

RESEARCH ARTICLE

Common palm civets *Paradoxurus hermaphroditus* are positively associated with humans and forest degradation with implications for seed dispersal and zoonotic diseases

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Abstract

1. Habitat loss and degradation can undermine wildlife communities and ecosystem functioning. However, certain generalist wildlife species like mesopredators and omnivores can exploit these disturbed habitats, sometimes leading to population increases (e.g. 'mesopredator release' in degraded areas). Although mesopredator release may cause negative effects on food webs and zoonotic disease management, some disturbance-tolerant species may help perpetuate important ecological interactions, such as seed dispersal.
2. We evaluated the habitat associations of common palm civets *Paradoxurus hermaphroditus*, which are widespread generalist mesopredators in Southeast Asia. Common palm civets are also high-quality seed dispersers, and potential zoonotic disease hosts.
3. We used published and new camera trapping data to map their probability of presence across Southeast Asia and evaluate regional-scale associations between capture rates and habitat variables such as elevation, ecoregion intactness and Human Footprint Index, among others. We also assessed the influence of habitat variables on their relative abundance at the local scale.
4. At the regional scale, we found that common palm civets showed significant positive associations with landscapes characterized by lower ecoregion intactness, higher Human Footprint Index and lower elevations. At the local scale, their relative abundance showed a significant positive association with higher Human Footprint Index, but only to a certain point, after which it started decreasing. They also favoured lower elevations at the local scale.
5. These multi-scale results indicate that common palm civets' abundance can increase under certain levels of human disturbances, consistent with the 'mesopredator release' hypothesis. This suggests they may be crucial seed dispersers in degraded forest landscapes, especially where more sensitive seed dispersers have disappeared. Our results are also consistent with previous studies

reporting that habitat degradation increases populations of potential zoonotic disease hosts, and thus risks of transmission to humans.

KEYWORDS

abundance modelling, camera trapping, deforestation, emerging infectious disease, wildlife

1 | INTRODUCTION

Forest loss, logging and hunting affect most remaining tropical forests in Southeast Asia (Harrison et al., 2016; Wilcove et al., 2013). These threats act synergistically to degrade ecosystems and their services (Benítez-López et al., 2017; Gallego-Zamorano et al., 2020), while also increasing overlap and potential pathogen transmission between remaining wildlife and humans (Gibb et al., 2020; Jones et al., 2013). Degraded tropical forests experience shifts in wildlife composition, replacing interior and sensitive species with disturbance-tolerant species (Filgueiras et al., 2021) that can reach relatively high abundances due to population release from predation and competition, or access to novel food subsidies like agriculture and trash (Luskin et al., 2017; Prugh et al., 2009). These shifts in species assemblage result in simplified communities and the loss of important ecological interactions and services, such as seed dispersal (Dirzo et al., 2014). Conversely, some disturbance-tolerant species may serve important roles perpetuating seed dispersal services where key seed dispersers have been lost (Pérez-Méndez et al., 2016). Changes in species assemblage driven by disturbances also seem to favour species that can carry zoonotic diseases, which, coupled with a higher wildlife-human overlap in degraded habitats, can increase the risks of zoonotic disease transmission (Gibb et al., 2020). Here, we evaluate the effect of habitat variables on the relative abundance of common palm civets (*Paradoxurus hermaphroditus* in Viverridae family). We also discuss implications for seed dispersal and zoonotic diseases, since these civets are widespread in Southeast Asia, high-quality seed dispersers, and civets are known hosts of zoonotic pathogens (Nakashima et al., 2010a; Veron et al., 2015; Wicker et al., 2017).

Common palm civets are small (~2–5 kg) nocturnal solitary mammals of the order Carnivora, and have a flexible omnivorous diet, eating mainly fruits and complementing with invertebrates and small vertebrates opportunistically (Fung et al., 2018; Nakashima et al., 2010a). They are predominantly arboreal and shelter in trees with dense covers during the daytime, while at night they forage both in trees and on the ground (Nakashima et al., 2013). Common palm civets have been observed in degraded and logged forest, as well as around human settlements and in plantations such as oil palm and coffee (Duckworth, 1997; Nakashima et al., 2013; Withaningsih & Pratiwi, 2019). However, they usually return to forest patches for shelter during the day (Jennings et al., 2015). A key question is whether common palm civets can persist or even increase in these degraded forests.

Common palm civets could play an important role supporting degraded and secondary forest plant communities and regeneration (Nakashima et al., 2010a). Many tropical plants rely on animals for seed dispersal; however, large and more vulnerable frugivores are often lost in degraded forests, especially in Southeast Asia (Dirzo et al., 2014). Passing through the gut greatly increases seed retention time, and thus dispersal distance (Wunderle Jr, 1997). Compared to other disturbance-tolerant species, such as sympatric wild pigs *Sus scrofa* or macaques *Macaca fascicularis* and *M. nemestrina* that regularly crush or discard seeds, common palm civets swallow relatively large seeds whole (Nakashima et al., 2010a; Nakashima & Sukor, 2010; Pedrosa et al., 2019). These civets retain seeds for an average 2.6 hr, disperse seeds non-randomly with benefits for seedling survival, and have an estimated seed dispersal distance of 216 m, a distance significantly larger than other disturbance-tolerant omnivores (Nakashima et al., 2010b; Nakashima & Sukor, 2010).

