodia (Figure 1e). Readers interested in leopard cats outside of forested areas may prefer Figure 4c showing all terrestrial areas. The MaxEnt SDMs can also help fill gaps in published information available on the species such as in Myanmar.

Landscape-level habitat associations

We collated 91 camera trapping studies from 42 landscapes conducted at sites with predominantly tropical rainforest and where the leopard cat is known to occur. This represented a total effort of 507,114 trap nights, with leopard cat detections at 31 (73.8%) landscapes and in 71 (76.5%) studies. The best landscape-level glmm included a nonlinear hump-shaped relationship with forest cover and a positive relationship with oil palm cover (Table 2 and Figure 2e,f).

Local-scale habitat associations

We obtained 286 independent captures from the 20 new camera trap arrays in 10 landscapes (1218

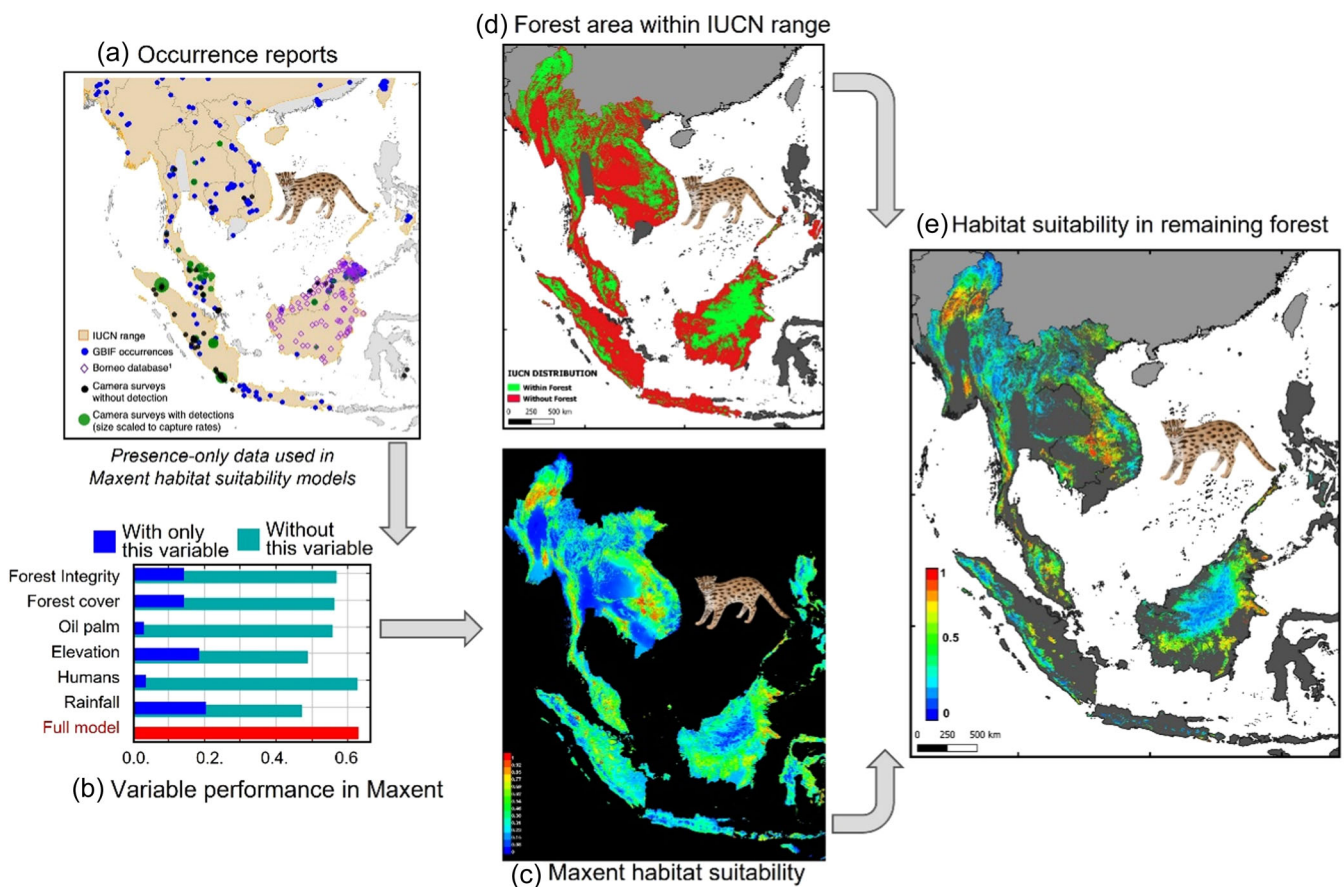


FIGURE 1 Leopard cat range and probability of presence in Southeast Asia, updated with contemporary occurrence records and forest cover data. (a) Extent of Occurrence “EOO” (shaded area) and the location of occurrence records, colored by data source (red points are observations out of the species range). (b) Jackknife graph of variable performance in the MaxEnt SDM using the regularized training gain. (c) Probability of presence throughout Southeast Asia, including non-forested areas. (d) Forest cover within the species range as of 2015. (e) Predicted probability of presence within remaining forests.

