

# Binturong ecology and conservation in pristine, fragmented and degraded tropical forests

ARATA HONDA, ZACHARY AMIR, CALEBE P. MENDES  
JONATHAN H. MOORE and MATTHEW SCOTT LUSKIN

**Abstract** The persistence of seed-dispersing animals in degraded habitats could be critical for ensuring the long-term conservation value and restoration of forests. This is particularly important in Southeast Asia, where > 70% of the remaining forest areas are within 1 km of a forest edge, and many are degraded (e.g. logged). We synthesized information on the habitat associations of the binturong *Arctictis binturong*, a large, semi-arboreal, frugivorous civet and one of the most important seed dispersers in the region, especially for figs (*Ficus* spp). We adopted a multiscale approach by employing ensemble species distribution modelling from presence-only records, assessing landscape-scale variation in detection rates in published camera-trap studies and using hierarchical occupancy modelling to assess local (i.e. within-landscape) patterns observed from 20 new camera-trap surveys. Contrary to prior reports that binturongs are strongly associated with intact forests, the species was equally present in degraded forests and near forest edges where sufficient forest cover was maintained (> 40% forest cover within a 20-km radius). The species also tolerates moderate incursions of oil palm plantations (< 20% of the area within a 20-km radius covered by oil palm plantations). The relative resilience of binturongs to habitat degradation could be in part because of behavioural adaptations towards increased nocturnal activity. These results support the notion that key seed dispersers can persist and maintain their ecological function in degraded forests.

**Keywords** *Arctictis binturong*, camera trap, civet, conservation, habitat associations, occupancy modelling, seed dispersal, Southeast Asia, Viverridae

ARATA HONDA\* ([orcid.org/0000-0002-7881-4413](https://orcid.org/0000-0002-7881-4413)) Department of Ecology and Evolutionary Biology, Yale University, New Haven, USA

ZACHARY AMIR ([orcid.org/0000-0002-8398-2059](https://orcid.org/0000-0002-8398-2059)) and MATTHEW SCOTT LUSKIN† (Corresponding author, [orcid.org/0000-0002-5236-7096](https://orcid.org/0000-0002-5236-7096), [m.luskin@uq.edu.au](mailto:m.luskin@uq.edu.au)), School of Biological Sciences, University of Queensland, 534 Goddard Hall, St Lucia, Queensland, Australia

CALEBE P. MENDES ([orcid.org/0000-0003-1323-3287](https://orcid.org/0000-0003-1323-3287)), Asian School of the Environment, Nanyang Technological University, Singapore

JONATHAN H. MOORE‡ School of Environmental Science and Engineering, Southern University of Science and Technology, Shenzhen, China

\*Also at: School of Earth and Environmental Sciences, University of Queensland, St Lucia, Australia

†Also at: Centre for Biodiversity and Conservation Science, University of Queensland, St Lucia, Australia

‡Also at: School of Environmental Sciences, University of East Anglia, Norwich, UK

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## Introduction

Southeast Asia has the highest number of threatened mammals of all terrestrial bioregions, with the primary threats being forest loss and hunting (Duckworth et al., 2012). More than 70% of remaining forest areas are within 1 km of a forest edge or are otherwise degraded (Haddad et al., 2015). Populations of large animals tend to decline at habitat edges and in degraded habitats but there are few species-specific assessments in Asia, especially for cryptic animals (Chutipong et al., 2014; Benítez-López et al., 2017; Haysom et al., 2021; Hughes et al., 2021; Amir et al., 2022). Here we examine the effects of forest degradation on binturongs *Arctictis binturong*, large frugivorous civets (Viverridae) that play a key ecological role in supporting the resilience of degraded forests through seed dispersal (Lambert, 1990; Shanahan et al., 2001; Colon & Campos-Arceiz, 2013; Nakabayashi et al., 2017; Nakabayashi & Ahmad, 2018; Allam et al., 2019; Nakabayashi et al., 2019; Ong et al., 2022).

Binturongs are the world's largest civets (adults can weigh > 20 kg) and range from north-east India through the mainlands and islands of Southeast Asia (Wilcox et al., 2016). They are semi-arboreal and mostly frugivorous, spending much of their time resting and feeding in the canopy of fig trees. They also consume smaller amounts of other fruits, leaves, birds, carrion and fish (Lambert, 1990; Lambert et al., 2014; Semiadi et al., 2016; Nakabayashi et al., 2017; Nakabayashi & Ahmad, 2018; Debrulle et al., 2020; Nakabayashi, 2020). Binturongs disperse a wide diversity of figs, including effective digestion and defecation of hemiepiphytes (strangler figs). They have rapid digestion rates, promoting seed germination, which in turn supports many other animals (Lambert, 1990; Shanahan et al., 2001; Colon & Campos-Arceiz, 2013; Nakabayashi et al., 2017; Nakabayashi & Ahmad, 2018; Nakabayashi et al., 2019; Nakabayashi, 2020). The importance of frugivorous species in the order Carnivora has often been overlooked (Draper et al., 2022), and binturong seed dispersal could be especially important in the Indo-Malayan region where there have been severe declines of larger herbivores including Sumatran rhinoceroses *Dicerorhinus sumatrensis*, primates, sun bears *Helarctos*

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*malayanus* and Asian elephants *Elephas maximus* (Scotson et al., 2017; Ong et al., 2022).

