

Living on the edge: forest edge effects on microclimate and terrestrial mammal activity in disturbed lowland forest in Sumatra, Indonesia

HELEN D. SLATER, PHILLIPA K. GILLINGHAM, VICTORIA PRATT, BEN EATON
SIMON FLETCHER, ABDULLAH ABDULLAH, SUPRIADI and AMANDA H. KORSTJENS

Abstract Species–environment relationships are often studied at large spatial scales, but effective conservation requires an understanding of local-scale environmental drivers and pressures. Widespread degradation and fragmentation of forests have increased the proportion of tropical mammal habitat that is affected by edge effects. Edge effects include greater exposure to anthropogenic disturbance and abiotic changes that synergistically influence how well populations can cope with climate change. We investigated relationships between distance to the forest edge, forest structure, microclimate and terrestrial mammal detections in a selectively logged forest at the boundary of Gunung Leuser National Park in Sumatra, Indonesia. We collected mammal detection data from motion-activated camera traps, microclimate data from automated climate data loggers and forest structure data from vegetation plots. Daily mean and maximum temperatures significantly decreased with distance from the forest edge, whereas tree height and minimum temperature increased. Mammal diversity was lower at the forest edge compared to the interior. Mammals were detected less frequently at the forest edge, although this relationship varied between mammal orders. Mammal detections were best explained by temperature, tree height and tree diameter at breast height. These results demonstrate that abiotic changes in forests brought on by edge effects have negative impacts on mammals, but these effects vary between mammal taxa because of differing sensitivities to human disturbance. Our findings highlight the importance of considering local-scale environmental drivers in determining species–environment relationships to identify key habitat features

such as microclimate refuges that should be prioritized in ecosystem management.

Keywords Camera trap, edge effects, forest edge, fragmentation, habitat use, Indonesia, mammals, remote monitoring

The supplementary material for this article is available at doi.org/10.1017/S0030605323000212

Introduction

Addressing key drivers of biodiversity loss such as habitat loss, fragmentation and climate change is essential to prevent mammal extinctions and establish healthy, resilient populations globally. High-quality data on species distribution and habitats are needed to do this effectively, but these are lacking for many species (Burivalova et al., 2019). Species distributions and habitat suitability are often inferred from outdated survey data or educated guesses based on expert knowledge (IUCN, 2021a). Research activities often focus on charismatic and/or threatened species, but effective conservation requires information on whole communities, including common and invasive species. Up-to-date species data, high-quality environmental data and ongoing monitoring are necessary to determine the status of biodiversity, examine the outcomes of conservation actions and facilitate adaptive management.

Accurate predictions of species responses to environmental changes are essential for effective long-term conservation. Most studies of species–environment relationships use species distribution models at large spatial and temporal scales. The environmental predictors used in species distribution models are often derived from remote sensing data with coarse spatial and temporal resolutions (e.g. annual climate data from WorldClim; Hijmans et al., 2015). Such large-scale data are generally unsuitable for local-scale conservation planning and practice because of their low precision at smaller scales, and their inability to account for local population stresses such as edge effects or exploitation (Tulloch et al., 2016). A modelling framework to determine species–environment relationships at local scales is needed to provide information on local drivers of population declines and biodiversity loss, and to facilitate long-term conservation planning. Developing such a framework requires

HELEN D. SLATER (Corresponding author, orcid.org/0000-0002-9362-5370, i7999848@bournemouth.ac.uk), PHILLIPA K. GILLINGHAM (orcid.org/0000-0002-9499-7627) and AMANDA H. KORSTJENS (orcid.org/0000-0002-9587-4020) Department of Life and Environmental Sciences, Bournemouth University, Fern Barrow, Poole, UK

VICTORIA PRATT (orcid.org/0000-0002-5969-0064), BEN EATON (orcid.org/0000-0001-8008-0415) and SIMON FLETCHER Invisible Flock, Yorkshire Sculpture Park, Wakefield, UK

ABDULLAH ABDULLAH* (orcid.org/0000-0002-8435-1005) Department of Biology Education, Syiah Kuala University, Banda Aceh, Indonesia

SUPRIADI Sumatran Orangutan Conservation Programme, Medan, Indonesia

*Also at: Research Centre for Elephant and Biodiversity Conservation, Banda Aceh, Indonesia

Received 29 March 2022. Revision requested 13 July 2022.

Accepted 20 February 2023. First published online 24 July 2023.

