LETTER

Sunda pangolins show inconsistent responses to disturbances across multiple scales

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Abstract
Pangolins are the most trafficked animals worldwide and are presumed to be restricted to pristine habitats due to poaching intensity in more accessible degraded areas or intrinsic habitat preferences. We tested the hypothesis that pangolins' could persist in degraded areas and near humans if poaching is controlled. We used occurrence records from new and published camera trapping studies from across Southeast Asia to conduct a multiscale analysis of habitat associations for the Critically Endangered Sunda pangolin, encompassing poached and non-poached areas. Our results were highly influenced by Singapore, where pangolins are common in urban settings and there is minimal poaching. Excluding Singapore, there were no significant landscape-level habitat associations, reflecting pangolins are habitat generalists. At local scales (including and excluding Singapore), occupancy was negatively correlated with active deforestation but not previously degraded forests. We conclude that with strong antipoaching enforcement, pangolins are unexpectedly adaptable, with Singapore exemplifying the potential for species recovery.

KEYWORDS
camera trapping, deforestation, occupancy modeling, urban ecology, wildlife

INTRODUCTION

Tropical forest habitat degradation and wildlife poaching threaten biodiversity, ecosystem services, and even human health via the risk of zoonoses (Gibb et al., 2020; Tilker et al., 2019). The nexus between forest degradation, wildlife conservation, and human health is manifest in the case of pangolins (family *Manidae*), a threatened and heavily poached group of insectivorous scaley mammals in tropical forests of Asia and Africa. Pangolins are reservoirs of multiple pathogens associated with ixodid ticks and possibly SARS-CoV and their poaching and consumption precipitate zoonotic disease spillover (Jabin et al., 2019; Khatri-Chhetri et al., 2016; Liu et al., 2019; Wacharapluesadee et al., 2021; Xiao et al., 2020). Demand for pangolin meat and products is driven by traditional Chinese medicine (TCM) despite the lack of scientific evidence to support the health

benefits (Challender et al., 2015; Harrison et al., 2016; Jacobs et al., 2019; Jin et al., 2020; Nijman et al., 2016). Pangolins are now "the most heavily trafficked wild mammal in the world" despite all species being internationally protected and CITES Appendix I (Challender et al., 2014, 2020; Heinrich et al., 2017), and pangolin trends continue to decline sharply with six out of eight extant Manidae species being Endangered or Critically Endangered (Challender & O'Criodain, 2020; Gaubert et al., 2018; Heinrich et al., 2016).

Disentangling the relative importance of habitat preferences versus hunting in shaping threatened wildlife distributions and population trends is a challenge. Poaching in tropical forests is regionally elevated in more densely populated areas and locally elevated in forest edges and in degraded forests that are more accessible to hunters (Benítez-López et al., 2017). Intense poaching in edges may create the appearance or pattern

of edge avoidance, even where a species prefers edges for habitat features or foraging. Here we seek to disentangle the relative importance of habitat preferences versus hunting underpinning pangolin occurrences in degraded forests and edges at multiple spatial scales.

Pending poaching can be controlled, a key question for the long-term conservation of pangolins is whether they can persist in edges and degraded forests (e.g., logged or fragmented). This is particularly important in Southeast Asia, which has the highest rates of deforestation globally and more than 70% of forests are now within 1 km of an edge (Haddad et al., 2015; Wilcove et al., 2013). Observations of several pangolin species in disturbed areas suggest that they can tolerate moderate levels of disturbance (Acosta-Lagrada, 2012; Mahmood et al., 2020; Schoppe et al., 2020; Wu et al., 2020). However, this perceived tolerance to modified habitats could also be due to increased detectability in areas that humans occupy, and their mere presence may not capture meaningful declines in their relative abundance or survival (e.g., edges could be population sinks). Approaches to account for detectability—such as hierarchical occupancy modeling—can be used to make conservative inferences, but the data available for pangolins has thus far been insufficient to run these robust analyses. We overcome this data limitation using a synthesis of occurrence records and dozens of camera trapping studies.

The Sunda pangolin (*Manis javanica*) was once common in Southeast Asia but now is listed as Critically Endangered by the IUCN Red List (Figure 1; Challender et al., 2019; Corbet & Hill, 1992). Sunda pangolin's natural history, ecology, and habitat associations are poorly understood due to their rarity and cryptic behaviors, such as nocturnality, burrowing, and climbing (Challender et al., 2019; Corbet & Hill, 1992). They also spend days hiding in tree hollows (in standing or fallen trees), burrows that are either freshly dug or modified from existing holes or among tall grasses (e.g., *Imperata cylindrica*) (Chong et al., 2020; Lim & Ng, 2008). Sunda pangolins have been reported from a wide range of natural habitat types, including tropical forests, peat swamp forests, and grasslands, but there is no consensus on their preferred habitats (Azhar et al., 2013; Chong et al., 2020; Ketol et al., 2009; Lim & Ng, 2008; Semiadi et al., 2009; Wearn, 2015). Many occurrence records come from low elevations <600 m yet this could be due to sampling bias (where people are looking) and we note the species has been recorded up to 1700 m on Mt. Kinabalu in Borneo (Payne et al., 2007). Their local abundance (within a landscape) has been associated with the availability of large trees (DBH > 50 cm) or other structures for denning and breeding sites such as dead wood hollows (Lim & Ng, 2008), as well as with the availability of insect prey species (Chong et al., 2020). This suggests Sunda pangolins may respond negatively to forest degradation such as logging that removes large trees (Morin et al., 2020; Pietersen & Challender, 2020).