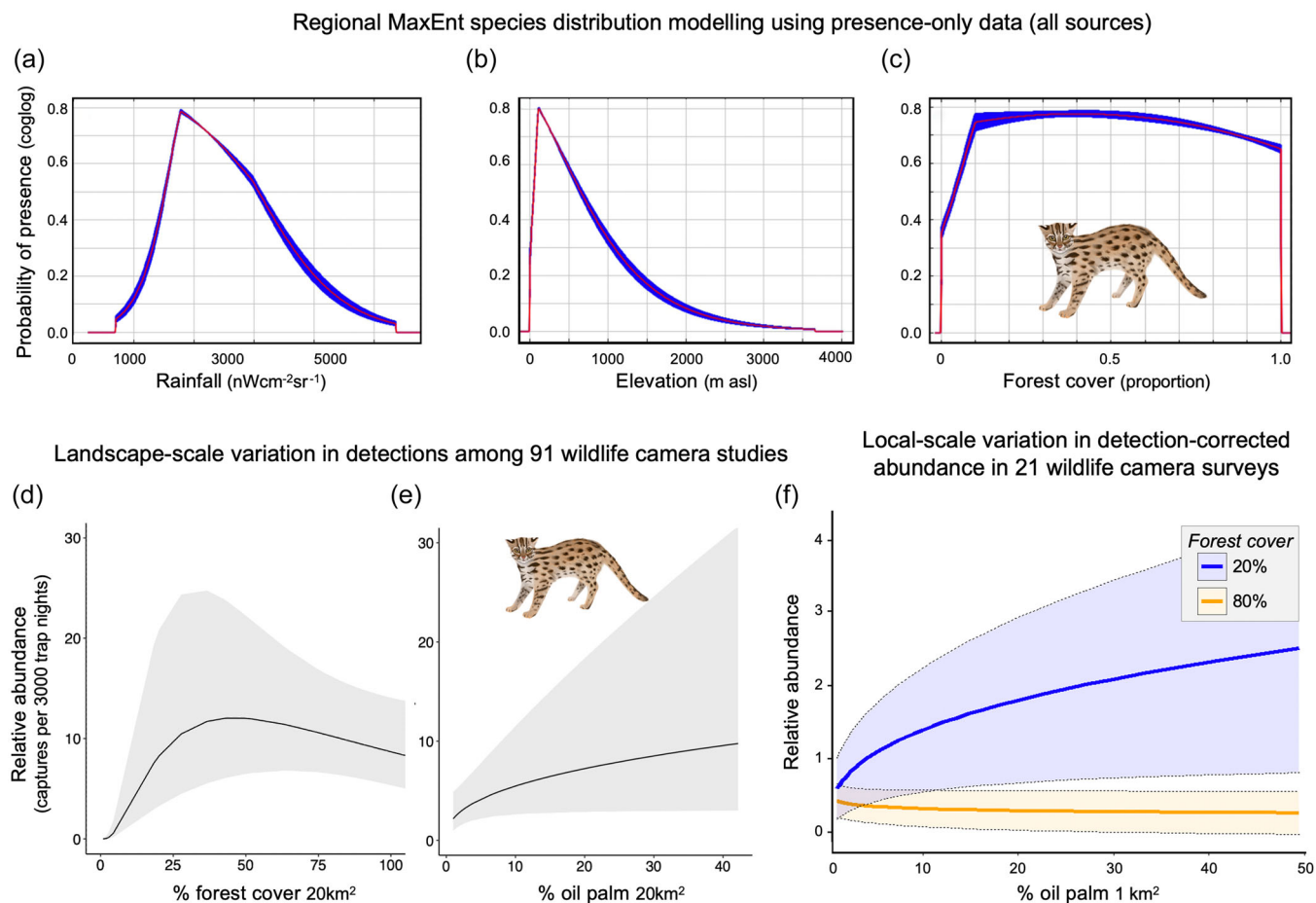


FIGURE 2 Habitat associations of leopard cats, assessed at different scales. (a–c) MaxEnt SDM relationships between habitat variables and the probability of occurrence in Southeast Asian tropical rainforests. The variables are ordered by declining importance from the Jackknife test (from left to right). (d, e) Variation in leopard cat detections in 91 camera trap studies, scaled to captures per 3000 trap nights. The covariates were calculated as the percentage area within a 20 km radius of the study. (e–f) Results from the top models based on the AICc model selection included forest and oil palm as additive effects (Table 2). The trends for each variable are shown while holding the other variable constant at its median value. All shaded areas show 95% CI. (f) Predicting local variation (within landscapes) in detection-corrected leopard cat abundance (per 3.45 km² grid cell) using RN hierarchical abundance models.

cameras and 58,608 trap nights). Khao Yai National Park in Thailand had the highest capture rates (1.238 captures per 100 trap nights), the highest naïve occupancy, and detection-corrected RN relative abundance among new camera trapping sessions (detected at 48% of all cameras; Supporting Information, Table S2). Leopard cats were rarely captured in rainforest interiors >2 km from a forest edge or in Singapore despite other disturbance-tolerant species recovering (Lamperty et al., 2023; Nursamsi et al., 2023). The RN model selection showed little support for the generic “distance to edge” covariate and strong support that leopard cats are more abundant near oil palm (Table 2). The best RN hierarchical