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Sun Bear Ecology and Conservation: Multiscale Habitat Associations in Southeast Asia

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ABSTRACT

Degraded tropical forests, defined here as logged, fragmented, and edge forests, constitute most of the remaining natural areas in Southeast Asia, potentially contributing to megafauna declines and extirpations. The sun bear (*Helarctos malayanus*) is a megafauna species native to Southeast Asian forests and is generally considered a forest specialist, and thus may be at risk from widespread forest degradation. To clarify the sun bear's responses to forest degradation, we assessed landscape- and local-level occurrence and diel activity across 38 landscapes throughout its range. First, we assess among-landscape variation in sun bear detections by comparing detection records from 185 camera studies. Second, we assess within-landscape variation in abundance using 19 new camera surveys in eight landscapes and Royle–Nichols hierarchical modelling to account for imperfect detectability. Finally, we assessed diel activity in intact versus degraded forests. Across the region (among landscapes), sun bear detections were higher in larger forests, but unexpectedly also in forests that neighbour humans. Within landscapes (i.e., local-scale), there were no significant responses to forest degradation but sun bears avoided oil palm plantations and had positive associations with elevation and humans. The diel activity analysis showed that sun bears are predominantly crepuscular and do not shift their activity patterns in degraded forests or near humans. These findings challenge prior work suggesting sun bears are specialists and suggest they are more tolerant of humans and forest degradation than previously realised. The sun bear's adaptability may be traced to its being a habitat generalist and omnivore, rather than to temporal partitioning to avoid humans. Our multi-scale synthesis suggests that, where hunting is low, degraded forests contribute to sun bear conservation.

1 | Introduction

Globally, megafauna, usually defined as terrestrial mammals with an average adult mass greater than 40 kg, are experiencing significant population declines (Harrison et al. 2016; Ripple et al. 2016, 2019). Southeast Asia, in particular, is suffering severe losses of megafauna in recent decades (Ripple et al. 2016; Mahmood et al. 2021; Amir et al. 2022), largely due to the widespread poaching (especially snaring), as well as deforestation and forest degradation (defined as logged, fragmented, and edge forests) (Hughes 2017; Strang and Rusli 2021). One Southeast Asian

Summary

Much of the natural environment in Southeast Asia has been degraded by humans, and along with hunting, these factors often contribute to declines of megafauna, such as sun bears (*Helarctos malayanus*). To determine the sun bear's response to forest degradation, we assessed sun bear detections at two spatial scales, regional (landscape-level) and locally (within a single landscape). We collated new and previously published camera trap studies and assessed how sun bear detection rates varied with environmental and anthropogenic factors. We also assessed the times at which sun bears were detected to determine whether they change their behaviour in disturbed habitats. At the regional/landscape scale, sun bears were detected most frequently in large forests but were also common in forests that neighboured humans. At the local scale, sun bears were associated with higher elevations and avoided oil palm plantations. We found that sun bears were mainly crepuscular and did not change their behaviour to avoid humans. These results suggest sun bears may be able to survive in areas with low-intensity forest degradation and although the reasons are not clear, it could be due to their omnivorous diet, and not by avoiding humans. Our findings suggest that some moderately degraded forests have high conservation value for sun bears.

- **Practitioner Points**
    - Across their range, sun bears are associated with large forests but are also present in forests near humans and infrastructure like roads.
    - Sun bears are predominantly crepuscular and do not shift their activity pattern to avoid humans.
    - Moderately degraded habitat (logged forests and forest edges) has significant conservation value for sun bears and should therefore be protected and managed to reduce hunting.

megafauna species that is threatened by these processes is the world's smallest bear species, the sun bear (*Helarctos malayanus*) (Meijaard 1999; Scotson et al. 2017a).

The sun bear's range extends from Yunnan Province in China southward through continental Southeast Asia and into Sumatra and Borneo (Linkie et al. 2007; Fredriksson 2012; Nazeri et al. 2014; Li et al. 2017). The species has an International Union for the Conservation of Nature Red List (IUCN-RL) classification of "Vulnerable" (Scotson et al. 2017a), as its population is declining due to acute and synergetic threats (Wilcove et al. 2013; Gallego-Zamorano et al. 2020). First, despite being listed in the Convention on the International Trade in Endangered Species (CITES) Supporting Information: Appendix I, sun bears are targeted by hunters and poachers for bushmeat, body parts such as claws for souvenirs, and especially gall bladders for bile used in traditional Chinese medicine (Shepherd and Shepherd 2010; Krishnasamy and Shepherd 2014; Gomez et al. 2020). Sun bear cubs are also targeted for the illegal pet trade (Scheffers et al. 2019). Second, Southeast Asian forests have undergone profound environmental changes in recent decades. There has been extensive land clearing for timber, as well as for crops such as rubber and oil palm. Additionally, over 70% of Asia's remaining forest is degraded by being within 1 km of an edge and is often selectively logged (Haddad et al. 2015; Grantham et al. 2020). As land clearing often requires the simultaneous construction of roads that provide access to poachers, these two key threats to sun bears (forest degradation and hunting) often interact synergistically (Laurance et al. 2009; Clements et al. 2014). Therefore, the sun bear's continued persistence largely depends on the degree of forest degradation it can tolerate and low hunting.