Understanding common palm civet habitat associations is also relevant to public health, because civet species (family: Viverridae) can carry a range of zoonotic diseases (Wicker et al., 2017). Some civet species host for several zoonotic diseases, including SARS (severe acute respiratory syndrome), avian influenza (HPAI H5N1), leptospirosis and variations of the rabies virus (Wicker et al., 2017). Notoriously, masked palm civets *Paguma larvata* in a live-animal market were the intermediary link for the SARS-CoV-1 outbreak in 2002 Southern China, which infected over 8,000 people (Guan et al., 2003). Civets are also being investigated as a potential vector for the current SARS-CoV-2 pandemic (COVID-19; Lu et al., 2020). Palm civets do carry less ticks than raccoons due to their grooming habits, reducing one transmission pathway (Doi et al., 2021). However, ongoing anthropogenic disturbances, poaching and wildlife farming all increase probability of pathogen exchange, and common palm civets experience each of these (Gottdenker et al., 2014). Reliable information on common palm civets' distribution and habitat associations can help assess and mitigate the risks of future zoonotic disease outbreaks.

Although common palm civets are ecologically important and of interest to public health, there is little robust information on their habitat associations. We conducted a multi-scale study to examine the regional and local factors that influence the abundance and occupancy of these civets. We used occurrence records gathered from a literature review of previous camera trapping studies, as well as new camera trapping conducted across the species range. First, we used Maxent species distribution modelling to map the common palm civets' probability of presence throughout the region.

Next, we tested how the variation in capture rates among camera trapping studies throughout the region was influenced by environmental and anthropogenic variables. We measured these variables across a 20 km radius around each study: average elevation, forest cover, oil palm, human population, ecoregion intactness, Forest Landscape Integrity Index and Human Footprint Index (henceforth: 'forest integrity' and 'human footprint'; Beyer et al., 2020; Grantham et al., 2020; Venter et al., 2016). Finally, we assessed the influence of the same variables (plus distance to forest edge) in 1 km² resolution on local relative abundance within landscapes using hierarchical abundance modelling that accounts for detectability. To our knowledge, this is the largest dataset and most comprehensive assessment of common palm civets to date.

We hypothesized that, at both the regional and local scales, relative abundance of common palm civets would be positively associated with certain anthropogenic pressures because the species is routinely observed in degraded habitats (Nakabayashi et al., 2016; Withaningsih & Prastiwi, 2019). We predicted a positive relationship with degraded habitats and human activity, unlike negative trends experienced by more sensitive interior forest specialists. We predicted a negative relationship with elevation since prior work suggested common palm civets prefer lowlands (Nakabayashi et al., 2016).

2 | MATERIALS AND METHODS

2.1 | Data collection

We compiled common palm civet occurrence data from four sources: (a) the Global Biodiversity Information Facility database (GBIF, *Paradoxurus hermaphroditus*, 2021), a global repository of biodiversity data including museum records and citizen science reports; (b) the Borneo Carnivore Database (Nakabayashi et al., 2016); (c) published reports of camera trapping studies; and (d) new camera trapping sessions conducted across our focal region (Figure 1a). Throughout our report, we define a 'study' as a continuous sampling effort using >5 cameras within a landscape (10–1,000 km²). We refer to the area sampled as a 'landscape', which was usually a national park or other protected area, production forest or collection of forest patches within a 100 km² area. Regional scale refers to trends across Southeast Asia, while local scale focuses on trends within 10 landscapes of Southeast Asia (new camera trapping). According to a recent study, common palm civets should be split from one species (*Paradoxurus hermaphroditus*) into three: *P. hermaphroditus*, *P. musangus*, and *P. philippinensis* (Veron et al., 2015). However, we do not differentiate them in this study due to identification difficulties where their ranges overlap. The only data on *P. philippinensis* (located in