abundance model included a positive effect from both forest cover and oil palm, with an interaction between forest cover and oil palm suggesting contingency (Table 2). Namely, detection-corrected leopard cat abundance increased with increasing oil palm cover in areas with low forest cover but was largely unaffected by oil palm in areas with high forest cover (Figure 2f).

DISCUSSION

Our results indicate that (i) abundances of a widespread forest-dwelling mesopredator were dependent on the adjacent nonforested landcover, (ii) there was a synergistic effect between habitat and food subsidies supporting a rise in mesopredators in forest edges, and (iii) mesopredator habitat associations were scale-dependent. Specifically, we found evidence that leopard cats are edge specialists in Southeast Asia and that their abundances are influenced by both forest cover and oil palm, the latter providing foraging subsidies because they eat rodents in plantations. First, leopard cat relative abundance showed a hump-shaped relationship with increasing forest cover suggesting they thrive where there is a mix of forest and nonforest cover, and we note their near-complete absence from interior forests (e.g., rarely detected where there was more than 80% forest cover within the 3.45 km² area around cameras; Figure 2g). They also showed a positive association with oil palm at the landscape and local scale. At the local scale (within

TABLE 2 Model selection results for linear mixed models (GLMMs, top section) and Royal–Nichols (RN, bottom section) hierarchical abundance models assessing variation in leopard cat independent abundance at a landscape and local scale, respectively.