Binturongs are threatened by habitat loss and degradation, their use in traditional medicine and the pet trade, indiscriminate snaring and some limited direct exploitation for bushmeat (Lau et al., 2010; D’Cruze et al., 2014; Bourgeois et al., 2020). Consequently, the species is categorized as Vulnerable on the IUCN Red List, with an inferred population decline of 30% over three generations (c. 18 years; Wilcox et al., 2016). However, binturongs are cryptic and their habitat associations remain poorly understood, limiting inferences on their conservation status and their role in supporting seed dispersal in degraded habitats (Debruille et al., 2020). Binturongs have been observed in both primary and secondary forests including logging concessions, areas near agricultural plantations and at elevations from sea level to >1,500 m (Semiadi et al., 2016; Wilcox et al., 2016). Prior studies have suggested they are tolerant to moderate logging but not open plantations or large clearings; however, most such work has suggested that the species prefers large expanses of intact lowland and hill forests (Grassman et al., 2005; Wilcox et al., 2016; Nakabayashi et al., 2017; Debruille et al., 2020).

We compiled information collected through previously published and new camera-trapping data to investigate binturong persistence and behaviour in degraded forests. We employed ensemble species distribution modelling, generalized linear mixed modelling (GLMM) and occupancy modelling using camera-trapping datasets to assess their habitat associations. We predicted that binturongs would avoid degraded habitats and edges at all spatial scales but that they would be positively associated with oil palm plantations because of the availability of fruit and high tree cover in these areas (Luskin & Potts, 2011; Luskin et al., 2014; Dehaut et al., 2022). We also sought to elucidate contrasting findings on binturong activity patterns, with reports ranging from them being strictly nocturnal to primarily diurnal, crepuscular or cathemeral (Grassman et al., 2005; Wilcox et al., 2016; Debruille et al., 2020). We tested whether these variations in diel activity are associated with different habitats or are driven by temporal avoidance of people, which has been noted for hunted species in other tropical forest regions (Frey et al., 2017; Cremonesi et al., 2021; Pardo et al., 2021; Negret et al., 2023).

## Methods

### Data collection

We compiled occurrence data from four sources: (1) the Global Biodiversity Information Facility database (GBIF, 2021), a presence-only repository that includes museum records and citizen science reports (we removed incomplete or erroneous records), (2) the Borneo Small

Carnivores Database (Kramer-Schadt et al., 2016), (3) published reports of camera-trapping studies, and (4) new camera-trapping sessions (Supplementary Fig. 1a). For regional species distribution modelling we used presences from all data sources. For all camera trapping we defined a single ‘study’ as a continuous sampling effort using more than five cameras within a landscape (10–1,000 km<sup>2</sup>) and we refer to the area sampled as a ‘landscape’, which was usually a national park, production forest or collection of forest patches within a 100-km<sup>2</sup> area (Supplementary Fig. 1). We use ‘regional scale’ when reporting results from presence-only species distribution modelling across the species’ range, ‘landscape scale’ when analysing variation amongst published camera-trapping studies and ‘local scale’ for hierarchical occupancy modelling of new camera-trapping sites.

### Collating detections from published camera-trapping studies

We located previous camera-trapping studies using a Web of Science (Clarivate, Philadelphia, USA) search with the following key terms: camera trap\* AND (Asia\* OR Thai\* OR Malay\* OR Indonesia\* OR Singapore\* OR Borneo\* OR Cambodia\* OR Vietnam\* OR Lao\* OR Myanmar\* OR Burm\* OR Sumatra\*). We examined the references in these matches for additional studies. We included studies written in English, conducted after the year 2000 and that reported sampling effort (number of cameras and deployment duration or number of total trap-nights) and number of independent detections (generally defined based on a 30–60 min interval between detections of the same species). To control for detectability, we only included studies that used unbaited cameras placed at < 0.4 m height in forests, usually facing trails or other areas frequently used by wildlife. This is the standard deployment approach used widely in the region and is suitable for the majority of semi-terrestrial species > 1 kg (Rovero & Ahumada, 2017). We recorded the data on locations (landscape name and coordinates), detections, sampling effort and a variety of other covariates (Supplementary Table 1). We grouped multiple studies from the same landscape per year by summing detections and effort and averaging the covariate values.