Sun bears are often considered forest specialists that predominantly occupy intact, undisturbed, lowland, dipterocarp tropical forests (Augeri 2005; Wong et al. 2013; Nazeri et al. 2014). This paradigm has been challenged by studies demonstrating that sun bears can persist in regenerating forests previously degraded by logging, provided poaching is low (Linkie et al. 2007; Brodie et al. 2015; Guharajan et al. 2021; Hwang et al. 2021; Guharajan et al. 2022). Our work follows from that of Guharajan et al. (2021, 2022), and Hwang et al. (2021)—who identified that sun bears can persist in recently or currently logged forests. We assess this by analysing sun bear camera detections relative to forest and anthropogenic covariates on a larger scale. Guharajan et al.'s (2021, 2022), and Hwang et al.'s (2021) work were confined to relatively small geographic areas and may be subject to site-specificity, while our datasets cover a larger portion of the species' range and utilises data sourced from multiple countries. Finally, we conducted analyses at two spatial scales (within and among landscapes), which is informative to managers who operate across different scales, from park rangers working in a single landscape up to regional, national, or international level planning.

Anthropogenic activity may not only reduce the habitat available to sun bears but may also affect their behaviour. Many diurnal and crepuscular animals are known to adjust their behaviour in areas with humans by becoming more nocturnal in order to avoid times of the day when humans are most active (Gaynor et al. 2018; Negret et al. 2023; Lee et al. 2024). Disturbed forests are likely to contain humans, such as people hunting or collecting non-timber forest products like firewood (Fotang et al. 2021), so measures of degradation can be used as a proxy for human presence. However, it is important to acknowledge that forest degradation is not a perfect proxy for human activity, and poachers may focus on intact forests (O'Kelly et al. 2018). Research on sun bear diel activity is limited, with studies from intact forests suggesting that they are predominatly diurnal (Te Wong et al. 2004; Augeri 2005; Gouda et al. 2020) and possibly more nocturnal closer to forest edges (Griffiths and Schaik 1993; Tee et al. 2021). This shift to nocturnality could potentially allow sun bears to avoid humans during daylight hours when they are more likely to be present in the landscape (Lee et al. 2024). However, we did not identify any research that suggests that sun bears adapt their diel activity near humans or in degraded forests.

With the exception of Scotson et al. (2017b) and Guharajan et al. (2022), the latter only utilising data from Sabah, Malaysian Borneo, there is a dearth of range-wide ecological research, syntheses, or comparative analyses for sun bears, with the majority of studies focused on small geographic areas (Linkie et al. 2007; Wong and Linkie 2013; Guharajan 2016; Lee et al. 2019). We expand on these earlier studies by including a larger dataset and analysing diel activity alongside habitat associations. In this study, we examine relationships between sun bear occurrence records collected from several sources across multiple landscapes in the species' range alongside anthropogenic and habitat variables at landscape and local scales. We expected variation in the strength of relationships with the same covariate across the two spatial scales, but that the primary drivers and directions of effects would be consistent. We predicted that sun bears would be positively associated with habitat covariates, including forest size, forest quality, and the Forest Landscape Integrity Index. Likewise, we predicted they would be negatively associated with anthropogenic covariates, including human population, night lights, the Human Footprint Index, and oil palm plantations. This last prediction was less certain as sun bears, like many other animals, are known to enter oil palm plantations where they consume both fruit and insects (Normua et al. 2004; Abidin et al. 2018; Guharajan et al. 2018). However, sun bears may be vulnerable to snaring in plantations, so oil palm and nearby forests may be population sinks (Luskin and Potts 2011; Luskin et al. 2014; Luskin et al. 2018), and they still require neighbouring forests to retreat (Cheah 2013; Guharajan et al. 2018). We therefore predicted that, overall, the extent of oil palm plantations would negatively affect sun bear detections. Finally, we hypothesised that sun bears would shift their diel activity towards nocturnality near humans and in degraded forests, consistent with other species' responses (Lee et al. 2024).

2 | Methods

This paper is modelled after several previously published papers (Dehaudt et al. 2022; Dunn et al. 2022; Carr et al. 2023; Decœur et al. 2023; Hendry et al. 2023; Honda et al. 2023; Luskin et al. 2023a; Nursamsi et al. 2023; Mendes et al. 2024b), hence the similarities in many parts of the methods.

2.1 | Study Region, Data Sources, and Approach

We defined the region of focus for this study as the tropical forest range of the sun bear in Southeast Asia, which specifically includes Myanmar, Thailand, Cambodia, Laos, Peninsular Malaysia, Sumatra, and Borneo [the species has been extirpated from Singapore for over 75 years; (Amir et al. 2022; Brodie et al. 2023; Sartor et al. 2024)]. While sun bears also occur in South Asia (i.e., Northeast India) and infrequently occur in Yunnan province in China, we limited our analysis to the tropical rainforests of Southeast Asia. To make inferences at different scales, we compiled presence and absence data for the sun bear from two sources: (1) survey-level total detections reported in published camera trapping studies and (2) camera-level detection histories from new camera trapping sessions conducted across eight landscapes in Southeast Asia. Presence data consisted of georeferenced occurrence records, defined as the coordinates of a location where a sun bear was observed. We defined a camera study as a continuous sampling effort using at least 10 cameras within a landscape (10–1000 km^2). We refer to the sampling area as a "landscape"—usually a national park, a production forest, or a collection of nearby forest patches within a 20-km radius area (1256 km^2). When comparing landscape-level surveys, camera sampling likely reflects population-level metrics, since individual sun bears have relatively small home ranges compared to other bear species (approx. 15 km^2 from one study—Te Wong et al. 2004). On the contrary, detection histories from landscapes partitioned into many 10 km^2 grid cells likely reflect individual-level habitat associations.