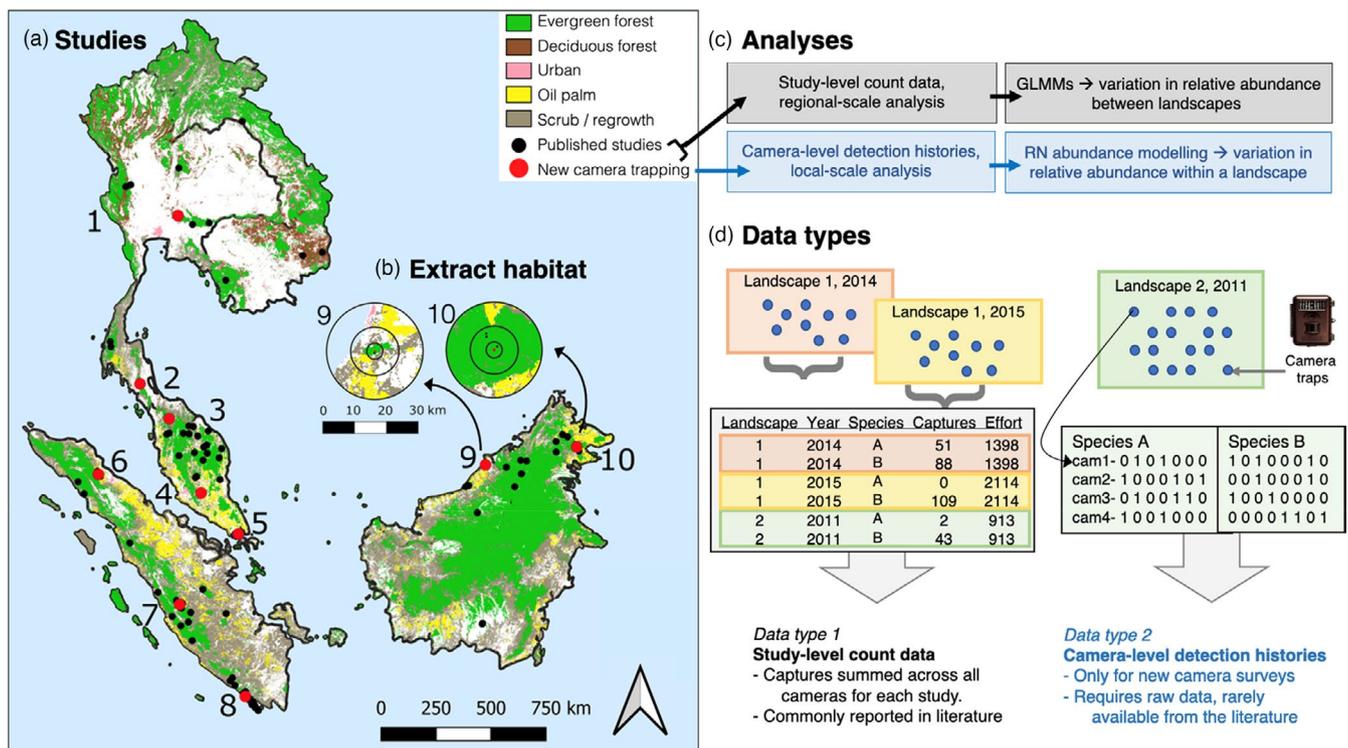


FIGURE 1 Study area and diagram of camera trapping data types and analyses. (a) Study sites where camera trapping was undertaken, with black circles showing where published camera trapping studies were located and red circles showing locations of new camera trapping. The map inset (b) shows the process of extracting habitat covariates, which were averaged in a 20 km radius around studies for the regional-scale analyses, and in 1 km radius around each camera for the local-scale analyses. The left side of panel (c) shows the structure of the study-level species counts per landscape that was analysed using zero-inflated Poisson generalized linear mixed models, where the 'landscape' was the sampling unit (regional). The right side of panel (c) shows the camera-level capture histories that were used in hierarchical abundance modelling (local). Panel (d) summarizes the data flow for both scales of analyses

the Philippines) are from GBIF and thus only included in the Maxent analysis.

We collated results of existing camera trapping studies from the literature using key terms: “camera trap*” AND Asia* or Thai* or Malay* or Indonesia* or Singapore* or Borne* or Cambodia* or Vietnam* or Lao* or Myanmar* or Burm* or Sumatra*. We only kept studies written in English, conducted after the year 2000, and that reported sampling effort and number of independent captures. We then used snowball sampling by examining references in key papers yielded by the first search. From each study, we recorded the location (area name and coordinates), capture and effort data, and a variety of other covariates available.

We also conducted 20 new camera trapping sessions in 10 landscapes with varying levels of disturbance (Figure 1a). We deployed between 18 and 112 passive infrared camera traps (Bushnell and Reconyx models) across areas ranging from 10 to 813 km² at each landscape. We placed cameras within a pre-mapped grid and spaced them at least 500 m apart in large forests (>100 km²) and 100–500 m apart in smaller forest patches (e.g. Pulau Ubin, Singapore). To reduce variation in detection probability between cameras we standardized methods between all deployments, attaching passive infrared camera traps to trees 0.2–0.3 m above-ground along hiking trails or natural wildlife trails. We deployed cameras for approximately 60–90 days at each landscape from December 2013 to March 2019. To ensure that model outputs were spatially comparable across multiple landscapes and to prevent spatial pseudo-replication, we resampled the capture data into hexagonal grid cells with a short diagonal of 1 km following Rayan and Linkie (2020). In most cases, each sampling unit contained only one camera associated with a unique value for each habitat covariate. We averaged covariate values when multiple cameras fell within the same grid cell. We considered captures independent if they occurred at least 30 min apart (Rovero & Zimmermann, 2016). We produced detection history matrices based on a sampling occasion of 5 days, and containing presence/absence data (0 = species not detected; 1 = species detected; NA = inactive sampling unit or occasion). See Table S3 for complete deployment details for all new camera trapping sessions. Permit numbers are also provided in the Supporting Information. Our universities did not require ethical approval for non-invasive camera trapping.