### New camera-trapping sessions

We conducted 20 new camera-trapping sessions in 10 landscapes across Thailand, Peninsular Malaysia, Sumatra, Borneo and Singapore (Supplementary Table 2), with varying levels of human disturbance and forest degradation. We deployed 18–112 passive infrared camera traps (various models from Bushnell, Overland Park, USA, and Reconyx, Holmen, USA) across areas of 10–813 km<sup>2</sup> in each landscape.

We placed cameras within a pre-mapped grid and spaced at least 500 m apart in large forests (> 100 km<sup>2</sup>) and 100–500 m apart in smaller forest patches (e.g. Pulau Ubin, Singapore). We standardized methods between all deployments, attaching camera traps to trees 0.2–0.3 m above the ground along hiking or wildlife trails. We deployed cameras for c. 60–90 days in each landscape during December 2013–March 2019. To ensure that model outputs were comparable spatially across multiple landscapes and to prevent spatial pseudo-replication, we resampled the capture data into hexagonal grid cells with an apothem of 1 km (Rayan & Linkie, 2020). In most cases, each sampling unit contained only one camera associated with a unique value for each habitat covariate, but we averaged covariate values when multiple cameras fell within the same grid cell. We considered captures to be notionally independent if they occurred at least 30 min apart. 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 Supplementary Table 2 for the complete deployment details for all new camera-trapping sessions.

#### Regional habitat associations

We projected the habitat suitability for binturongs using an ensemble species distribution model considering eight algorithms (Generalized Linear Model, Generalized Boosted Regression, Multivariate Adaptive Regression Splines, Classification Tree Analysis, Random Forest, Maximum Entropy, Artificial Neural Networks and Support Vector Machine; Liu et al., 2019). We employed the *SSDM* package in *R* 4.0.4 (Schmitt et al., 2017; R Core Team, 2020) using presence-only data and spatial environmental variables with 1-km resolution. We selected a suite of anthropogenic and biogeographical variables that have been shown to influence the detection, occupancy and distribution of other civet species in the region (Dehaudt et al., 2022; Dunn et al., 2022). We included only presences recorded after the year 2000 from the four data sources described previously to reduce the effect of historical records in areas where the species or habitat could have been subsequently lost (Fig. 1a). To address sampling bias, we spatially thinned presences to reach a nearest-neighbour distance of at least 10 km amongst all points as binturongs have a home range of 1.54–6.90 km<sup>2</sup> (Grassman et al., 2005; Chutipong et al., 2015; Nakabayashi & Ahmad, 2018). We removed covariates when Pearson's correlation  $r > 0.7$ , to reduce multicollinearity (Supplementary Fig. 2). We generated pseudo-absences following Barbet-Massin et al. (2012), setting the number, repetition and geographical sampling space according to parameters proposed to improve the performance of each algorithm. We combined the top models

from each algorithm after 10 repetitions (inclusion threshold of area under the curve > 0.75) using the area under the curve-weighted mean. We assessed variable importance using the Pearson's correlation between a full model and those reduced by each variable (calculated as a score of  $1 - r \times 100$ ; denoted as  $1 - r$ ). Finally, we calculated the area of remaining forest and the percentage of protected area within the species' extant range, based on the IUCN Red List range map (Wilcox et al., 2016) using the IUCN World Database on Protected Areas (Protected Planet, 2020).

#### Landscape-scale habitat associations

We explored variation in binturong detections in camera-trap studies using GLMMs with zero-inflated Poisson error distribution. Our response variable was counts and we included fixed effects to control for study effort (measured in trap-nights) and random effects for landscape. We note that this approach does not account for variation in detection probability and there is unexplained variation because of differences in equipment and deployment methodology amongst studies. Both sources of measurement error could reduce our modelling power and our ability to detect true relationships (Sollmann et al., 2013).

We selected a suite of biophysical and disturbance variables (Supplementary Table 1) that have been shown to influence the detection, occupancy and distribution of other civet species in the region (Dehaudt et al., 2022; Dunn et al., 2022). The covariate values describe the area within a 20-km radius around the centroid of each landscape. We used this vast study area (1,256 km<sup>2</sup>) to account for some large camera-trapping grids and the possible low precision of centroid coordinates provided or inferred from the landscape descriptions in some studies. We tested each variable independently and with a non-linear term. High collinearity amongst covariates inhibited multivariate analyses and testing for interactions. We used the Akaike information criterion corrected for small sample size (AICc) to identify the most parsimonious model. All GLMMs were implemented in package *GLMMadaptive* in *R* (Rizopoulos, 2019).