It is essential to acknowledge that any observed variation might be due to differences in methodologies at different scales, but this likely introduces noise rather than bias.

2.2 | Collating Published Camera Studies

We compiled published camera trap records by searching Web of Science with the following criteria: 'camera*' AND Asia* or Thai* or Malaysia* or Indonesia* or Borneo* or Cambodia* or Vietnam* or Lao* or Myanmar* or Burm* or Sumatra*. We selected from the list of returned studies those that were written in English and reported relevant results for the sun bear, including sampling effort (number of cameras, and deployment length or total trap nights), and number of independent detections using a 30–60 min interval between detections of the same species, referred to as "independence period" (Rovero and Zimmermann 2016). We examined the references listed in key papers to identify and include further sources. We included all tropical forest camera studies that used unbaited cameras placed < 0.4 m high, usually facing trails or other areas used by wildlife. This is the standard deployment approach used in the region and suitable for most semi-terrestrial species > 1 kg (Rovero and Zimmermann 2016). From each study, we recorded the location (forest name and coordinates), detection, and effort (number of trap nights). We grouped multiple studies from the same landscape in the same year by summing detections and effort among the studies and averaging the covariate values (Greco et al. 2025). We assumed that all studies that occurred in regions where the sun bear is sympatric with the Asiatic black bear (*Ursus thibetanus*) correctly distinguished between these two species. The full dataset is publicly available (Mendes et al. 2024a).

2.3 | New Camera Trapping Sessions

We conducted a total 19 new camera trapping sessions in eight tropical forest landscapes in Thailand, Peninsular Malaysia, Sumatra, and Borneo between December 2013 and June 2020. These sessions occurred in seven different landscapes in the sun bear's range as recognised by the IUCN (Scotson et al. 2017a). One session of camera trapping also occurred outside the sun bear's IUCN range, in Lambir Hills National Park in Sarawak (taking the total number of landscapes where new camera trapping occurred to eight). Further details on the new camera trapping sessions are provided in Supporting Information: Table S1.

We deployed between 18 and 78 passive infrared Bushnell Trophy and Reconyx HC500 Hyperfire cameras across sampling areas ranging from 10 to 813 km^2. We standardised deployment methods across all landscapes. Cameras were placed within a pre-mapped grid and spaced at least 500 m apart in large, forested landscapes (> 50 km^2) and 100–500 m apart in smaller forest patches. Cameras were attached to trees 0.3 m above ground along hiking trails or natural wildlife trails and deployed for approximately 60–90 days. Sun bear detections were considered independent if they occurred at least 30 min apart (Rovero and Zimmermann 2016). We differentiated sun bears from Asiatic black bears based on body shape and size, as well as fur colour. Research permissions are provided in Supporting Information: Table S7.

2.4 | Landscape-Level Habitat Associations Using GLMMs of Sun Bear Detections

We used both the published and new camera trap data to investigate landscape-scale relationships between the number of sun bear detections and various environmental and anthropogenic factors using generalised linear mixed-effect models (GLMMs) with a negative binomial error distribution (Mendes and Luskin 2025). We treated detections as count data and included a fixed continuous term to control for study effort (measured in trap nights) and a random categorical term for landscape, because some landscapes had multiple studies. Following Ash et al. (2020), we used raw count data as opposed to a relative abundance index (RAI, independent photos per 100 trap nights) to enable use of a negative binomial distribution. We note that these approaches do not account for variation in detection probability, and thus we are implicitly assuming that detection probability among studies does not vary, and acknowledge this may introduce measurement error and that detections do not linearly reflect true abundance (Sollmann et al. 2013). We also acknowledge that there is unexplained variation in detections owing to slight differences among studies in equipment, deployments, and data curation. Furthermore, sun bear detectability could vary due to the availability of fruit across time, such as in masting years when there may be a reduced need to travel (Fredriksson et al. 2006; Dehaudt et al. 2024b). All sources of measurement error reduce our power of detecting statistically significant or 'true' relationships, but do not lend themselves to directional bias.

We used GLMMs to test the effect of 10 environmental and anthropogenic predictor variables (covariates) on sun bear detections reported in published camera studies conducted across different landscapes. Our covariate values were derived from GIS layers and describe the area within a 20 km radius around the centroid of each landscape. Forest sizes were determined from the IUCN Red List protected areas database (UNEP-WCMC and IUCN 2021) or, for unprotected areas, from the original papers' reporting. Sources for covariate data are listed in Supporting Information: Table S2. We used this study area (1256 km^2) to account for large sampling grids and unclear centroids inferred for some landscapes. We also used the year of camera trapping as a covariate (resulting in 11 total covariates tested) to determine if and how the amount of sun bear detections has changed over time. Details of the references, study sites, camera effort, and sampling periods are available in the CamTrapAsia database (Mendes et al. 2024a).