Species distributions and habitat associations are essential for developing conservation action plans (Cuttelod et al., 2009). For example, the IUCN Red List uses the extent of occurrence (EOO) and more recently, the area of occupancy (AOO), to assess species


Practitioner points

- Sunda pangolins are rainforest habitat generalists and—if poaching is eliminated—can persist in degraded rainforest patches, even nearby urban areas. Small protected areas can support pangolin conservation through increased anti-poaching efforts and enforcement, such as undertaken in Singapore.
- Sunda pangolins are extremely susceptible to poaching. To reduce demand for pangolin products, public awareness campaigns promoting scientifically supported medicinal alternatives should focus on East Asian markets where products are primarily consumed.
- To reduce the supply side of the pangolin poaching problem, campaigns could focus on educating rural communities about poaching laws and penalties, and tourism or other values.
- Foster international cooperation to reduce pangolin trade.

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threat levels (IUCN, 2020). The AOO is especially important for species that are patchy or rare within their range, such as the Sunda pangolin (Anderson, 2023). We posit that Sunda pangolin associations with degraded and edge forests are crucial to properly mapping and interpreting the AOO. For example, if their occasional presence in degraded forests and edges accurately reflects that this species can thrive in such habitats, the species may have a larger effective AOO and lower threat status than currently appreciated. Alternatively, if Sunda pangolins show dramatic declines in degraded forests and edges, their effective AOO may need to be refined to the interiors of primary forests.

Habitat associations can vary at different spatial scales and this affects management options. Local-scale factors such as specific resource availability (a large tree hollow for a den) and human activities influence an individual's movement within its home range, while regional factors such as weather, vegetation composition, topography, habitat fragmentation, or poaching, may shape species' relative abundance among forest patches, among landscapes, or regionally (Chase & Knight, 2013; Suárez-Castro et al., 2018). For on-the-ground conservation management at local scales, this may focus on creating beneficial features such as artificial dens versus landscape and regional-scale policy interventions or campaigns to reduce poaching or on protected area planning.

We evaluated Sunda pangolin distribution, occupancy, and habitat associations using occurrence records available in the peer-reviewed literature and online databases. To disentangle the effects of habitat versus poaching in shaping Sunda pangolin habitat associations, we compare landscapes with poaching to those in Singapore, where strict regulations and enforcement have nearly eliminated all forms of hunting (Lamperty et al., 2023). Other Southeast Asia countries have documented problems with hunting (Harrison et al., 2016) including cases of Sunda
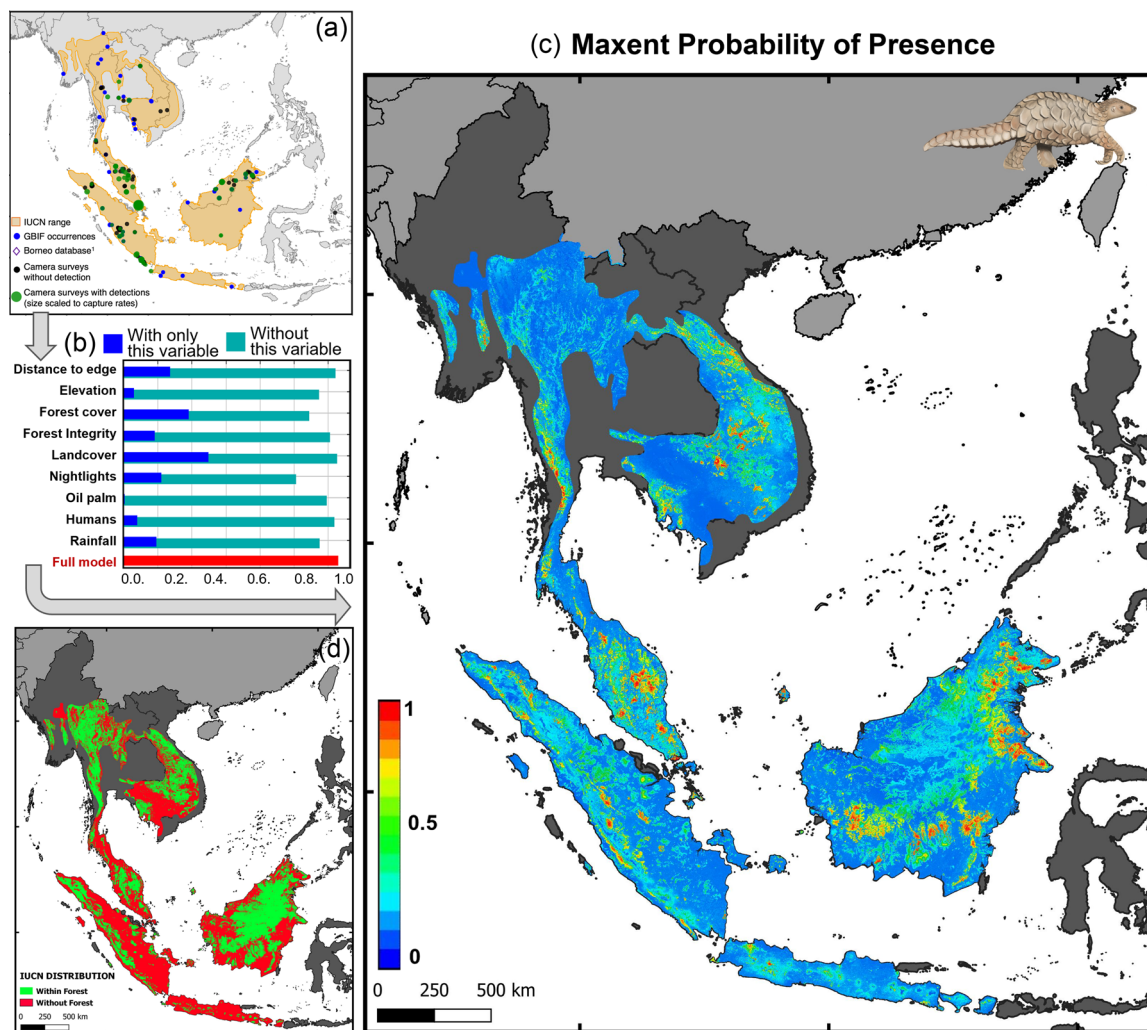
FIGURE 1 The Sunda pangolin range and probability of presence. In (a), the shaded area shows the IUCN Red List range (extent of occurrence or "EOO") and the location of occurrence records, colored by the data source. (b) The MaxEnt Jackknife graph of variable importance using the regularized training gain. The dark blue bars show the training gain of a model using only the denoted variable, while the teal bars show the good fit of the full model to the training data except for the denoted variable, the latter highlighting whether the variable captures unique information. (c) The MaxEnt SDMs predicted probability of presence throughout the IUCN range in Southeast Asia, including nonforested areas. (d) Forest cover within the species range as of 2015. Methods for MaxEnt SDMs are provided in the Supporting Information. The map was created using the aforementioned dataset in QGIS ver. 3.20.0 (www.qgis.org: accessed August 20, 2022) and MaxEnt software ver. 3.4.4 (https://biodiversityinformatics.amnh.org/open_source/maxent/: accessed August 20, 2022).