#### Local-scale (within-landscape) habitat associations

We used single-season occupancy modelling to explore binturong occupancy within landscapes sampled using new camera-trapping sessions (MacKenzie et al., 2002). Detection probability is expected to be low when studying semi-arboreal binturongs using ground-based camera traps; we counteracted this with our immense trapping effort. Furthermore, ground-based camera traps have previously been shown to record the majority of arboreal mammals at the area of deployment (Rovero & Ahumada, 2017; Moore et al., 2020). To reduce the effects of spatial dependence between nearby camera traps, we resampled

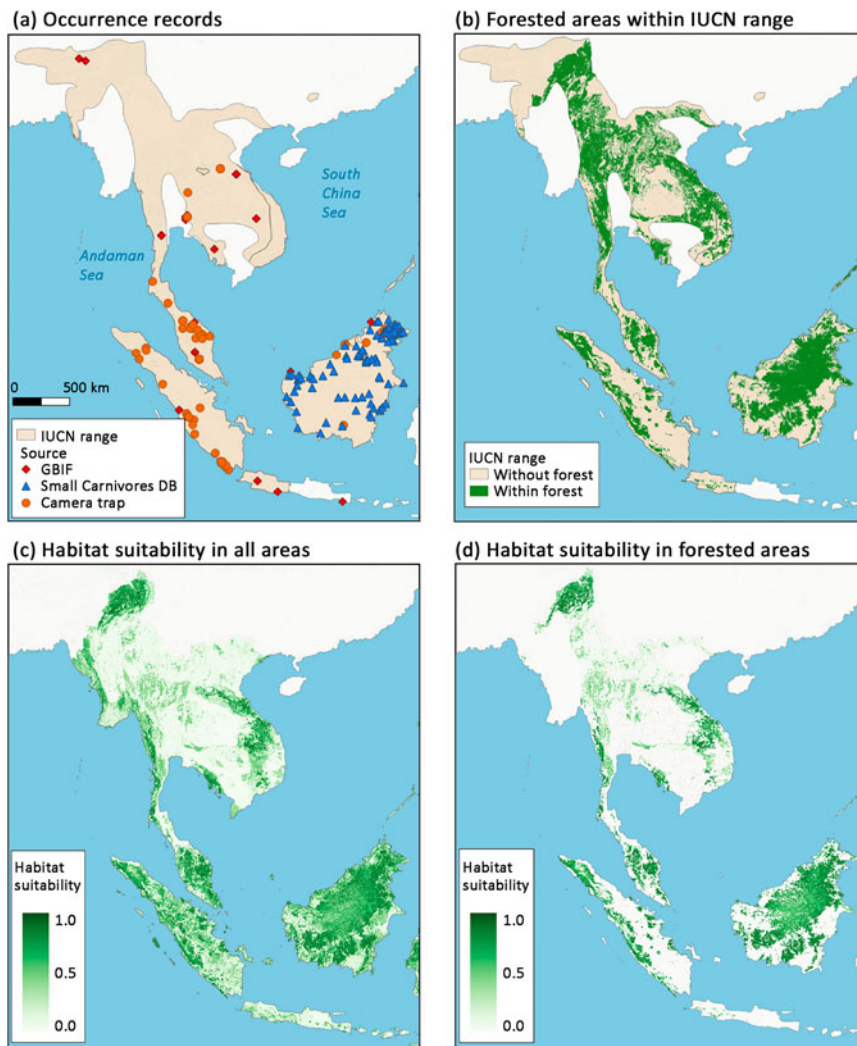


FIG. 1 Binturong *Arctictis binturong* range and habitat suitability. (a) The species' extant range according to IUCN and the locations of occurrence records, by data source: Global Biodiversity Information Facility (GBIF; GBIF, 2021), Small Carnivores Database (DB; Kramer-Schadt et al., 2016) and camera-trap records. (b) Forest cover within the species' range as of 2015, with non-forested areas assumed to be unoccupied. (c) Projection from the top ensemble model visualizing the habitat suitability for binturongs, including areas outside forests and the IUCN-estimated range of the species. (d) The top ensemble model projection of the habitat suitability for binturongs within the remaining forest.

the data into hexagonal grid cells with an apothem of 1 km and defined these 2.6-km<sup>2</sup> cells as sampling units. In most cases, each sampling unit contained only one camera associated with a unique value for each habitat covariate, but we averaged covariate values when multiple cameras fell within the same grid cell. We included a study as a fixed effect to maintain the spatial and temporal independence of our sampling units and to satisfy the assumption of population closure in the models. We extracted covariate values in the 1-km radius around camera traps (Supplementary Table 1) as well as the distance to the nearest forest edge and the nearest river.