We tested each variable independently with linear and nonlinear (quadratic) univariate models and used AICc model selection to identify the most parsimonious models (Burnham and Anderson 2002). We used the conventional cut-off of 2.0 to identify clear differences in models. Nonlinear models allowed us to identify peaks of sun bear detections that could exist at mid-levels of a covariate value. We also tested bivariate models. To avoid multicollinearity, we tested correlation among our covariate pairs by creating a correlation matrix and excluding all covariate pairs that had a correlation coefficient of 0.4 or greater. All GLMMs were implemented using the R package "glmmTMB" (version 1.1.8) (Brooks et al. 2017).

2.5 | Local-Scale Habitat Associations Using Royle–Nichols Hierarchical Modelling

We assessed the effect of habitat variables on sun bear abundance at the local scale using Royle–Nichols abundance models (Royle and Nichols 2003) (see Supporting Information: Table S4 for details of sampling effort, detection rates, and naïve occupancy). For this, we only used data from our 19 new camera trapping surveys. We use the Royle–Nichols model, which uses presence–absence data to derive a relative abundance metric by exploiting the positive relationship between variation in individual detection probability and the species' abundance (Royle and Nichols 2003). RN models reveal habitat associations by estimating abundance relative to a gradient of a covariate while accounting for imperfect detection (Kéry and Royle 2021). Hierarchical abundance modelling, such as N-mixture models, often face assumption violations when using camera trap data, so we conservatively interpret the results of our model and avoid inferring that these values reflect the actual abundance or density. Rather, relative abundance is only informative when being predicted by covariates to reflect spatial variation in abundance (Gilbert et al. 2021).

To ensure that model outputs were spatially comparable across multiple landscapes and to prevent detecting the same sun bear at different sampling units, we resampled the data into 10 km^2 hexagon grid cells, as suggested by Rayan and Linkie (2020), which is smaller than one estimate of the average home range of sun bears of 14.8 km^2 (Te Wong et al. 2004). We produced a sun bear detection history matrix based on a sampling occasion of 3 days containing presence/absence data (0 = sun bear not detected; 1 = sun bear detected; NA = inactive sampling unit or occasion). Each sampling unit (hexagon) contained at least one camera, but for those with two or more, sun bear presence/absence per sampling unit and sampling occasion was informed by all active cameras in the sampling unit they occurred in, and we averaged their covariate values. We included "study" as a fixed effect to account for potential variation in abundance associated with each set of deployments, and to maintain the spatial and temporal independence of our sampling units, as well as satisfy the assumption of population closure. We also included the total effort, in trap nights, per sampling unit as a fixed effect in the detection formula to account for multiple cameras grouped in a spatially explicit sampling unit (e.g., multiple cameras in one grid cell). We tested the effect of local-scale predictors such as elevation, percentage of oil palm plantations, human population, and percentage of degraded forest, which were all calculated using a 1 km radius around each camera's coordinates (3.14 km^2 area; sources for all covariate data are listed in Supporting Information: Table S2). Degraded forest included 'combined land cover of oil palm, lowland mosaics, lowland open ground, and regrowth/

plantations' and is sourced from Miettinen et al. (2016). The variable present in the GLMM analysis but not the RN analysis were forest size, forest cover, roughness, and night lights. We addressed potential issues with collinearity among covariates by limiting our investigations to univariate models as we did not obtain sufficient detections at many sites to test multivariate models. We used AICc to identify the most parsimonious univariate model and implemented all analyses in the R packaged 'unmarked' (Fiske and Chandler 2011). The conventional cut off of 2.0 AICc points was again used to identify clear differences in models.

2.6 | Diel Activity Patterns

We used time-stamped detections from our new sampling to investigate if forest degradation affects the sun bear's diel activity by comparing Kernel density estimates of sun bears in degraded and non-degraded (intact) forests. Specifically, we split detections based on the median value of the forest degradation variable (sourced from Miettinen et al. 2016) and ran a bootstrap procedure to simulate 1000 distributions of activity pattern data to conduct a Wald test using the function compareAct() in the R package "activity" (Rowcliffe et al. 2014). For this analysis, we calculated forest degradation at a 1.0 km radius around each camera (3.14 km^2) because diel activity is more likely to be affected by local conditions. The coefficient of overlap was calculated using the R package 'overlap' (Ridout and Linkie 2009).

3 | Results

3.1 | Landscape-Level Habitat Associations

From both the new and previously published camera trap studies, we obtained 3360 independent detections of sun bears from 127 camera studies at 38 landscapes in six different countries, as well as 58 studies in the sun bear's range that did not detect the species (Table 1, Figure 1). The bivariate GLMM model containing forest size and night lights (a measure of proximity to humans) was the best predictor of sun bear detections (Table 2 and Supporting Information: S5), with a significant positive relationship for both covariate terms ($p < 0.001$ for forest size and $p = 0.014$ for night lights; Figure 2, Table 2). Examples of forests in the top 20% of sun bear detection rate, human population, and night lights were in Sumatra (Bukit Barisan Selatan National Park, the eastern area of the Gunung Leuser Ecoregion, and Kerinci Seblat National Park) and central Peninsular Malaysia (eastern area of Taman Negara and near Jerteh). Similar to the night lights variable, the human population also had a significant positive influence on sun bear detections ($p = 0.03$, Table 2 and Supporting Information: S5).