pangolin poaching in Myanmar (Nijman et al., 2016), Thailand (Kitamura et al., 2010), Lao (Nooren & Claridge, 2001), Vietnam (Newton et al., 2008; Nuwer & Bell, 2014; MacMillan & Nguyen, 2014), Cambodia (Gray et al., 2017), Malaysia (Jayasilan, 2018; Mohd-Azlan et al., 2018), and Indonesia (Semiadi et al., 2009; Shepherd, 2009). To account for different habitat relationships emerging at different spatial scales, we used a collection of analyses that leveraged different quantities and resolutions of occurrence observations. First, we used comparatively large presence-only datase to conduct regional species distribution modeling (SDMs). Next, we evaluated the landscape-scale habitat associations of Sunda pangolins by compiling a data set of count records (including zeros) from 123 new and published camera trapping sessions. For landscape-level analyses (i.e., variation detection rates among surveys), we used generalized linear mixed models (GLMMs). Finally, we assess local-scale response (i.e., variation within landscapes) using hierarchical occupancy modeling with 20 new camera trapping sessions conducted

at 10 landscapes, including Singapore. We hypothesized there would be significant and consistent negative effects of habitat degradation and humans on Sunda pangolins at all spatial scales.

Pangolin's ability to persist in degraded forests and edges may be dependent on their behavioral plasticity, of which their activity patterns are often examined using cameras. Diurnal humans may impact nocturnal pangolins at dusk and dawn, and thus we predicted Sunda pangolins would shift any crepuscular activity toward later hours (e.g., peaking 2200-0400) nearer humans, as has been shown for a variety of other wildlife species (Gaynor et al., 2018).

METHODS

Data collection

We compiled presence and absence data for Sunda pangolin from three sources: (1) the Global Biodiversity

Information Facility database (GBIF, 2019), an online global repository of biodiversity data including museum records and citizen science reports (presence-only); (2) published reports of camera trapping sessions (presence-absence); and (3) new camera trapping sessions conducted spanning our focal region (complete detection histories). Presence-only records include georeferenced observations (any number of times) by any means (direct visual observation or camera trapping). Presence/absence data is the georeferenced coordinate records of the camera traps or camera trapping studies. We included camera trapping sessions located within its IUCN Red List range. We define a "camera trapping session" as a continuous sampling effort using >5 cameras within a landscape (10–1000 km^2) by a single author or group. We refer to these areas sampled as a "landscape," which was usually a national park, production forest, or collection of forest patches, such as those left in plantations to qualify for green certifications.

Collating published camera trapping studies

We collated camera trapping data from 103 published camera trapping sessions in 49 landscapes by searching the Web of Science with the following criteria: "camera trap*" AND Asia* or Thai* or Malay* or Indonesia* or Singapore* or Cambodia* or Vietnam* or Lao* or Myanmar* or Burma* or Sumatra* or Borneo*. We included studies written in English and reported relevant results for the species of interest, including sampling effort (number of cameras and deployment length or total trap nights) and number of independent captures (generally defined based on a 30–60 min interval between captures of the same species, referred to as "independence period"). We examined the references listed in key papers to identify and include further sources. We further limited the inclusion criteria to all tropical forest camera trapping studies that used unbaited cameras placed <0.4 m in height, usually facing trails or other areas determined by researchers to be used by wildlife. This is the standard deployment approach used in the region and is suitable for the majority of semi-terrestrial species >1 kg (Rovero & Ahumada, 2017). From each study, we recorded the landscape (forest name and coordinates), the number of independent captures, and the sampling effort, and extracted a variety of spatially derived environmental variables (Supporting Information: Table S1). We grouped multiple studies from the same landscape each year by summing the number of independent captures and sampling efforts among the studies and averaging the environmental variable values (Dehaudt et al., 2022; Dunn et al., 2022; Hendry et al., 2023).