2.2 | Mapping range and probability of presence

First, we estimated the probability of presence for common palm civets across Southeast Asia using Maxent software (Version 3.4.1; Phillips et al.), which accepts species presence-only data and spatial environmental variables (Phillips & Dudík, 2008). We used all occurrence records from the four data sources described previously, but limited inclusion to observations after the year 2000 in order to remove historical records in areas where the species may no longer occur (mapped in Figure 2a). The environmental spatial layers included the following biophysical and anthropogenic factors: elevation (m), landscape cover (categorical), mean annual rainfall

(mm), tree cover (binary), forest integrity (0–10), distance to forest edge (m), human population density, nightlights (scaled from 1 to 63 micro flick) and the presence of oil palm plantations. See Table S1 for description of covariates. We used a cloglog output format that scales the probability of presence from 0 to 1 to map their distribution in the region (Figure 2c). We also ran a jackknife test to estimate the relative contribution of each variable to the model (Figure 2b). Lastly, we calculated the area of remaining forest and the percentage of protected areas within common palm civets' range, based on the 2015 forest layers described in Table S1 (Miettinen et al., 2016) and on geographical data obtained from the IUCN World Database on Protected Areas (UNEP-WCMC and IUCN, 2021).

2.3 | Regional-scale relative abundance with habitat characteristics

Next, we used both the published and new camera trap data to investigate regional-scale relationships between the number of common palm civet captures and various environmental and anthropogenic factors. Our sampling unit was a study, for which we combined the total number of independent captures of common palm civets across all cameras (Table S2). To account for multiple studies from the same landscape, we resampled our data per landscape per year, summing captures and effort among studies and averaging the covariates. Based on location, each study received a value for seven different habitat variables of interest: average elevation, forest cover, forest integrity, ecoregion intactness, oil palm, human population and human footprint. We extracted each variable at 1 km² resolution and calculated the sum or average values (depending on the variable) within a 20 km² radius around the centroid of cameras for each study. We analysed the study-level count data using generalized linear mixed models (GLMMs) with zero-inflated Poisson error distribution. We included study effort (measured in trap nights) as a fixed effect and landscape as a random effect, because some landscapes had multiple studies and effort varied. We used the number of independent captures as a proxy for relative abundance after controlling for study effort and landscape. We note that this does not account for variation in detection probability and thus does not linearly reflect true abundance (Sollmann et al., 2013). We tested each variable independently, and with a nonlinear term if relevant (e.g. average elevation). We inspected the effect size and *p*-values, and we compared our different models with Akaike information criterion (AIC). All GLMMs were implemented in the R package ‘GLMMADAPTIVE’ in R version 4.0.3 (R Core Team, 2020; Rizopoulos, 2019).

2.4 | Local-scale relative abundance spatial predictors

Finally, to understand how common palm civets respond to fine scale habitat and anthropogenic influences we used Royle–Nichols (RN) abundance models on the new camera trapping data (Royle