This is an Open Access article, distributed under the terms of the Creative Commons Attribution licence (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted re-use, distribution, and reproduction in any medium, provided the original work is properly cited.

Oryx, 2024, 58(2), 228–239 © The Author(s), 2023. Published by Cambridge University Press on behalf of Fauna & Flora International doi:10.1017/S0030605323000212
<https://doi.org/10.1017/S0030605323000212> Published online by Cambridge University Press

more empirical research into fine-scale species–environment relationships.

Tropical forests are heterogeneous environments with significant variation at finer temporal and spatial resolutions (Marsh et al., 2022). Landscape-scale models often do not include fine-scale variations in topography, logging intensity, forest structure and microclimate because they use categorical land units (e.g. primary forest, logged forest, agricultural land; Wearn et al., 2017). Microclimate variations (i.e. sub-annual variations with spatial scales < 1 km²) are important drivers of mammal distributions, behaviour and phenology (McCain & King, 2014; Buckley et al., 2018; Tamian et al., 2022). The inclusion of microclimate variables in species distribution models has improved their performance for several mammal species (e.g. McCain & King, 2014; Varner & Dearing, 2014; Mathewson et al., 2020; Tamian et al., 2022), but the influence of microclimate on mammal habitat choice in tropical forests has not yet been tested.

Microclimate variations are likely to be more extreme in fragmented forests and near forest edges. Edge effects have been observed up to 1 km into forest patches (Laurance, 2004; Pohlman et al., 2007). Approximately 70% of forested areas are within 1 km of a forest edge (Haddad et al., 2015) and therefore a large proportion of forest habitat is likely to be subject to edge effects. Proximity to forest edges also leads to increased human disturbance from hunting and extraction of other resources. These changes are widely assumed to negatively affect mammals, with some studies reporting lower abundances of certain species at forest edges (e.g. Kinnaird et al., 2003). Species respond differently to these changes, and the most effective conservation strategies vary depending on the target species. Few studies to date have investigated how edge-related abiotic changes relate to mammal distribution and habitat use.

In this study, we measured edge effects on forest structure and microclimate, and examined their impacts on forest mammals in a region of recovering secondary tropical forest near the edge of a protected area in Sumatra, Indonesia. Our data on fine-scale species–environment associations provide urgently needed information for the conservation of mammals in the region. We hypothesized that edge effects create an environment that is less favourable for terrestrial forest mammals, resulting in them spending less time near forest edges. We also predicted that trees would be smaller and less well connected at the forest edge, resulting in increased light penetration through the canopy and higher temperatures. Our final prediction was that mammals would spend less time near forest edges, and that mammal detections would thus be associated negatively with temperature and light intensity, and positively with distance from the forest edge, larger trees and increased canopy connectivity.

Study area

We collected data from Aras Napal in the Sikundur region on the boundary of Gunung Leuser National Park in the North Sumatra province in Sumatra, Indonesia (Fig. 1). Sikundur comprises secondary lowland forest that was selectively logged before the establishment of the Park in 2004 (Orangutan Information Centre, 2009). Despite its protected status, illegal logging and hunting still occur in the area (Roth et al., 2020), although no data are available on the frequency and impacts of these activities. Aras Napal, which consists of c. 150 households, is adjacent to the Sikundur forest. Subsistence and smallholder agriculture are the predominant land uses outside the protected forest in Aras Napal, whereas the area to the north of the village comprises larger commercial rubber and oil palm plantations. Except for a few primate studies (Harrison et al., 2020; Roth et al., 2020; Hankinson et al., 2021, 2022), there are no published data on mammals in Sikundur.

Methods

We investigated fine-scale species–environment interactions and determined abiotic edge effects on terrestrial mammals by measuring forest structure, microclimate and mammal detections along four transects (Fig. 1). We liaised with landowners in Aras Napal to identify starting locations in orange plantations adjacent to the forest edge and the boundary of the National Park. We generated 2-km transects with survey points at 0.5-km intervals from these starting locations using *ArcGIS Pro* (Esri, 2010). Where possible, we set up monitoring locations within 50 m of these points. In some cases, monitoring locations had to be placed further apart because the intended survey points were inaccessible on foot. We conducted camera-trap and climate monitoring in all locations concurrently over 60 days during August–October 2019. To minimize disturbance-related changes in animal behaviour, we collected vegetation data only after we had completed the remote monitoring period.