New camera trapping sessions

We conducted 20 new camera trapping sessions in 10 landscapes in Thailand, Peninsular Malaysia, Singapore, Sumatra, and Borneo between December 2013 and March 2019 (see Supporting Information: Table S2 for landscape characteristics, and Supporting Information for a full description of study sites, camera deployments, and data curation [Amir et al., 2022; Luskin et al., 2017]). Detailed study site descriptions are also available at Amir et al. (2022). We deployed between 18 and 78 passive infrared cameras, with standardized deployment methods, across sampling areas ranging from 10 to 813 km^2 (Supporting Information: Figure S1 and Table S2). Cameras were placed within a pre-mapped grid and spaced at least 500 m apart in large landscapes (>100 km^2) and 100–500 m apart in smaller forest patches and islands (e.g., Pulau Ubin in Singapore), attached to trees 0.2–0.3 m above ground along hiking trails or natural wildlife trails and deployed for 60–90 days. The data from our new camera trapping sessions includes the full detection histories from all camera traps that denote the fine-scale spatiotemporal variation in detections and nondetections, and this fine-scale information is not available from published camera trapping studies.

Regional-scale SDM with MaxEnt

We compared the Sunda pangolin's EOO with our own estimate of their AOO in the region to assess if the EOO accurately reflects the species' actual distribution. The EOO, measured in km^2, corresponds to the area covered by the species' known range that we extracted directly from the IUCN Red List range map (IUCN, 2020). We calculated the AOO, in km^2, from the remaining forest area within the species' EOO, based on the remotely sensed habitat layers obtained in 2015 (Supporting Information: Table S1) (Miettinen et al., 2016). As all remaining forest patches may not be occupied, our estimate of the AOO is conservative and should be interpreted as the remaining available habitat. Moreover, since Sunda pangolins have been observed in forest edges and even nonforest plantations, we also included the result of Sunda pangolins' probability of presence (from MaxEnt) outside of AOO but within the EOO. Finally, we also calculated the percentage of protected areas inside the remaining forests in the species' range based on the protected terrestrial layer data obtained from the IUCN World Database on Protected Areas (UNEP-WCMC & IUCN, 2021). All of the mappings and calculations were performed in QGIS (QGIS.org, 2021) and in R (R-Core-Team, 2021) with the "sf" package (Pebesma, 2018).

We conducted SDM using MaxEnt (Phillips et al., 2006) with presence-only data and environmental layers. We used all presence-only records from the three data sources described previously but limited inclusion to observations within the current IUCN range (plus a 35 km buffer) and observations after the year 2000 to remove historical records in areas where the species may not currently occur. Moreover, to avoid sampling bias due to the high number of occurrence points in Singapore, which does not adequately represent the majority of Sunda pangolin habitat characteristics, we implemented the "systematic sampling" selection method presented by Kramer-Schadt et al. (2013) and Fourcade et al. (2014). We created a grid of 0.02-degree cell size (which is larger than the variables' 0.01-degree cell size) in Singapore and

randomly selected one occurrence per grid cell. Moreover, to reduce the false-negative rate, we feed the setting with a bias file to represent the sampling effort across the study area and to limit areas for MaxEnt to extract background (pseudo-absence) data with a maximum number of 5000 (Barbet-Massin et al., 2012; Fourcade et al., 2014; Kramer-Schadt et al., 2013; Stolar & Nielsen, 2015). Our environmental layers included biogeographical variables such as elevation, land cover, mean annual rainfall, forest cover, Forest Landscape Integrity Index (forest integrity hereafter, as defined by Grantham et al. [2020]), and distance to edge, as well as anthropogenic variables associated with human presence and hunting including human population density, the Human Footprint Index (HPI) and night lights (Supporting Information: Table S1). Further adjusted MaxEnt settings, sampling bias file creation, and other attempts to reduce model error (e.g., false-negative) are explained in the Supporting Information section for reproducibility.

Landscape-scale habitat associations with ZIP GLMMs

We assessed landscape-scale associations between the capture rates of published and new camera trapping sessions and landscape-level anthropological and environmental variables using GLMMs. We used a zero-inflated Poisson (ZIP) distribution as we treated detections as count data and included sampling effort per camera trapping session (measured in trap nights) as a continuous fixed effect and landscape as a random effect. Our sampling unit was a camera trapping session (one set of camera deployments from a single landscape), and all variables were calculated for the entire session. We chose to run GLMMs on the raw count data as an improvement on using linear mixed models with relative abundance index (RAI, usually the number of independent captures per 100 trap nights) following Ash et al. (2020) while acknowledging that either approach does not account for variation in detection probability and thus do not linearly reflect true abundance (Sollmann et al., 2013). Therefore, in this analysis, we are implicitly assuming that detection probability does not vary between camera trapping sessions and acknowledge that this approach may introduce unexplained variation in captures owing to slight differences in equipment and deployment methodology between sessions. These sources of measurement error may reduce our chances of detecting significant "true" relationships.

We used AICc model selection to test for relationships with three biophysical descriptors (latitude, annual precipitation, average elevation), three indicators of habitat degradation (forest patch size, percentage of forest cover, and forest integrity) and three indicators of human presence and potential hunting intensity (human population density, night lights, and the HFI; sources listed in Supporting Information: Table S1). These variables describe the area within a 20 km radius around the centroid of each landscape (1256 km^2) to account for the large areas covered by some camera

trapping grids and consider the spatial scale relevant to persistence between landscapes. While few studies have examined Sunda pangolin movements, other pangolin species have home ranges >10 km^2 and have population densities <0.16/km^2 (Pietersen et al., 2014), inferring a single viable interacting population of >160 pangolins across a landscape >1000 km^2. We also tested multivariate additive models after filtering highly correlated variables ($|r| > 0.6$) (Burnhan & Anderson, 2002). Detections in Singapore may influence regional results, so we present GLMM including and excluding Singaporean surveys (Elith et al., 2011; Phillips et al., 2017). More details on data set curation and analytical approach are provided in the Supplementary Methods.