#### Diel activity patterns

We used time-stamped detections from our new camera-trapping sessions to investigate variability in the diel activity of binturongs across sampling units and between landscapes and to compare these activity patterns to those of humans. We computed von Mises kernel density estimates in *R* using the *densityPlot()* function from the *overlap* package (Meredith & Ridout, 2020), with default smoothing parameters. We

excluded camera sessions with insufficient detections ( $n < 4$ ). To compare the distributions of capture times between landscapes, we computed coefficients of overlap using the *R* package *overlap* (Ridout & Linkie, 2009) and performed an Anderson–Darling *k*-sample test using the *R* package *kSamples* (Scholz & Zhu, 2019). We tested for significant differences in diel activity patterns between various habitat types (e.g. degraded vs non-degraded, using the median values of the disturbance variables) using a bootstrap procedure to simulate 1,000 distributions of activity pattern data to conduct a Wald test using the function *compareAct()* in the *R* package *activity* (Rowcliffe et al., 2014).

## Results

### Regional habitat associations

We gathered 215 geo-referenced occurrence records of binturongs for our species distribution models, including 80 from new and published camera-trapping surveys, 34 from the Global Biodiversity Information Facility database

(GBIF, 2021), and 101 from the Borneo Carnivore Database (Kramer-Schadt et al., 2016; Fig. 1). We retained 149 records after thinning for spatial independence with a minimum nearest-neighbour distance of 10 km. Individual algorithm projections are shown in Supplementary Fig. 3, details on model performance are provided in Supplementary Table 3 and the top ensemble species distribution model results are shown in Fig. 1(e). The habitats with the highest suitability for binturongs were in central Borneo, central and western Sumatra, much of Peninsular Malaysia, northern Myanmar, central Viet Nam, south-eastern Lao People's Democratic Republic and western Cambodia. Habitat suitability was lowest in western Thailand, central Myanmar, central Cambodia and the northern and southern regions of Viet Nam. The variables containing the highest amount of information when used in isolation in the top ensemble model were annual rainfall ( $1 - r = 51.77$ ), followed by elevation ( $1 - r = 9.73$ ), forest cover ( $1 - r = 9.11$ ) and human density ( $1 - r = 7.72$ ). The top ensemble models include projections with moderate pairwise correlations to single model projections ( $r = 0.492 - 0.792$ ).

The extant range of binturongs (as defined by the IUCN Red List) within our study region was 2.651 million km<sup>2</sup>. Only 38% of this range was forested as of 2015 and 11% was protected (Supplementary Table 4).

#### Landscape-scale habitat associations

We used GLMMs with zero-inflated Poisson error distribution to assess the variation in 181 independent binturong captures from 91 studies in 41 landscapes. The three best predictors (based on AICc) were night lights (negative effect;

$\beta = -10.330 \pm \text{SE } 7.252$ ;  $P = 0.155$ ), forest cover (positive, non-linear effect;  $\beta = 1.296 \pm \text{SE } 0.410$ ;  $P = 0.002$ ) and human footprint (negative effect;  $\beta = -0.853 \pm \text{SE } 0.316$ ,  $P = 0.007$ ; Table 1). After removing surveys from Singapore where the species was never detected, the best predictors were oil palm (negative, non-linear effect;  $\beta = -0.700 \pm \text{SE } 0.303$ ,  $P = 0.020$ ) and forest intactness (negative effect;  $\beta = -0.290 \pm \text{SE } 0.172$ ,  $P = 0.097$ ). There were no studies detecting binturongs in landscapes that retained < 40% forest cover within the 1,256 km<sup>2</sup> covering the sampling areas (Supplementary Fig. 4).

#### Local-scale habitat associations

The new camera-trapping effort included 10 landscapes, 20 sessions, 1,218 cameras and 58,608 trap-nights (Supplementary Table 2). We obtained 54 independent captures of binturongs from nine landscapes (e.g. Plate 1); we did not detect the species in Singapore. Encounter rate (0.315 detections per 100 trap-nights) and naïve occupancy (detected by 10.2% of all cameras) were highest in Ulu Muda in Peninsular Malaysia. Details on the compiled published and new camera-trapping data by landscape are in Supplementary Tables 5 & 6.

We used AICc model selection and determined that the top variable in our hierarchical occupancy modelling was elevation, which showed a positive effect ( $\beta = 2.350 \pm \text{SE } 1.117$ ;  $P = 0.035$ ; Fig. 2). Distance to rivers ( $\beta = 0.798 \pm \text{SE } 0.502$ ;  $P = 0.112$ ) and concentration of oil palm plantations ( $\beta = -0.796 \pm \text{SE } 0.677$ ;  $P = 0.240$ ) also performed better than the null model (Table 2). Disturbance variables including degraded forest, human population, human footprint, forest integrity, forest loss and distance to forest

TABLE 1 Model selection explaining the variation in camera-trap detections of binturongs *Arctictis binturong* amongst the landscapes assessed in this study (Fig. 2). The table shows univariate model selection criteria from the zero-inflated Poisson generalized linear mixed modelling assessing variation in independent detections of the binturong, including study effort and landscape as random effects. All covariates were averaged for the 20-km radius areas surrounding the study area, then centred and standardized so that effect sizes can be interpreted relative to each other. The sample sizes were 181 detections from 72 studies in 38 landscapes excluding Singapore, and 181 detections from 91 studies in 41 landscapes including Singapore.