Forest structure

We measured forest structure in 25 × 25 m plots at all monitoring locations. Within each plot, we recorded the total number of trees with a circumference at breast height of > 31.4 cm. For each tree, we recorded circumference at breast height (cm), total height (m), bole height (m), north–south crown width (m), east–west crown width (m) and crown connectivity with neighbouring crowns (%). We used the tree circumference to calculate the diameter at breast height (cm), and estimated crown area (m²) from the crown widths in north–south and east–west directions.

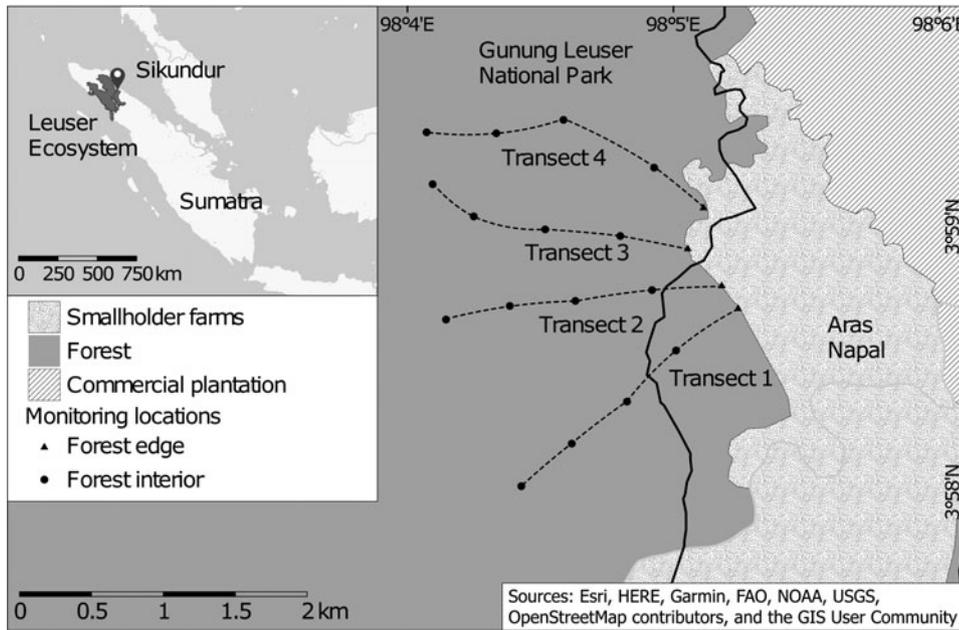


FIG. 1 Monitoring locations in Sikundur and Aras Napal and the Sikundur region within the Leuser Ecosystem in Sumatra, Indonesia.

Microclimate

At each monitoring location, we recorded below-canopy hourly ambient temperature ($^{\circ}\text{C}$) and light intensity (lux) using Onset HOBO UA-002-08 8 K Pendant Waterproof Temperature & Light Intensity Loggers (Onset, Bourne, USA). Because of a software issue, we were only able to collect microclimate data for 49 out of the 60 days. We placed the loggers in a shaded location to minimize the risk of greenhouse effects within the sensor casing from direct sunlight; despite this, there were still some instances of elevated temperature and light intensity measurements. To minimize the effect of these records in the final dataset, we removed data points for which the recorded light intensity exceeded 32,000 lux (level of direct sunlight; Hiscocks, 2011, in Marsh et al., 2022). We also excluded data points for which temperature increased by $> 5^{\circ}\text{C}$ between consecutive hourly recordings, and the two data points immediately following them (to ensure loggers had sufficient time to return to ambient temperatures). Overall, 223 data points were removed from the analysis. Finally, we summarized climate data for the entire sampling period (including both nighttime and daytime temperatures) and for each 24-h period.

Mammal occurrence

We used mammal detections to determine the occurrence of detectable terrestrial mammal species at each sampling location. At each location, we deployed one SpyPoint Force-Dark remote trail camera (Eurohunt, Harztor, Germany), using 20 cameras in total. These cameras feature 42 no-glow light-emitting diodes and take infrared images at night, thereby avoiding the disturbance of wildlife with camera flashes. We secured cameras at a height

of c. 0.5 m from the ground, facing towards animal signs or probable trails. We removed any vegetation directly in front of the cameras to provide a clear field of view. We did not bait camera locations to avoid influencing animal movements. We set the cameras to take one image followed by a 30-s video when triggered by movement.