Local-scale habitat associations using hierarchical occupancy modeling

We assessed variation in Sunda pangolin occupancy within landscapes due to environmental and anthropogenic variables using single-season, single-species occupancy models (MacKenzie et al., 2002). We used the detection histories generated from our 20 new camera trapping sessions to develop our occupancy models that account for imperfect detection. To ensure model outputs were spatially comparable across multiple landscapes and to prevent spatial pseudo-replication, we spatially resampled our data into hexagonal sampling units with a short diagonal of 1 km (0.87 km^2), following Amir et al. (2022). Each sampling unit often contained only one camera and a unique variable value, but values were averaged when multiple cameras fell within the same grid cell (Rayan and Linkie 2020). Captures were considered independent if they occurred at least 30 min apart. We produced detection history matrices based on a sampling occasion of 3 days and containing detection-nondetection data (0 = species not detected; 1 = species detected; NA = inactive sampling unit or occasion). We never managed to detect more than a single pangolin in any images from our cameras. We included the camera trapping session identifier as a fixed effect in the occupancy formula to maintain our sampling units' spatial and temporal independence, and we included sampling effort per camera (in trap nights) in our detection formula to account for unequal sampling.

We assessed relationships using the environmental and anthropogenic variables described previously for the landscape-scale GLMMs and additional local-scale indicators of habitat degradation and disturbance: distance to the forest edge, percentage of oil palm plantation cover, percentage of forest loss, and percentage of degraded forest, this time calculated within a 1 km radius around each camera (Supporting Information: Table S1). We ran univariate models with each variable and implemented multivariate models when univariate models had competing delta AIC scores (<2). We noticed the large proportion of data from Singapore, so we also tested the effect of this outlier by excluding data from Singapore and compared the result when including data from Singapore.

Behavioral changes (diel activity patterns)

We used time-stamped detections from our new camera trapping sessions to investigate variability in the Sunda pangolin's diel activity within the study areas. We tested if forest degradation (forest integrity and distance from forest edges) or variables associated with human presence and hunting (human population density, HPI, night lights) affect Sunda pangolin behavior by testing for significant differences in diel activity patterns. Specifically, we split our time-stamped detections based on the median value of the disturbance variable and ran a bootstrap procedure to simulate 1000 distributions of activity pattern data to conduct a Wald test using the function compare Act() in the R package "activity" (Rowcliffe et al., 2014). When significant differences in activity patterns were detected, the coefficient of overlap was calculated from the R package "overlap" (Ridout & Linkie, 2009). We also used the Schmid and Schmidt (2006) Dhat estimator to compute the coefficient of overlap for each type of disturbance variable, where we used $Dhat_1$ (over $Dhat_4$) because we generated less than 60 independent detections.

RESULTS

Regional-scale SDM

For the MaxEnt SDM, we collected 152 georeferenced presence records, including all observations from GBIF, published, and new camera trapping sessions (Supporting Information: Figure S1 and Table S3). The IUCN Red List EOO for Sunda pangolin was 4.39 million km^2, of which 19% were forested as of 2015, and 12.2% were forests within protected areas (Table 1; Figure 1 and Supporting Information: Figure S1). Our SDM results showed a good discrimination ability (mean AUC = 0.879) and performed better than models with random variables (Fourcade et al., 2018; Peterson et al., 2011). There were isolated hotspots with a high probability of presence in Peninsular Malaysia, northern Vietnam, southern Thailand, eastern Borneo, and Singapore. Areas with a medium-to-high probability of presence (>0.32) accounted for only about 43.3% (391,102 km^2) of the forested EOO within IUCN. Sunda pangolins were forest-dependent, with less than 1% (12,220 km^2) of areas

with a high probability of presence (>0.5) located outside forests and 62.7% of these nonforest areas were oil palm plantations nearby forests, but GIS layers may not accurately capture differences in natural versus plantation tree cover types. The three variables with the largest contributions to the SDM were forest cover (positive), nightlights (positive), and a unimodal effect of rainfall (peak occurrence at 2000–3000 mm year^{-1}; Supporting Information: Figure S2). The cumulative contributions of these three variables alone accounted for 73.4% of the model's predictive power (Supporting Information: Table S4).