Covariate	Estimate	AICc <sup>1</sup>	LogLik <sup>2</sup>	$\Delta\text{AICc}^3$	Akaike weight
Model selection excluding data from Singapore					
Oil palm	-0.70	276.9	-131.2	0.0	0.69
Forest intactness	-0.29	279.9	-134.0	3.0	0.16
Reduced (effort only)	0.83	280.0	-135.4	3.1	0.15
Model selection including data from Singapore					
Night lights	-10.10	280.2	-134.2	0.0	0.87
Forest cover	-0.88	285.3	-135.5	5.1	0.07
Forest cover	1.20	287.3	-137.8	7.1	0.03
Forest integrity	-1.36	287.6	-136.6	7.4	0.02
Human footprint	-1.15	288.7	-137.2	8.5	0.01
Null	1.30	296.4	-143.7	16.2	0.00

<sup>1</sup>AICc, Akaike information criterion corrected for small sample size (lower values indicate better model performance).

<sup>2</sup>LogLik, log-likelihood (higher values indicate better model fit).

<sup>3</sup> $\Delta\text{AICc}$ , difference of AICc to the best-performing model.



PLATE 1 Camera-trap image of a binturong *Arctictis binturong* in Danum Valley, Malaysian Borneo.

edge performed worse than the null model, suggesting no local-scale habitat associations with those variables (Supplementary Table 7).

### Diel activity patterns

We analysed the diel activity of binturongs from camera-trap data. Pooling all observations, the kernel density estimation showed a crepuscular trend, with peaks in activity before sunrise and after sunset (Fig. 3a; Supplementary Fig. 5a,b). There was substantial variability in the activity patterns across sampling units with moderate overlap ( $\Delta_1 = 0.338$ – $0.748$ ) but no clear pattern for differences (Anderson–Darling  $k$ -sample test = 3.036;  $P = 0.733$ ). In the more intact forests that were  $> 1$  km from edges,

binturongs had a third activity peak around noon ( $\Delta_1 = 0.636$ ; SE = 0.099;  $P = 0.062$ ). Other disturbance and human-associated variables showed similar impacts on the diel activity of binturongs (Supplementary Figs 5 & 6).

### Discussion

This multiscale synthesis of binturongs largely failed to find significant habitat associations with habitat degradation and suggests binturongs demonstrate more habitat plasticity than previously thought. However, binturongs never persisted in small forest patches ( $< 10$  km<sup>2</sup>), which could explain why we did not record them in Singapore, although the common palm civet *Paradoxurus hermaphroditus* and other large herbivores persist there (Dehault et al., 2022; Lamperty et al., 2023). In more highly forested landscapes, binturongs were equally common in intact and degraded/logged forests and interior forest and habitats near forest edges. The species' avoidance of oil palm plantations at the landscape and local scales contradicted our hypothesis and differs from other crop-using frugivores such as pigs (*Sus scrofa* and *Sus barbatus*), macaques (*Macaca nemestrina* and *Macaca fascicularis*) and other civet species (Luskin et al., 2017; Dehault et al., 2022). Binturongs altered their diel activity at forest edges and in disturbed forests to become more nocturnal, suggesting a behavioural adaptation to avoid people (Negret et al., 2023). We conclude that where sufficient forest cover is retained in the larger landscapes (i.e.  $> 40\%$  in a 1,256-km<sup>2</sup> area), binturongs