3.2 | Local-Scale Habitat Associations

There were 416 independent detections of sun bears in our 19 new camera trapping sessions across eight landscapes, including detections of multiple sun bears together (usually mothers with a single cub). Using the Royle–Nichols (RN) abundance models, elevation was the best predictor (2.88 AICc points lower than the next best performing model) and produced a significant positive relationship ($p < 0.001$, Table 3, and Supporting Information: S6; Figure 3a). The next best models included a

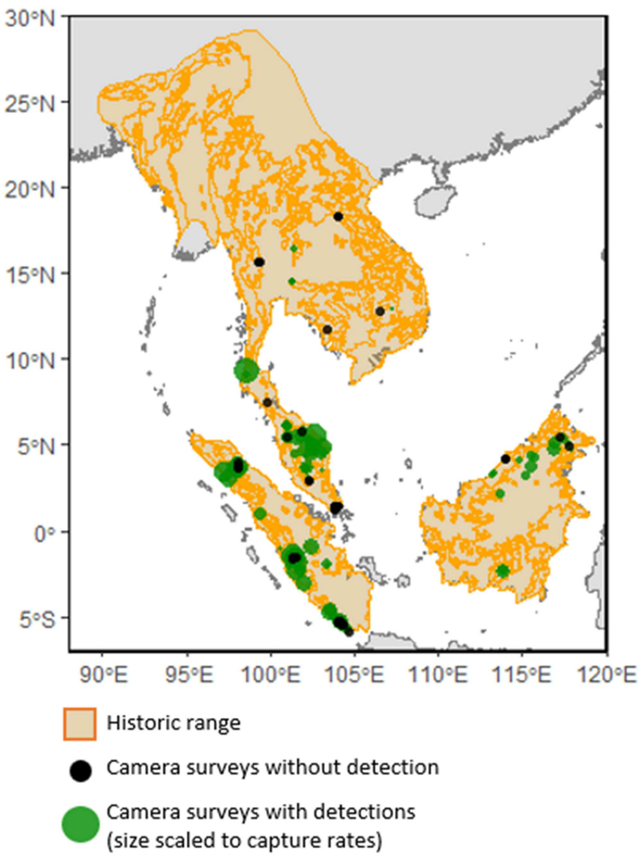

FIGURE 1 | The sun bear's historic range (shown in orange) with points showing the location of sun bear occurrence records used in this study. The historic range data is sourced from the IUCN Red List (Scotson et al. 2017a).

TABLE 1 | Data sources and sample sizes (detections) for the three analyses of this study. Data from new camera trapping data sets were also included in the GLMM analyses.

Analysis	Records
Camera trap count data for GLMMs (landscapes, surveys with detections, surveys without detections)	38, 127, 58
Independent detections for GLMMs	3360
New camera data for RN models and diel activity (landscapes, surveys)	8, 19
Independent detections for RN models and diel activity	416

Abbreviations: GLMMs, generalised linear mixed-effect models; RN, Royle and Nichols.

TABLE 2 | Top five GLMM models assessing sun bear detections among landscapes as determined by AICc model selection.

Model ranking	Terms	Estimate	Std. error	*p*-value
Model 1	Forest size (log)	0.50	0.11	< 0.01*
	Night lights	0.38	0.16	0.01*
Model 2	Forest size (log)	0.49	0.11	< 0.01*
	Human population (log)	0.29	0.14	0.03*
Model 3	Forest size (log)	0.42	0.11	< 0.01*
	Year	−0.31	0.15	0.04*
Model 4	Forest size (log)	0.44	0.13	< 0.01*
	Elevation	−0.06	0.14	0.64
Model 5	Forest size (log)	0.39	0.12	< 0.01*
	Forest cover	0.06	0.17	0.74

Note: We used AICc model selection criteria to compare negative binomial GLMMs. The full model ranking table, which includes the AICc and ΔAICc values, is Supporting Information: Table S5. The response variable was independent sun bear detections in 185 published camera trap studies, and we included study effort as a fixed effect and landscape as a random effect. All covariates were averaged for the 20 km radius area surrounding the study site, then centred and standardised so effect sizes could be interpreted relative to each other, with the exceptions of Forest size, which was measured in km^2 and year, which refers to the year that a camera trapping study began. Correlations among predictors were checked and predictor pairs that had a correlation coefficient of 0.4 or greater were included. Only linear covariates were used for the multivariate models. Sources for covariate data are listed in Supporting Information: Table S2. The asterisks (*) denotes significant results.
Abbreviations: AIC, Akaike information criterion; GLMMs, generalised linear mixed-effect models.