Landscape-scale habitat associations

We identified 123 new and published camera trapping studies with a total effort of 485,770 trap nights within the species range (Supporting Information: Tables S1 and S5). The naïve occupancy (landscapes detecting the species at least once) was 86% in Sumatra, 67% in Borneo and 63% in mainland Southeast Asia (Supporting Information: Tables S5 and S6). Singapore reported 3–5-fold higher relative abundance (detections per 100 trap nights) than other regions (mean of 0.33 vs. 0.03–0.08 detections per 100 trap nights). The top ZIP GLMM explaining variation in the number of Sunda pangolin captures between landscapes included a linear positive effect of Human Footprint ($\beta = 0.78$, SE = 0.21; $p < 0.01$; Figure 2; Table 2) and a nonlinear positive effect of Nightlights^2 ($\beta = 0.40$, SE = 0.08; $p < 0.01$; Figure 2; Table 2). When excluding surveys from Singapore (an outlier with a large number of detections for a small area), no variable outperformed the null/reduced model or had significant p-values, suggesting Singapore drives the positive relationship with Human Footprint.
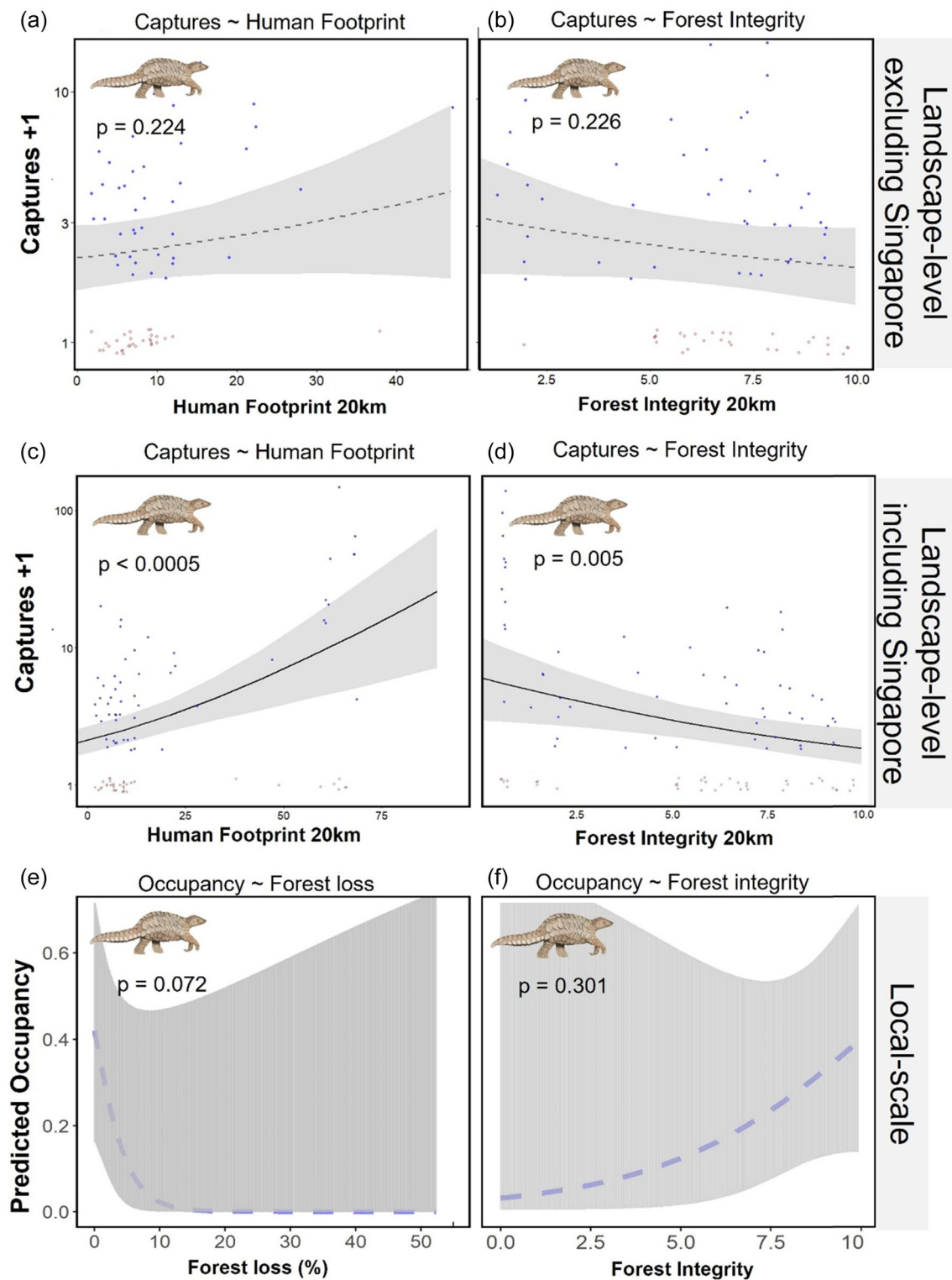
Local-scale habitat associations

Our new camera trapping sessions set 1102 cameras across 10 landscapes within our species' range and yielded detections in 9 of 10 landscapes and a total 69 independent detections (Supporting Information: Table S8). The new camera trapping recorded very high detection rates (0.4–0.6 detections per 100 trap nights) at a large remote forest on the Thai-Malaysia border (Ulu

TABLE 1 Sunda pangolin range and forest cover in Southeast Asia.

Region	IUCN EOO range (km^2)	Forested EOO (km^2)	Forested EOO (%)	Protected range (%)
Borneo	1,468,320	321,601	21.9	6.7
Mainland SE Asia	1,763,376	376,349	21.3	19
Sumatra	860,069	84,888	9.9	7.6
Southeast Asia	4,354,717	828,891	19	12.2

Note: EOO refers to the extent of occurrence, which we calculated as the total area within the IUCN Red List range in each region (km^2). AOO is the area of occupancy (km^2), which we defined here as the forested area in 2015 remaining within the EOO (Miettinen et al., 2016), which is an overestimate because it assumes all remaining forest is occupied. Therefore, it may be interpreted more correctly as the remaining habitat available. "Percent forested" is the AOO divided by the EOO and the "Percent protected" is the forested area within protected areas divided by the EOO. Protected areas were taken from the Protected Planet database (UNEP-WCMC, 2016). We also present all results separated for each country (Supporting Information: Table S7).

FIGURE 2 Habitat associations for the Sunda pangolin based on detections from camera trapping studies. All variables were centered and standardized before modeling. (a–d) Landscape-scale habitat associations were assessed using ZIP GLMMs, with each data point reflecting the detections for an entire camera trapping session (red denotes absences [jittered] and blue for presences; $N = 123$ surveys from 49 landscapes) and the variables describe the 20 km radius area covering the camera trapping session's landscape (Table 2). (e, f) Local habitat associations were determined from hierarchical occupancy modeling, where variables were measured in the 1 km radius area around each camera (note that linear relationships can appear curved due to the log-link function).

Muda). We recorded high detection rates in the highly urbanized areas of Singapore, in a degraded strip of forest in southern Thailand (Khao Ban Tat) and in the fragmented forest of Lambir Hills in Borneo (all 0.2–0.3 detections per 100 trap nights). There were surprisingly low detection rates in the well-protected areas of Bukit

Barisan Selatan in Sumatra and Khao Yai in Thailand (0.14 and 0.03 detections per 100 trap nights, respectively).