Model	df	cAIC	Δ AIC	ω
GLMMs (variation among landscapes)				
Oil palm + Forest cover ²	7	507.56	0	0.33
Oil palm + Forest integrity ²	7	509.40	0.96	0.20
Forest integrity ²	6	509.76	1.83	0.13
Forest cover ²	6	509.81	2.20	0.11
Oil palm * Forest cover ²	8	509.91	2.34	0.10
Oil palm * Forest integrity ²	8	510.54	2.97	0.07
Oil palm + Forest integrity	6	513.84	6.27	0.01
Forest integrity	5	515.17	7.61	0.01
Human footprint	6	515.46	7.89	0.01
Oil palm	5	516.76	7.92	0.01
Oil palm + Human footprint	6	516.89	8.58	0
Oil palm ²	6	517.12	9.19	0
Oil palm + Human footprint ²	7	518.55	9.32	0
Reduced_null	4	522.00	11.80	0
RN models (local variation within landscapes)				
Oil palm * Forest cover	24	2918.02	0	1
Forest cover ²	23	2934.75	16.72	0
Forest cover	22	2935.27	17.24	0
Oil palm + Forest cover	23	2936.1	18.08	0
Human footprint + Forest cover	23	2936.53	18.5	0
Human footprint * Forest cover	24	2937.98	19.96	0
Oil palm	22	2938.42	20.4	0
Oil palm * Forest integrity	24	2938.81	20.79	0
Human footprint + Oil palm	23	2939.14	21.12	0
Oil palm + Distance to edge	23	2940.2	22.18	0
Oil palm + Forest integrity	23	2940.38	22.36	0
Nonlinear distance to edge	23	2941.24	23.22	0
Reduced_null	21	2941.25	23.23	0

Note: For RN models, the df column shows the number of parameters. The reduced_null models include an effort covariate and random effects to account for spatial pseudoreplication where there were multiple surveys at the same landscape. Elevation and other variables that performed worse than the null models are not shown. Quadratic relationships are denoted with superscripts, for example, Forest cover².

landscapes), there was an interaction between forest cover and oil palm wherein oil palm has a stronger positive effect where there are more edges (e.g., when there was <20% forest cover). The synergistic effect of oil palm and forest edges on leopard cats is important because these conditions co-occur throughout much of the region. For example, Malaysia has approximately 150,000 km² of forest edge and 70,000 km² of oil palm (Cheng et al., 2019). Taken together, leopard

cats are a common and widespread mesopredator that thrives in forest edges, especially in forest-oil palm habitat mosaics.

In terms of our hypotheses, leopard cats' hump-shaped relationship of relative abundance with forest cover supported the intermediate disturbance hypothesis (H3) over the persistence hypothesis (H1) or the edge preference hypothesis (H2). Leopard cats also had a positive relationship with oil palm where they are known to hunt rodents in oil palm plantations, supporting the cross-boundary food subsidy hypothesis (H4). For our spatial scales hypotheses, there was support for climate (rainfall) and biogeographic factors (elevation) being the most important factors explaining regional occurrence patterns (H5), while forest cover and oil palm were the most important at the landscape and local scales (H6 and H7).

These results contribute to understanding population trends through time and how their habitat associations differ across environmental gradients. For example, the regional results suggest leopard cats likely benefited from drier climates in the Holocene that created mixed forest-grassland mosaics in Southeast Asia (Amir, Moore, et al., 2022). Leopard cats likely became much rarer during the last few millennia, as wetter conditions prevailed, through until the 19th century. Then during the 20th and 21st centuries, leopard cats likely increased again with the combined effect of logging and oil palm expansion. In terms of modern environmental gradients, the habitat associations we describe are limited to areas with predominantly tropical rainforests where the preponderance of our sampling occurred. However, in predominantly dry evergreen and deciduous forests in northern Thailand and evergreen-deciduous mosaics in Cambodia, Petersen et al. (2019) and Pin et al. (2022) found that leopard cats had higher densities in intact than regenerating forests and in more evergreen than deciduous forests, respectively. When considering prior work in context with our MaxEnt SDMs, landscape- and local-scale analyses, leopard cats appear to show a regional preference for drier lowland habitats, including interior forests, while in rainforests they shift to being comparatively edge and disturbance specialists.