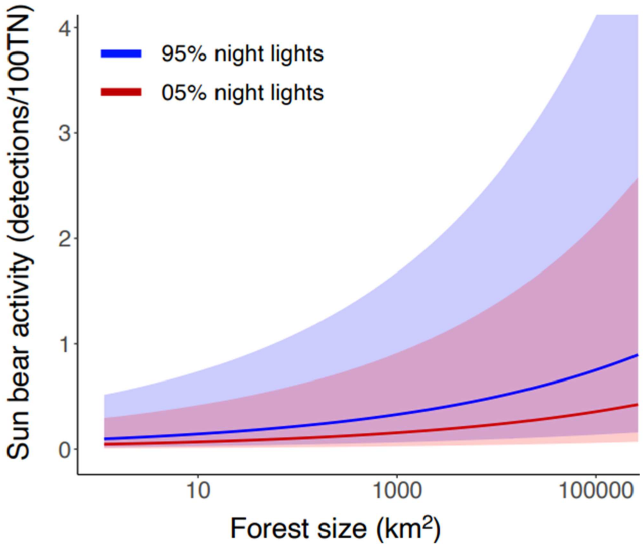

FIGURE 2 | Sun bear detections (per 100 trap nights) from 185 published and new camera trap studies, as predicted by the top GLMM (Table 2), which contained both forest size and night lights as predictors. The blue line shows the model at the 95th percentile night light value associated with a camera trap survey conducted in the sun bear's range, whereas the red line shows the model at the 5th percentile for night lights. The blue and red ribbons represent the 95% confidence interval for both conditions, however there is considerable overlap between these ribbons resulting in a purple ribbon and only a small section of red ribbon in the bottom right corner of the graph. GLMM, generalised linear mixed-effect model.

positive effect of human population ($\Delta AICc = 2.88$; $p = 0.001$) and a negative effect of oil palm ($\Delta AICc = 5.51$; $p = 0.024$; Table 3, and Supporting Information: S6; Figure 3b,c). Intact and degraded forests had a positive and negative influence on sun bear abundance, respectively, although these were not the best performing models based on AICc model selection (Supporting Information: Table S6).

TABLE 3 | Top five abundance models assessing sun bear habitat associations at a local scale (within landscapes), as determined by AICc model selection.

Terms	Estimate	Std. error	*p*-value
Elevation	0.3	0.09	< 0.01*
Human population	0.25	0.08	< 0.01*
Oil palm	−0.31	0.14	0.02*
Forest intactness	0.32	0.17	0.07
Degraded forest	−0.28	0.17	0.1

Note: The full model ranking table, which includes the AICc and ΔAICc values, is Supporting Information: Table S6. We fit Royle–Nichols abundance models with camera trapping session as a covariate to account for variation among landscapes and between surveys in the same landscape and effort affecting detection probability (per 10 km^2 sampling unit). Sources for covariate data are listed in Supporting Information: Table S2. The asterisks (*) denote significant results.
Abbreviation: AIC, Akaike information criterion.

3.3 | Diel Activity Patterns

Using the 416 independent detections of sun bears from our new camera trapping, we assessed sun bear diel activity using kernel density estimates. Sun bears showed a clear bi-modal activity peaks inferring a crepuscular activity pattern, with a first activity peak at dawn and a more prominent activity peak at dusk and shortly thereafter (Figure 4). For our activity pattern comparison between sun bears living in degraded and non-degraded forests, the median forest degradation value was zero. There were 724 cameras classified as intact forest and 372 cameras classified as degraded (noting that we excluded degraded landscapes with no sun bear detections). There was no change in diel activity when comparing intact versus degraded forests (Wald test $p = 0.271$; Figure 4).

4 | Discussion

Using detections sourced from 127 camera trap studies from 38 landscapes, sun bear detections were highest in large forests

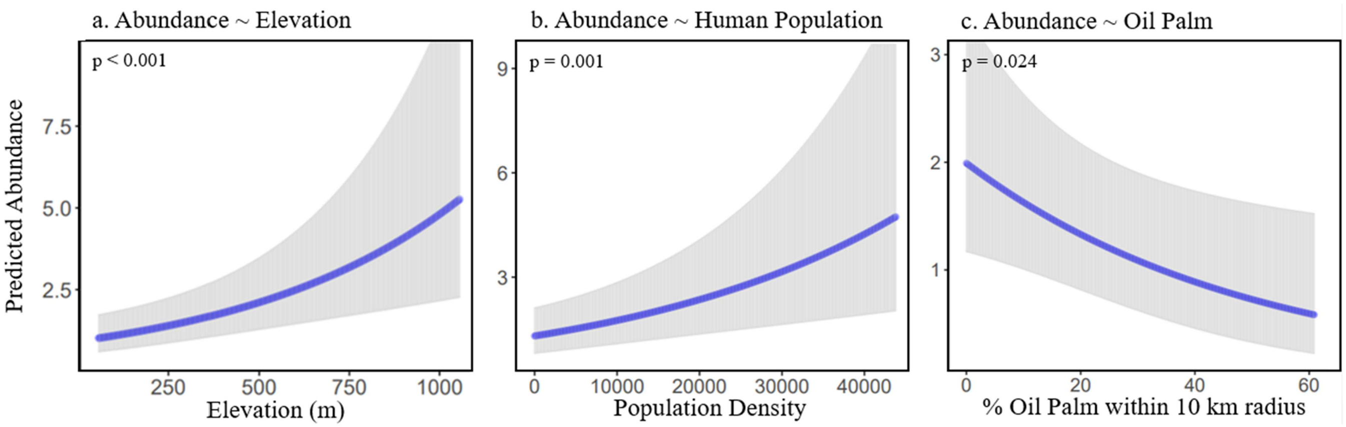

FIGURE 3 | Local variation in sun bear predicted abundance determined from detection-correction Royle–Nichols hierarchical modelling of camera trapping from eight landscapes in Southeast Asia (the three best performing models are shown; Table 3 and Supporting Information: S6). The y-axis is predicted sun bear relative abundance per 10 km^2 sampling unit. All covariates were centred and standardised prior to modelling, so effect sizes can be compared between variables.