Our hierarchical occupancy model revealed that only recent forest loss ($\beta = -1.48$; SE = 0.83; $p = 0.072$) performed better than the null/reduced model

TABLE 2 Variables associated with landscape-scale variation in camera trap detections (including and excluding Singapore).

Model	β	97.5% confidence interval	AICc	ΔAIC	AICwt
Model selection *excluding* data from Singapore					
Null/reduced	0.80	(0.52, 1.08)	281.3	0	0.24
Forest integrity	−0.19	(−0.50, 0.12)	282.5	1.22	0.13
Human footprint	0.13	(−0.08, 0.34)	282.6	1.29	0.12
Oil palm	−0.13	(−0.42, 0.15)	283.1	1.79	0.1
Model selection *including* data from Singapore					
Nightlights^2	0.40	(0.25, 0.55)	526.6	0	0.98
Human footprint	0.78	(0.43, 1.12)	537.1	10.49	0.01
Human footprint^2	0.03	(−0.22, 0.29)	539.8	13.19	0
Human footprint_log	0.55	(0.13, 0.98)	542.8	16.19	0
Null/reduced	0.93	(0.78, 1.06)	544.9	18.29	0

Note: AICc model selection for univariate linear and nonlinear ZIP GLMMs, with all models controlling for study effort as a fixed effect and landscape as a random effect. Variables were averaged for the 20 km radius areas surrounding the study, then centered and standardized so effect sizes could be interpreted relative to each other. Independent captures were defined as photos separated by 30 min.

TABLE 3 Local-scale Sunda pangolin habitat associations determined from occupancy modeling.

Model	β	AICc	ΔAIC	AICwt
Recent forest loss	−1.48	668.3	0	0.23
Null/Reduced		672.1	3.71	0.03
Oil palm	−1.49	672.9	4.58	0.02
Forest integrity	0.57	672.9	4.59	0.02
Human population	−0.46	673.1	4.76	0.02
Forest cover	0.22	673.6	5.27	0.02
River distance	−0.16	673.7	5.38	0.01
Forest edge	0.11	673.9	5.60	0.01
Elevation	0.02	674.1	5.80	0.01

Note: Results from hierarchical occupancy models. We include models that performed worse than the Null/Reduced model that included sampling effort and camera trapping session, because these addressed specific a-priori hypotheses. Recent forest loss was measured in the year of sampling within a 1 km radius of every camera. Full model outputs are presented in Supporting Information: Table S9.

(only controlling for sampling effort and camera trapping session; Figure 2; Table 3). Further, the R^2 values of all models were low, including when variables had significant p-values, suggesting poor explanatory power generally (Gardener, 2017).

Behavioral changes (diel activity patterns)

We analyzed the Sunda pangolin's diel activity pattern based on 65 independent captures across five landscapes

from our new camera trapping sessions in which there were five or more detections. The kernel density estimation confirmed the nocturnal nature of the species, with activity increasing after 6:00 p.m., peaking around 03:00 a.m., and then decreasing toward sunrise. We found no significant differences in diel activity patterns of Sunda pangolins detected at cameras near areas with high amounts of human disturbance compared to cameras near areas with minimal human disturbance (Figure 3a). Similarly, we found no significant change in diel activity patterns in Sunda pangolins detected at cameras at forest edges compared to cameras in interior forests (Figure 3b). The overlap between activity patterns was high, with the coefficient of overlap values (Dhat$_1$) ranging from 0.781 to 0.898 (all p-value > 0.05; Figure 3; Supporting Information: Table S10).

DISCUSSION

We had predicted Sunda pangolins would avoid areas where interactions with humans would be more common due to poaching and due to the general dogma regarding threatened wildlife being negatively impacted by human disturbance and forest degradation (logging, edges, and fragmentation). However, Sunda pangolins did not exhibit declines near these threats except in the most extreme circumstance where there was locally active deforestation, as measured by forest loss within 1 km of a camera occurring within the year of sampling (local-scale response from occupancy modeling assessing variation within-landscapes). There were also no clear associations with natural habitat variables like elevation or water sources at the local- or landscape-scale. While the highest detection rates within our new camera trapping surveys came from a large remote forest (Ulu Muda on the Thai-Malaysia border), Sunda pangolins also showed consistently high occurrence and detection rates in Singapore. Taken together, Sunda pangolins are habitat generalists with surprising tolerance to degradation and can coexist with humans if poaching is controlled. Pangolins are significant reservoirs for zoonoses so their presence in urban areas of Singapore should be carefully monitored, such as with disease prevalence testing.