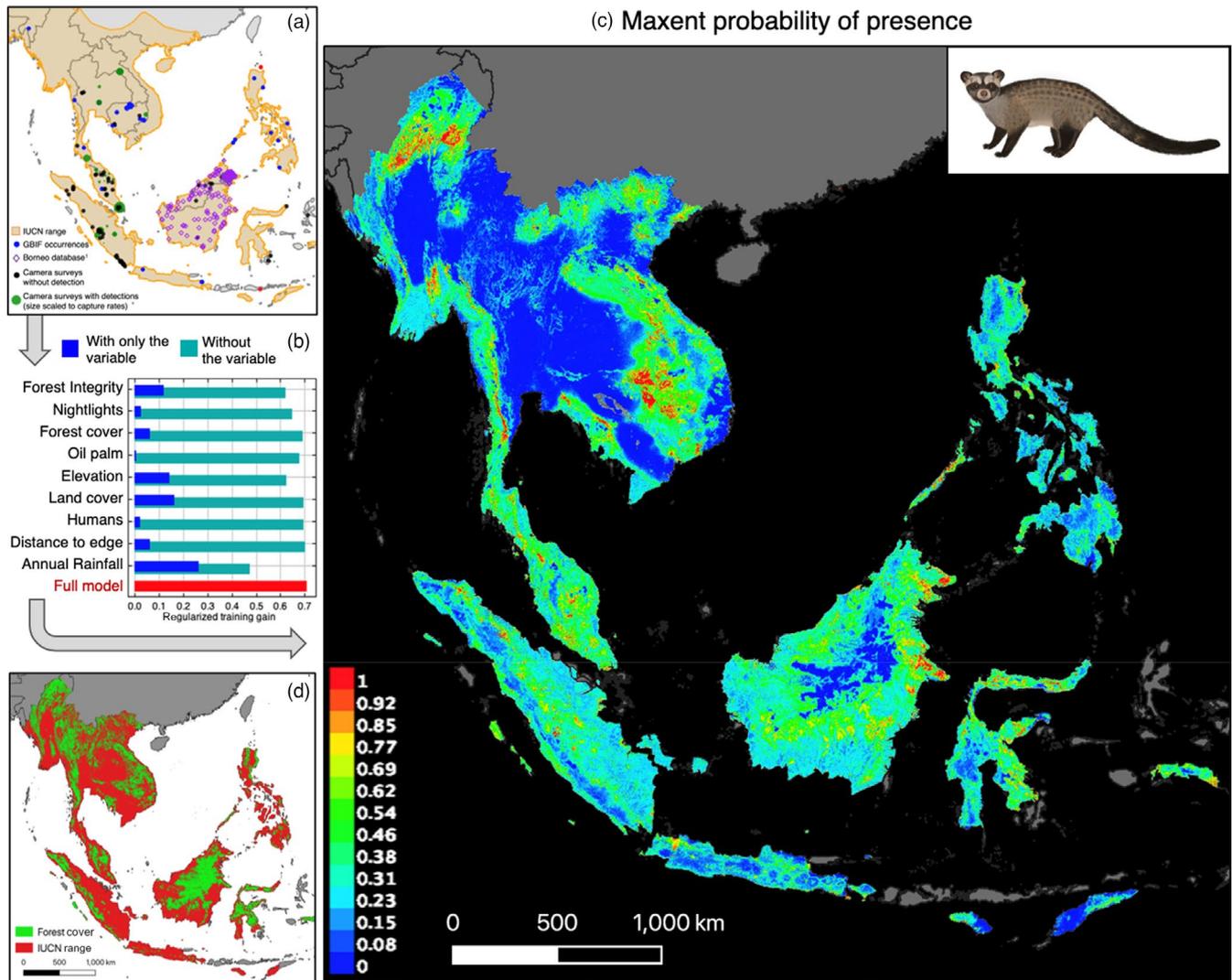


FIGURE 2 Common palm civets' range and probability of presence in Southeast Asia. Panel (a) shows the occurrence records differentiated by source (GBIF = blue, Borneo database = purple diamonds, surveys without detection = black, surveys with detection = green), and IUCN range (orange layer). (b) Jackknife graph of environmental variable performances in the Maxent modelling. The dark blue bars show the variable's explanatory power in models using only the denoted variable, while the teal bars show the predictive power of the full model excluding the denoted variable. The latter highlights whether the variable captures unique information. (c) Maxent probability of presence throughout its Southeast Asian range. (d) Forest cover remaining as of 2015 (green) that falls within the IUCN range (red)

& Nichols, 2003). The relative abundance from RN abundance models serves as an unbiased metric compared to capture rates because it accounts for imperfect detection of species (Sollmann et al., 2013). Instead of interpreting the RN model outputs as true densities, we consider that the observed variation in abundance due to covariates reflects true differences (Gilbert et al., 2021). We also note that home range size can fluctuate with food availability, which could affect results (Nakashima, 2020). We converted raw counts to a detection history (present or absent in each cell for each capture period). We defined a capture period as 5 days and limited our analysis to landscapes where we detected these civets at least once to reduce zero-inflation in the count data. We included the camera trapping session as an abundance covariate on all models to account for three landscapes having multiple

trapping sessions. To account for differing effort per sampling unit, we included the number of trap nights as a detection probability covariate on all models. Other than for effort, we assumed detection probability was consistent across cameras because we placed them on wildlife trails in similar rainforest habitats. We tested if the estimated relative abundance of common palm civets between sampling units varied with elevation, distance to river, forest cover, forest integrity, distance to forest edge, human footprint, human population and oil palm plantations. We tested each variable independently, inspected the effect size and p -values, and compared our different models using AIC scores. We also tested nonlinear models for certain variables if relevant. All RN abundance models were implemented in the R package 'UNMARKED' (Fiske & Chandler, 2011).

3 | RESULTS

3.1 | Mapping range and probability of presence

We obtained 2,173 geo-referenced occurrence records of common palm civets for the Maxent analysis. Their presence was confirmed in 72 of the published camera trapping studies, and in 13 of our new camera trapping sessions, while 1,944 records are from GBIF, and 144 from the Borneo Carnivore database (Nakabayashi et al., 2016). These different records are mapped in Figure 2a, along with the IUCN range for the common palm civet *Paradoxurus hermaphroditus* (Duckworth et al., 2016).