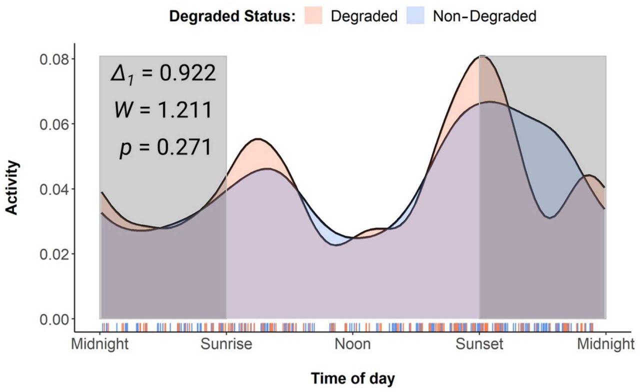

FIGURE 4 | Diel activity pattern of the sun bear in degraded (orange) and non-degraded forests (blue) determined from 416 independent detections during 19 camera trapping surveys at eight landscapes across their range in Southeast Asia. Time-stamped sun bear detections were assigned to the degraded or non-degraded forest category based on whether the detection occurred in intact versus degraded forest. Degradation included any forest with oil palm plantations, lowland mosaic forest, lowland open ground, and regrowth forests within a 1.0 km radius of a camera trap in our new camera trapping sessions (Supporting Information: Table S2). Δ_1 refers to the extent of overlap in activity of sun bears in the two different forest categories. *W* refers to the Wald test result comparing these two distributions and *p* refers to the *p* value associated with this Wald test. The tick marks (rugs) at the bottom of the figure show the exact time of each sun bear detection, coloured-coded to match the degradation status of the location in which it occurred.

and areas with more night lights, a proxy for humans and their infrastructure. Two notable areas with high detections of sun bears near night lights (humans) were landscapes in Sumatra and central Peninsular Malaysia, where there are many towns directly bordering large parks. This result was consistent with the local scale Royle–Nichols (RN) hierarchical modelling from eight landscapes, which also showed sun bears being positively associated with humans and also elevation, but negatively associated with oil palm plantations. Taken together, a parsimonious explanation for these results is that sun bears are frequently detected at the edges of large forests in areas close to humans (where there are night lights), and within these large forested landscapes (local scale), they show a preference for higher elevations and an avoidance of oil palm plantations. These results provide a rationale to be cautiously optimistic for the conservation of the species in degraded forests.

A key inference from this work was that forest size appeared more important for sun bears than forest quality. The importance of large forests may be due to their large 15 km^2 home ranges and low densities (Te Wong et al. 2004; Abidin et al. 2018). Hwang et al. (2021) also proposed that sun bears can persist in disturbed forests because the greater amount of dead wood in such forests supports insects for sun bears to feed on (Luke et al. 2014; Kimber and Eggleton 2018), and invertebrates comprise a major part of the sun bear diet, particularly in non-masting years when there is less fruit (Wong 2002; Te Wong et al. 2005).

The positive associations with humans in both analyses were unexpected because sun bears are poached, and most megafauna populations decline near humans (Shepherd and Shepherd 2010; Benítez-López et al. 2017; Hughes 2017; Ripple et al. 2019; Gomez et al. 2020; Edinur et al. 2022). The positive associations with humans may be an artifact of high detection of sun bears in Sumatra and Peninsular Malaysia, where there happened to be many towns bordering the large parks. If true, sun bears were not "attracted" to areas with more people and lights, but may be able to survive there.

The negative influence of oil palm was expected, but still interesting because sun bears are known to forage in oil palm plantations (Normua et al. 2004; Abidin et al. 2018; Guharajan et al. 2018). This is likely due to the increased risk of snaring and the access for poachers that oil palm plantations provide and we note that sun bears that utilise plantations still require nearby forests (Cheah 2013; Azhar et al. 2014; Guharajan et al. 2018).

Sun bears are primarily frugivores, and megafauna seed dispersers are crucial for maintaining forest tree community dynamics (Dehaudt et al. 2024a; Anderson et al. 2025; Deblauwe et al. 2025). Large frugivores are often at higher risk (Joshi et al. 2025) and there are numerous ecological cascades that may result from declines in large seed dispersers (Luskin et al. 2017; Williams et al. 2021; Brodie et al. 2025).

4.1 | Scale-Dependency

We expected there to be variation in the strength of habitat covariates among our analyses because sun bear local habitat preferences may differ from those of the entire region they occupy, and the analyses used different data. Interpreting multiple analyses together can provide richer insights but requires nuance. A key example was elevation, which was not a key variable in the landscape-level analyses (Supporting Information: Table S5) but was the top variable in the local-scale analysis (Supporting Information: Table S6). One explanation is that the local analysis cameras were predominantly placed between 0 and 800 m asl, while the landscape-level studies had a range of 9 to 5000 m asl. Taken together, this may indicate a preference for hill forests (e.g., 400–800 m asl) and an avoidance of the lowest and highest areas of the sun bear's range, such as peat swamps < 50 m asl and montane forests > 1000 m asl. This finding is consistent with other studies (Linkie et al. 2007; Steinmetz et al. 2011, Wong et al. 2013).