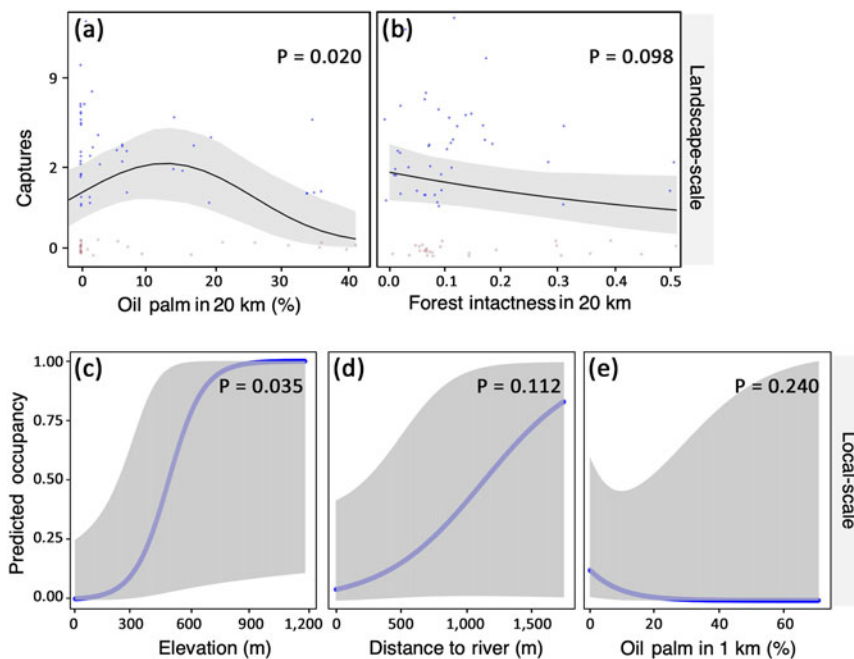


FIG. 2 Variation in binturong detections amongst the landscapes assessed in this study, and local occupancy (Table 1). Binturong captures are shown in relation to (a) % of the area within a 20-km radius covered by oil palm plantations and (b) the forest intactness within a 20-km radius. Data points show raw capture data (jittered for clarity; red points indicate zero detections). Predicted occupancy is shown in relation to (c) elevation, (d) distance to the nearest river and (e) % of the area within a 1-km radius covered by oil palm plantations. We centred and standardized all covariates prior to modelling, so that effect sizes can be compared. We calculated P-values based on the covariate  $z$ -values. Trend lines in all panels were drawn using the *predict()* function in R and grey areas represent the 95% confidence intervals. We assessed landscape-scale trends using zero-inflated Poisson generalized linear mixed models (a,b) and local-scale trends using hierarchical occupancy models (c–e).

TABLE 2 Model performance for assessing local (within-site) variation in binturong occupancy amongst the landscapes assessed in this study. No multivariate models improved performance by  $> 2$  AICc points from the null/reduced model, which contained the sampling unit effort as a covariate in the detection formula and the trapping session as covariate affecting occupancy, which were included in all models.

Variable included	Estimate $\pm$ SE	P-value	K	$\Delta$ AICc	Akaike weight
Elevation	2.350 $\pm$ 1.120	0.035	20	0.0	0.839
Distance to river	0.798 $\pm$ 0.502	0.112	20	4.9	0.074
Oil palm	-0.796 $\pm$ 0.677	0.240	20	5.7	0.049
Null/reduced model	NA	NA	19	6.2	0.038

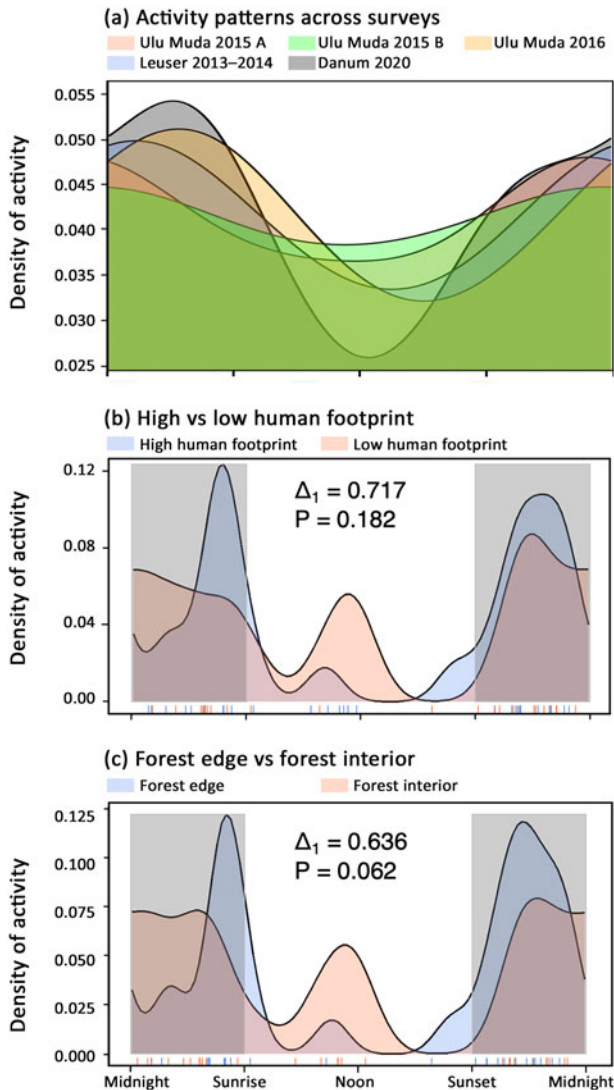


FIG. 3 Binturong diel activity patterns. (a) Variation amongst three different landscapes (Ulu Muda, Leuser and Danum) and amongst three surveys at Ulu Muda in Peninsular Malaysia (A and B refer to different locations within the Ulu Muda landscape). Activity patterns differed amongst forests with (b) high vs low Human Footprint Index values and (c) at cameras that were within 1 km of a forest edge vs cameras at forest interior sites. We considered sites with a Human Footprint Index  $> 3$  to have a high human footprint. (Readers of the printed journal are referred to the online article for a colour version of this figure.)

can retain their keystone role of dispersing fig seeds in degraded forests and edges, especially in mid-elevation habitats.