Mesopredators persisting in and around agriculture can provide pest control ecosystem services, such as leopard cats preying upon rodents in oil palm plantations (Chua et al., 2016; Hood et al., 2019; Silmi et al., 2021). Leopard cats thus join a group of other native generalist omnivores and mesopredators that directly or indirectly benefit from oil palm including macaques, wild pigs, and common palm civets in Asia (Dehaudt et al., 2022; Holzner et al., 2019; Luskin & Ke, 2017; Luskin, Brashares, et al., 2017) and crab-eating foxes (*Cerdocyon thous*) in South America (Pardo et al., 2021). Rodents reduce yields (Hood et al., 2019) and trigger declines in biodiversity (Moore et al., 2022), so leopard cat predation may provide comparable ecosystem services to rodent-eating macaques (Holzner et al., 2019). This rise in native mesopredators thus moderates rodent proliferation in anthropogenically disturbed areas and forest edges. At the same time, abundant mesopredators in forest edges can also impose

abnormally high predation on native species and undermine conservation (Prugh et al., 2009; Ritchie & Johnson, 2009). For example, Rajaratnam et al. (2007) recorded a diversity of native forest mammals consumed by leopard cats in oil palm and forest boundaries, including rodents that may not benefit from oil palm presence, and the Whitehead's spiny rat (*Maxomys whiteheadi*), which is Vulnerable to extinction. Hence, there may be a trade-off for oil palm managers and green certification schemes in terms of balancing the beneficial pest control from leopard cats versus the negative impact from leopard cat increased predation pressure on native vertebrates (Cazzolla Gatti et al., 2019; Laurance et al., 2010). These trade-offs can be partially navigated for leopard cats because their activity in oil palm is linked to plantation vegetation management (Hood et al., 2019; Jennings et al., 2015; Silmi et al., 2021). Resolving mesopredator diets in forests nearby oil palm plantations will aid our understanding of their benefits for pest control versus their deleterious effects from high predation on native biodiversity, which may explain low bird diversity in forest fragments (Edwards et al., 2010).

Our findings support the IUCN Red List listing of "Least Concern" for leopard cats because we confirmed they are widespread in human-modified landscapes and they are not acutely threatened by poaching and roadkill (Bashir et al., 2014; Castelló, 2020; Choi et al., 2012; Kim et al., 2019; Lau et al., 2010; Ross et al., 2015). However, leopard cats still rely mostly on forests to rest during the day, and for breeding success and long-term fitness, so the high rate of forest loss may eventually threaten the species (Miettinen et al., 2016). Leopard cats carry zoonotic diseases that affect humans (toxoplasmosis) and there is potential zoonotic disease transmission (carnivore protoparvovirus (CPPV-1), feline immunodeficiency virus (FIV) and feline leukemia virus) between feral and domestic cats with whom they can hybridize (Beatty et al., 2014; Chen et al., 2019; Gibb et al., 2020; Saka et al., 2018).

Future research directions

Research gaps on leopard cat ecology and conservation include their response to different oil palm ages and management over the 20–30 year oil palm plantation lifecycle since semiarborescent species require a closed canopy, which only older palm trees can offer (Hendry et al., 2023; Luskin & Potts, 2011). Second, leopard cats' impacts on forest-dwelling small vertebrates in forest edges abutting oil palm and interactions with domestic cats may be key issues. Third, there are opportunities to use camera trap data to estimate densities and movement with mark-recapture analyses since leopard cats can be uniquely identified based on their coat patterns. Finally, there is little known about the role of apex predators in mediating smaller felid habitat associations and the mesopredator release in the region but the camera trap datasets collated for this study could be used with

coabundance modeling to address this question (Amir, Sovie, et al., 2022; Decœur et al., 2023; Luskin, Albert, et al., 2017).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and R code required to reproduce the results are available via the FigShare DOI:10.6084/m9.figshare.24115263.

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SUPPORTING INFORMATION

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

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