4.2 | Sun Bear Diel Activity

Many animals—especially persecuted megafauna—adopt a more nocturnal activity pattern in degraded areas to avoid encounters with humans (Gaynor et al. 2018; Lee et al. 2024). For example, both Tee et al. (2021) and Fredriksson (2012) found that sun bears living near forest edges are more nocturnal than conspecifics residing in forest interiors. Instead, we found sun bears were consistently crepuscular (Figure 4). This is consistent with Guharajan et al. (2018) but conflicts with Te Wong et al. (2004) and Cheah (2013), who reported sun bears as being diurnal but become more nocturnal when feeding in oil palm plantations. Methodological differences may explain these inconsistent results, as Guharajan et al. (2018) and Tee et al. (2021) utilised camera traps while Fredriksson (2012) and Te Wong et al. (2004) used radio collars. Future studies utilising radio or GPS collars could resolve discrepancies in sun bear behaviour near humans and forest degradation.

4.3 | Comparison to Previous Studies

Aside from Scotson et al. (2017b), previous analyses of sun bear detection data have been limited to small geographic areas (Guharajan et al. 2021; Hwang et al. 2021; Guharajan et al. 2022). These studies identified that canopy cover and or comparable habitat covariates are positively associated with sun bear detections and persistence in moderately degraded habitat (Hwang et al. 2021). Our study expands on these previous studies by sourcing sun bear camera trap detections from multiple countries and also analysing more covariates than these previous studies, including both habitat and anthropogenic covariates. A key covariate that was analysed in this study was the extent of oil palm plantations. The conversion of rainforest into oil palm plantations is a major conservation issue in the region, so understanding the response of sun bears to oil palm plantations is crucial for their conservation. Overall, our paper concurs with Scotson et al. (2017b) and Guharajan et al. (2022) who identified that large expanses of forested habitat are important for sun bears, but the species can also persist in areas with moderate degradation (Guharajan et al. 2021; Hwang et al. 2021). Together, these findings suggest that sun bears may not avoid humans in space or time.

4.4 | Sun Bear Conservation

Scotson et al. (2017b) and Wong et al. (2013) suggest recent sun bear declines are due to forest loss and poaching (Edinur et al. 2022). Approximately 90% of the potentially suitable habitat for sun bears lies outside protected areas, where poaching may occur (Scotson 2019). Our analyses suggest there is a considerable opportunity to safeguard the species by targeting the protection of large, unprotected forests, which is consistent with other recent analyses in the region (Scotson et al. 2017b; Hwang et al. 2021). Namely, there are large expanses of natural and native timber production forests in the region that may be targeted for this purpose, alongside the enforcement of regulations against poaching and wildlife trade (Linkie et al. 2015; Edinur et al. 2022).

One ray of hope comes from Lambir Hills National Park in Sarawak, Malaysian Borneo, which contains 70 km^2 of intact lowland and hill forest that previously experienced severe poaching. Sun bears were not detected in camera surveys conducted at Lambir Hills in 2002 and 2006, suggesting they may have been extirpated (Shahanan and Debski 2002; Azlan and Lading 2006). There has since been a renewed emphasis on park management and enforcement to reduce poaching, and our 2017 survey detected a sun bear at Lambir Hills National Park. Another potential positive is that the recent outbreak of African Swine Fever may reduce competition with wild boars and improve foraging opportunities for sun bears (Luskin et al. 2021; Luskin et al. 2023b; Lieb et al. 2025).

4.5 | Future Research Directions

To determine whether degraded forests are population sinks or sustain viable populations, longitudinal work across the degradation gradient is needed (Dehaudt et al. 2025). The continued use of cameras among many different groups presents opportunities for collaborations to achieve longitudinal work (Bruce et al. 2025). We also recommend that more camera trap surveys be conducted in regions north of Peninsular Malaysia (e.g., Thailand, Myanmar, and Cambodia), as much of the data for this study was sourced from Peninsular Malaysia, Sumatra, and Borneo. Movement studies to understand how sun bears use degraded forests and corridors will enable better conservation planning. Diet studies are also required to test the hypothesis that sun bears become more insectivorous in degraded forests (Hwang et al. 2021) and the degree to which they consume oil palm and other agricultural products in degraded forests (Cheah 2013). More information on sun bear health, such as variation in their body condition and reproduction, would be especially useful, particularly if such research spans masting and non-masting years and is repeated in intact versus degraded forests. Finally, there is a need to determine whether sun bears are habituating to humans at forest edges and whether human-wildlife conflict is occurring, such as through altered diets.

Author Contributions

Alexander Hendry: formal analysis, writing – original draft preparation, writing – review and editing. **Harsh K. Pahuja:** formal analysis, writing – original draft preparation, writing – review and editing. **Zachary Amir:** data curation, formal analysis, methodology, supervision, visualisation, writing – review and editing. **Ilyas Nursamsi:** formal analysis, visualisation. **Jonathan H. Moore:** data curation, formal analysis, fieldwork. **Matthew Scott Luskin:** conceptualisation, data curation, formal analysis, funding acquisition, fieldwork, methodology, supervision, writing – original draft preparation, writing – review and editing.

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Ethics Statement

Ethical approval for non-invasive camera sampling was not required for this study.

Conflicts of Interest

The authors declare conflicts of interests.

Data Availability Statement

Data available in FigShare: https://figshare.com/articles/dataset/Sun_Bear_Data/23993505. The data that support the findings of this study are openly available in FigShare at https://figshare.com/articles/dataset/Sun_Bear_Data/23993505, reference number 23993505.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.
Sun Bear Supporting Information 20260105.