Our study has three important caveats. Firstly, hunting pressure was estimated indirectly through variables such as human access and infrastructure (i.e. the Human Footprint Index, and distance to nearest river and nearest human settlement), so these results need to be interpreted with caution. Secondly, many assumptions are necessary in assessing detection rates amongst a variety of studies within a single framework. The resulting noise in the data limited our ability to detect trends amongst landscapes, including in terms of how the detectability of semi-arboreal binturongs by terrestrial cameras could be influenced by forest degradation (Chutipong et al., 2014; Gregory et al., 2014; Haysom et al., 2021). For example, a previous camera-trapping study of orangutans in Borneo suggests that although these primates naturally sometimes travel on the ground, increased use of terrestrial substrates was associated with higher levels of logging (Ancrenaz et al., 2014). Other studies have noted hunting-induced behavioural changes amongst arboreal animals (Whitworth et al., 2019), and future studies with access to more data should include this in the detection function of their occupancy models. Finally, although this is the largest synthesis of binturong data to date, we still had small sample sizes for some analyses and were unable to include additional covariates in the detection function of our local-scale occupancy model (we recorded only 54 independent detections over 58,608 trap-nights). Our findings are thus preliminary and we encourage researchers working in underrepresented areas (e.g. Cambodia, Lao People's Democratic Republic and Viet Nam) to publish the summary data from their camera-trap studies to fill in these gaps. Because of the low number of detections, we were unable to assess regional trends, which have been shown to vary between Sundaic and non-Sundaic areas (Ke & Luskin, 2019). Most other sampling methods (e.g. line transects) present challenges in detecting nocturnal and/or cryptic species such as binturongs (Whitworth et al., 2016; Bowler et al., 2017). Binturong detectability may be improved by using arboreal camera traps, as suggested by 41 independent binturong detections recorded previously over 2,973 trap-nights (Debruille et al., 2020), which is a capture rate 10 times higher than that reported here, using terrestrial cameras.

Future research could examine the influence of the vertical structure of forests on habitat associations (Deere et al., 2020; Stobo-Wilson et al., 2021). This could be especially important in helping species to find their ideal microclimates and for potential niche partitioning through vertical stratification, which may partly explain the high diversity of civets and many other arboreal mammals in Asia (Shanahan & Compton, 2001; Thiel et al., 2021). Data on these habitat layers are now available from the Global Ecosystem Dynamic Investigation (Dubayah et al., 2020). There is also a need for more systematic assessments of binturong hunting. The species' occurrence in fragmented and degraded habitats may correlate with areas of higher hunting pressure (Duckworth et al., 2012). We found that a large portion of the forested range of binturongs is unprotected and unsuitable for their habitation, raising concerns of further population declines. Given that binturongs persist in degraded habitats, it is imperative for future research to identify those populations most at risk from hunting and to propose strategies to minimize this risk. For example, restoration of fig trees and lianas in degraded habitats (Campbell et al., 2015; Cottee-Jones et al., 2016) could support arboreal locomotion and shelter, along with the plants providing fruits for the species and other wildlife (Shanahan et al., 2001; Lambert & Halsey, 2015; Nakabayashi & Ahmad, 2018; Debrulle et al., 2020). Binturong seed dispersal in degraded forests and edges may help offset the deleterious impacts of pigs, which are abundant in these habitats and are seed and seedling predators (Luskin et al., 2019; Luskin et al., 2021). Binturongs may also support the prey base for carnivores, including apex predators and medium-sized felids (Amir et al., 2022; Decœur et al., 2023). If binturongs can adopt behaviours to avoid people, for example by becoming more nocturnal and elusive in forest canopies (Whitworth et al., 2016), this could reduce their detection by hunters.

Our findings suggest that binturongs can persist in degraded and disturbed forests, probably through modulating their diel activity to become more nocturnal, and thus maintain their seed dispersal services in the widespread degraded forests of Asia. This provides hope for the restoration of plant and animal communities, especially via keystone plants (figs) and their dispersers (binturongs). Conversely, binturongs in degraded areas could face greater threat from hunting. Borneo and Sumatra are areas with highly suitable binturong habitat and the highest binturong detection rates in camera-trapping studies, but the lowest proportions of protected forest (6.6% and 7.6%, respectively).

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**Conflicts of interest** None.

**Ethical standards** This research abided by the *Oryx* guidelines on ethical standards and did not involve experimentation with animals or collection of specimens. We received ethical clearance for camera trapping from the University of California, Berkeley, Nanyang Technological University (NTU), and the University of Queensland (UQ). The camera-trap images of people were securely stored and not published or distributed, abiding by the ethical clearance from these institutions.

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