Using Maxent, we found that common palm civets had a medium to high probability of presence (≥ 0.5) in many parts of Southeast Asia (Figure 2c; Figure S2). The most informative variable when modelled in isolation was annual rainfall, followed by land cover and elevation (Figure 3b). Common palm civets were more likely to be found in habitats at lower elevations, and with mean annual rainfall between about 1,700 and 3,300 mm/year (Figure S1). A map showing where probability of presence is higher or equal to 0.5 and a map of probability of presence confined to remaining forests are included in Supporting Information (Figures S2 and S3). Only 34.6% of the common palm civet's Southeast Asian IUCN range remains forested as of 2015, and only 9.5% of this IUCN range is designated as protected areas (Table 1).

3.2 | Regional-scale relative abundance with habitat characteristics

At the regional scale, we found that ecoregion intactness, human footprint and average elevation had a significant effect on the

number of common palm civet captures. Based on AICc model selection (Table 2), ecoregion intactness was the best predictor of capture rates and showed a significant negative relationship ($p < 0.0001$; Figure 3a). We included results from the next two best models to address our hypotheses about the role of elevation and civet-human associations, but note these were >20 AIC points higher than the best model: capture rates showed a significant positive relationship with human footprint ($p < 0.0001$; Figure 3b), and a nonlinear relationship with average elevation peaking around 500 m elevation ($p < 0.005$; Figure 3c).

3.3 | Local-scale relative abundance spatial predictors

Our total new camera trapping effort included 10 landscapes, 20 sessions, 1,218 cameras and 58,608 trap nights (Table S4). We obtained 245 independent captures of common palm civets from seven landscapes and did not detect the species at three landscapes. Standardized capture rates (relative abundance index; RAI) and naïve occupancy are provided in Table S4 and shows that Khao Chong in southern Thailand had the highest capture rate (RAI = 2.3 per 100 trap night) and naïve occupancy (detected in 56.8% of all cameras).

Based on the AIC model selection of our RN hierarchical abundance models, we found that common palm civets' relative abundance at the local scale was best predicted by nonlinear human footprint (Table 3). Common palm civet relative abundance showed a significant positive relationship with human footprint until a certain point, after which it became negative ($p < 0.01$; Figure 4a). It also showed a significant negative relationship with elevation ($p = 0.012$;

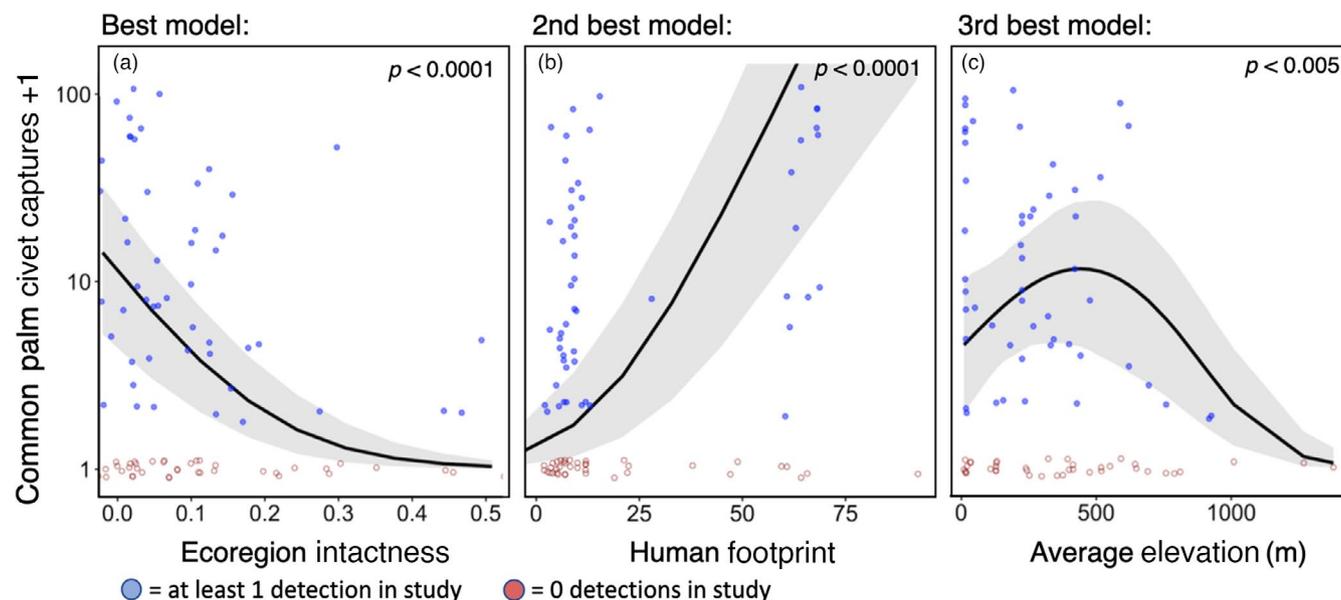


FIGURE 3 Regional-scale relationships between common palm civet captures and various habitat variables. Relationships assessed using zero-inflated Poisson GLMMs, where the response variable was detections per study ($n = 92$ studies from 42 landscapes). Trend lines were drawn using the predict() function in R and data points show raw capture data (jittered for clarity). We graphed the nonlinear model for average elevation