Our findings suggest the effectiveness of both large remote protected areas like Ulu Muda—where access for hunters may be difficult—or effective antipoaching measures in smaller forests like in Singapore. Protected area types that fall between these extremes had lower Sunda pangolin detection rates, such as highly degraded forests in Thailand (Khao Ban Tat) and Borneo (Lambir Hills) as well as well-protected forests in Thailand (Khao Yai) and Sumatra (Bukit Barisan Selatan). In the context of Southeast Asia, where there are persistently high deforestation rates, and given that only 12.2% of the Sunda pangolin range (EOO) remains as protected forests, both solutions—large remote parks and highly managed small parks—are critical to prevent their extinction. The success of Singapore's pangolin conservation, achieved in spite of the significant historical disturbance and fragmentation of its forests, underscores the immense conservation benefits of rigorous anti-poaching enforcement.
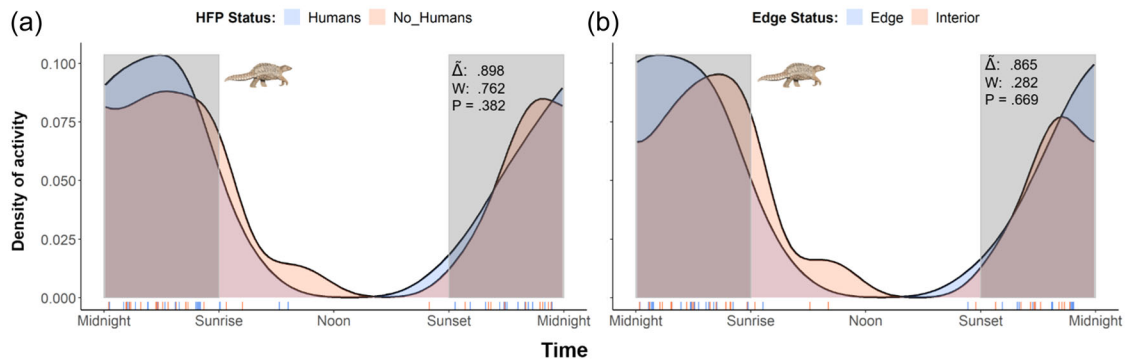
FIGURE 3 No variation in Sunda pangolin nocturnal activity patterns near humans. (a) Variation in the diel activity patterns with the Human Footprint Index (the human versus nonhuman cut-off was the median Human Footprint Index (HPI) value across all cameras). (b) Variation in the diel activity patterns in forest edges, with edges defined as being within 1 km of nonforest areas.

Pangolin tolerance to disturbances

There is mounting evidence from other sources that the Sunda pangolin tolerates some habitat disturbance on the strict condition that poaching is controlled. Khwaja et al. (2019) also demonstrated higher Sunda pangolin occupancy in unprotected than in protected areas, with unprotected areas more likely to suffer harvesting of timber and nontimber forest products, and Wearn (2015) found that Sunda pangolin abundance was higher in logged versus unlogged forests. Sunda pangolins have been observed in monoculture plantations like rubber and oil palm (Lim & Ng, 2008), degraded forests (Azhar et al., 2013; Lim T-Lon, 2008), and Singapore's urban parks and university campuses (M.S. Luskin, personal observation, Nash et al., 2020). Further, the three other pangolin species in Asia (Chinese pangolin, *Manis pentadactyla*, Indian pangolin, *Manis crassicaudata*, and Palawan pangolin, *Manis culionensis*) have also been observed in rubber plantations, tea-dominated home-garden, and logged-over lowland forest (Karawita et al., 2018; Lagrada, 2012; Pabasara et al., 2015; Schoppe et al., 2020; Wu et al., 2003, 2020). These results suggest the true Sunda pangolin habitat AOO may include some nonforest habitats such as tree plantations, pending poaching can be controlled. Sunda pangolin's ability to persist in degraded areas did not appear to be dependent on the behavioral plasticity of their diel activity pattern, whose nocturnality did not significantly shift nearby humans. However, Sunda pangolins may avoid active logging areas where poaching is more likely (this study), yet they may utilize previously logged areas with potential insect foraging opportunities (e.g., Wearn, 2015).

Scale dependency

We observed varying responses to forest degradation at different spatial scales. Forest cover was a positive predictor in the MaxEnt SDMs, and recent forest loss was a negative predictor in the local-scale occupancy (both analyses using covariates extracted at 1 km spatial grain). However, no forest cover variables were significant in the landscape-scale analyses. The landscape-scale analyses that included Singapore, where the 20 km radius included urban areas, may have driven the significant positive association with humans at this spatial scale (e.g., night lights and the Human Footprint Index). A more likely explanation is that Sunda pangolins are responding to the safe haven from poaching in Singapore at large scales (i.e., not that they prefer night lights). This interpretation is corroborated by the removal of those landscape-scale associations when excluding Singapore from the analyses. Further, our local-scale occupancy analysis (using a 1 km radius) did not reveal positive associations with humans or associated variables. Finally, local-scale pangolin tracking found that—within Singapore—pangolins do not prefer edges or degraded areas (Lim & Ng, 2008). Future research should carefully consider the effects of spatial gain on habitat associations.

Future research

Despite compiling the largest data set of occurrence records for this species to date, we urge conservative interpretations due to relatively low statistical power and small effect sizes. Further, much of the camera trapping included in our data set occurred in protected areas and thus, habitat associations derived from our analyses may be biased accordingly, so we urge new sampling to be located in unprotected forests. Research is also needed comparing pangolin diet, behavior, and overall fitness in pristine versus degraded habitats.

Conservation implications

Asia.Sunda pangolins have dramatically declined due to poaching across Southeast Asia but do not show strong avoidance of higher-risk areas (degraded forests, edges, and nearer humans). Where poaching is effectively controlled, such as in Singapore, our results demonstrate that Sunda pangolins can tolerate habitat degradation and humans more than previously perceived. Sunda pangolins may successfully coexist with humans through their strict nocturnality that reduces the risks of human-wildlife interactions.

Sunda pangolins are notable disease reservoirs so their persistence near humans should be coupled with disease monitoring and public outreach. Sunda pangolin conservation would be undermined if there is a spillover event that turns public opinion. Pending declines in deforestation rates and poaching can be controlled, our results suggest there is hope for the Sunda pangolins' long-term persistence in remaining fragmented and degraded areas of Southeast Asia.

AUTHOR CONTRIBUTIONS

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data and R code are available via the figshare Digital Repository https://doi.org/10.6084/m9.figshare.22566721.

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SUPPORTING INFORMATION

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