TABLE 1 Common palm civet IUCN range, remaining forested habitat and per cent protected

Region	IUCN range (km ²)	Forested area (km ²)	% Forested	% Protected
Borneo	734,160	321,601	43.8	6.7
Mainland SE Asia	1,988,438	684,570	34.4	10.7
Malay Peninsula	131,475	46,053	35	12.5
Sumatra	430,034	84,888	19.7	7.6
SE Asia Total ^a	3,284,107	1,137,112	34.6	9.5

^aExcluding the Philippines.

TABLE 2 Regional-scale GLMM model selection of covariates associated with common palm civet detections. We do not show models that performed worse than the null (forest integrity). We also did not include irrelevant nonlinear models and any multivariate models due to high correlation between best-performing variables

Model	AICc	ΔAICc	AICwt
Ecoregion intactness	956.3	0	1
Human footprint	984.7	28.4	0
Average elevation ²	1,015.91	59.61	0
Average elevation	1,032	75.7	0
Forest integrity ²	1,033.31	77.01	0
Forest cover ²	1,038.61	82.31	0
Oil Palm	1,040.3	84	0
Forest cover	1,046	89.7	0
Human population (log)	1,047.1	90.8	0
Null model	1,048.5	92.2	0

Figure 4b), which had the second lowest AIC of the models. We note that the AIC values of this model was >10 AIC points higher than the best model. Combining both human footprint and elevation into a multivariate model did not improve the AIC score (Table 3).

4 | DISCUSSION

The loss of seed dispersing fauna and spread of zoonotic diseases are key concerns in degraded forest landscapes, especially in Southeast Asia. At the regional scale, we found strong support that common palm civets, a seed dispersing mesopredator and zoonotic disease host, are positively associated with landscapes with lower ecoregion intactness and higher human footprint (Figure 3). While common palm civets are forest-dependent, our regional results likely reflect common palm civets' ability to adapt to some types of human disturbance, like logging, edges and secondary forests. At the local scale, their relative abundance was positively associated with human footprint but only up to a certain extent, after which it decreased (Figure 4). Their local positive association with moderate human footprint indicates that they are not confined to forest interiors, and may suggest they benefit from human resources, such as scavenging from gardens or trash. However, this nonlinear

relationship suggests a threshold after which human footprint affects them negatively, possibly due to high poaching or complete deforestation (Shepherd, 2012). Elevation was also an informative natural environmental variable, and there was strong support across multiple scales for their preference for low elevation habitats.

Why did we observe a positive association between common palm civets and some types of anthropogenic disturbance? One possible explanation is the availability of food subsidies at edges, a mechanism that also bolsters other Asian generalists and disturbance-tolerant species such as wild boars *Sus scrofa*, especially where they crop raid in oil palm plantations (Luskin et al., 2017). Although nonsignificant ($p = 0.059$), common palm civets' relative abundance and oil palm had a positive relationship at the local scale, suggesting the possibility of such a mechanism. We also propose that release from predation or competition are other potential explanations, since forest-specialist predators and competitors decline in disturbed forests (De CQ Portela & Dirzo, 2020; Trewby et al., 2008). However, this study does not specifically test these hypotheses. Taken together, the results of our multi-scale study support the mesopredator release hypothesis for common palm civets in degraded landscapes.

Common palm civets are one of few frugivores that can disperse relatively large seeds effectively and that are also disturbance tolerant (Nakashima et al., 2010a). Unlike many other mesopredators, common palm civets may cause fewer negative cascading effects on lower trophic levels since they eat primarily fruits, while also perpetuating seed dispersal services. Loss of seed dispersal services in tropical ecosystems due to hunting and habitat loss is a pressing issue (Harrison et al., 2013). Common palm civets, who can tolerate certain anthropogenic pressures, may become keystone species in degraded landscapes for their large seed dispersal where larger dispersers often decline (Corlett, 2017; Dirzo et al., 2014). They may also assist with secondary forest regeneration when travelling outside forest patches (Wunderle Jr, 1997).

Civets can host a variety of zoonotic diseases (Wicker et al., 2017) and populations at unnatural proximities to humans are more likely to transmit pathogens (Jones et al., 2013). Due to habitat degradation, a substantial portion of their habitat overlaps with human-modified landscapes (Figure 2). Our results suggest that common palm civets can do well in these disturbed areas and near humans, which is consistent with other studies reporting an increase in the proportion of wildlife able to host zoonotic pathogens in degraded habitats (Gibb et al., 2020). This makes their hunting,

Models	K	AIC	Δ AIC	AICwt
Human footprint ²	17	1,486.20	0	0.982
Elevation	16	1,496.40	10.20	0.006
Elevation + Human footprint	17	1,496.49	10.29	0.006
Human footprint	16	1,497.29	11.09	0.004
Oil palm	16	1,500.57	14.37	0.001
Null model	15	1,501.08	14.88	0.001

TABLE 3 Local-scale Royle Nichols model selection. We do not show models that performed worse than the null: Distance to river, forest integrity, forest cover and distance to forest edge

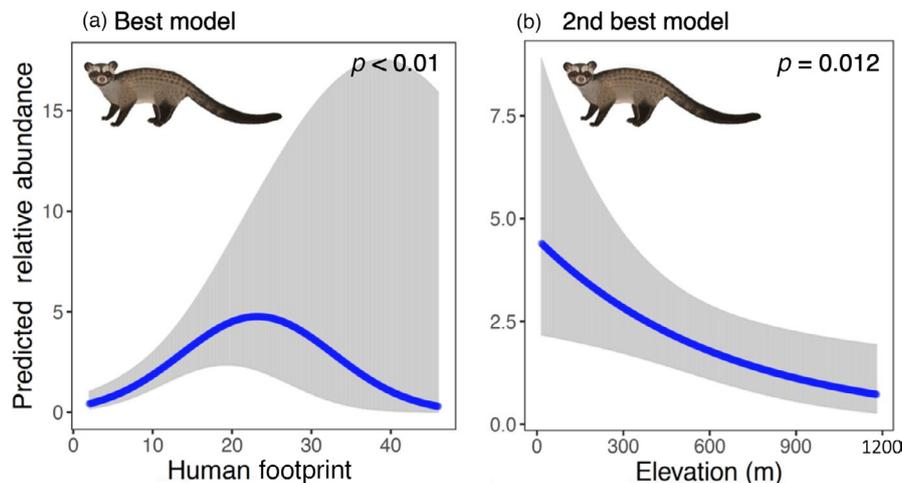


FIGURE 4 Relationships between common palm civets predicted relative abundance and local-scale habitat variables from Royle Nichols hierarchical models. Relative abundance estimates were generated using the predict() function in R while varying the covariate of interest across the observed range of values. We graphed the nonlinear model for human footprint. The shaded areas around the blue trend line represent the 95% confidence interval (CI). The wide CI for panel (a) stems from limited data at the upper range of the covariate

exploitation and associated interactions with humans a key concern. Civets are frequently captured and traded for meat, traditional medicine or for captivity to produce the increasingly popular kopi luwak coffee (made from beans defecated by common palm civets; Shepherd, 2012). Live-animal markets create an environment where stressed, sick and injured animals from various species are crowded together and near humans, favouring zoonotic disease transmissions (Wicker et al., 2017). Thus, different forms of human exploitation of Southeast Asian forested ecosystems (e.g. deforestation and wildlife trading) can act synergistically to increase the probability of zoonotic disease transmission.

Common palm civets are currently listed as least concern but declining by the IUCN Red List (Duckworth et al., 2016). Our habitat mapping and analyses generally support this assessment based on the limited forest cover remaining. Civets face threats from poaching due to increasing kopi luwak coffee production, and from hunting for meat and for crop protection (Nakashima et al., 2010a; Shepherd, 2012). Abating poaching, wildlife trade and deforestation are necessary to stop current common palm civet declines, and to limit pathways for zoonotic pathogens transmissions. Our study also highlights why selectively logged forests, although not equal to primary forests in terms of biodiversity, can still be refuges for certain tolerant species and thus are preferable to deforested areas and plantations (Gibson et al., 2011; Rayan & Linkie, 2020). We

note that although the generalist common palm civets can thrive in degraded forests and near plantations, the lack of protected areas and expansion of oil palm threaten many sympatric forest specialists and the region's biodiversity (Wilcove et al., 2013). In Southeast Asia, where most forests are degraded in some aspect, it is necessary to limit civet-human interactions by reducing wildlife exploitation, and to maintain viable populations of wild common palm civets to preserve valuable ecological functions in rainforest communities.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHORS' CONTRIBUTIONS

B.D., Z.A. and M.S.L. designed the study; M.S.L. and J.H.M. collected the data; J.H.M., Z.A., C.M. and M.S.L. prepared the data; B.D., Z.A., H.D., J.H.M., A.S. and M.S.L. analysed the data; B.D. and M.S.L. wrote the paper, and all authors contributed to editing the final manuscript.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.8cz8w9gs1> (Dehaudt et al., 2022).

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