At the end of the monitoring period, we collected the cameras and identified captured species in individual images using the Integrated Taxonomic Information System database (ITIS, 2021). We attached a metadata tag with the standardized common name of the identified species to each image. We extracted image metadata and tabulated all mammal detection events with the *camtrapR* package in *R* 4.0.0 (Niedballa et al., 2016; R Core Team, 2020). We applied a minimum delta time (i.e. the time between two subsequent detection events of the same species at the same location) of 1 h to prevent captures of the same individual being counted multiple times at one location. For each location, we counted the total number of mammal detections and the number of detections grouped by mammal order. We calculated the naïve occupancy (i.e. the proportion of sites at which a species was detected) of each detected mammal species or family. We checked that the sampling effort was sufficient to capture all detectable families using a species accumulation curve plotted with the *vegan* package in *R* (Oksanen et al., 2019). We did this at the family level as some small mammals could not be identified to species level.

Data analysis

We pooled data from all locations and grouped them by distance from the forest edge (0.0, 0.5, 1.0, 1.5 and 2.0 km). We estimated mammal species richness by calculating the

mean number of detected species from all locations at each distance from the edge. We determined the relationship between distance from the forest edge, environmental conditions and detections using generalized linear mixed models (GLMMs) fitted with the R package *glmmTMB* (Brooks et al., 2017). As our data collection followed a nested sampling design, we included location and transect ID as random intercepts in all models to account for non-independence between samples.

We summarized environmental predictors for each location. We calculated mean temperature and light intensity for the entire sampling period (including night-time and daytime temperatures). We also calculated the daily mean, maximum and minimum temperature and light intensity at each sampling location. We summarized forest structure for each plot into the following variables: mean tree height, mean bole height, mean diameter at breast height, mean crown area, mean connectivity and number of trees per plot. The environmental variables used in the models are provided in Supplementary Table 1, and R-code used to run the models is provided in Supplementary Material 1.

We first tested for the effect of distance from the edge on microclimate and forest structure. The GLMMs for microclimate variables also included the day of the year and hour of the day as random intercepts. We next tested for significant associations between detection events and distance from the forest edge using Pearson's χ^2 tests. We then tested the effects of microclimate and forest structure variables on overall mammal detections using a Poisson generalized linear model with a log link function fitted with the R package *MASS* (Venables & Ripley, 2002). We used a correlation matrix to check for co-linearity amongst predictor variables. For those with a correlation coefficient > 0.7, we selected only one to be included in the model. We determined which combination of variables produced the best model performance based on the Akaike information criterion (AIC) using automated model selection with the R package *MuMIn* (Bartoń, 2020).

Finally, we tested for the effects of microclimate and forest structure variables on the occurrence of each mammal order by fitting a negative binomial GLMM with *glmmTMB*. Order was included as a random intercept. As in the GLMM, we first selected independent variables using a correlation matrix and used automated model selection with *MuMIn* to select the best combination of variables based on the model AIC.

Results

Edge effects on forest structure and microclimate

Forest structure Tree height increased significantly with increased distance from the forest edge ($P < 0.05$; Table 1,

TABLE 1 Coefficient estimates for the generalized linear mixed model with a Gaussian distribution testing the effects of distance from the forest edge on forest structure variables (N = 217 trees) at Aras Napal, Indonesia (Fig. 1). AIC, Akaike information criterion.

		Dependent variables						
		Tree height ± SE (m)	Bole height ± SE (m)	Diameter at breast height ± SE (cm)	Tree basal area ± SE (cm ²)	Tree height:diameter at breast height ratio ± SE	Crown area ± SE (m ²)	Canopy connectivity ± SE (%)
Distance from edge (m)		0.002** ± 0.00	0.002*** ± 0.00	-0.001 ± 0.00	0.00 ± 0.00	0.006*** ± 0.00	-0.0005 ± 0.00	0.001 ± 0.00
Intercept		17.72*** ± 1.05	8.45*** ± 0.68	33.25*** ± 1.50	0.10*** ± 0.01	55.53*** ± 1.83	45.29*** ± 4.12	43.41*** ± 3.03
Random effects¹								
σ^2		65.93	33.38	184.94	0.01	267.97	1,356.24	538.29
τ_{00}		1.13	0.20	0.00	0.00	0.00	0.00	9.87
AIC		1,544.51	1,397.02	1,764.32	-382.04	1,844.04	2,192.69	1,996.05

* $P < 0.1$; ** $P < 0.05$; *** $P < 0.01$.
¹ σ^2 , residual variance; τ_{00} , random intercept variance.

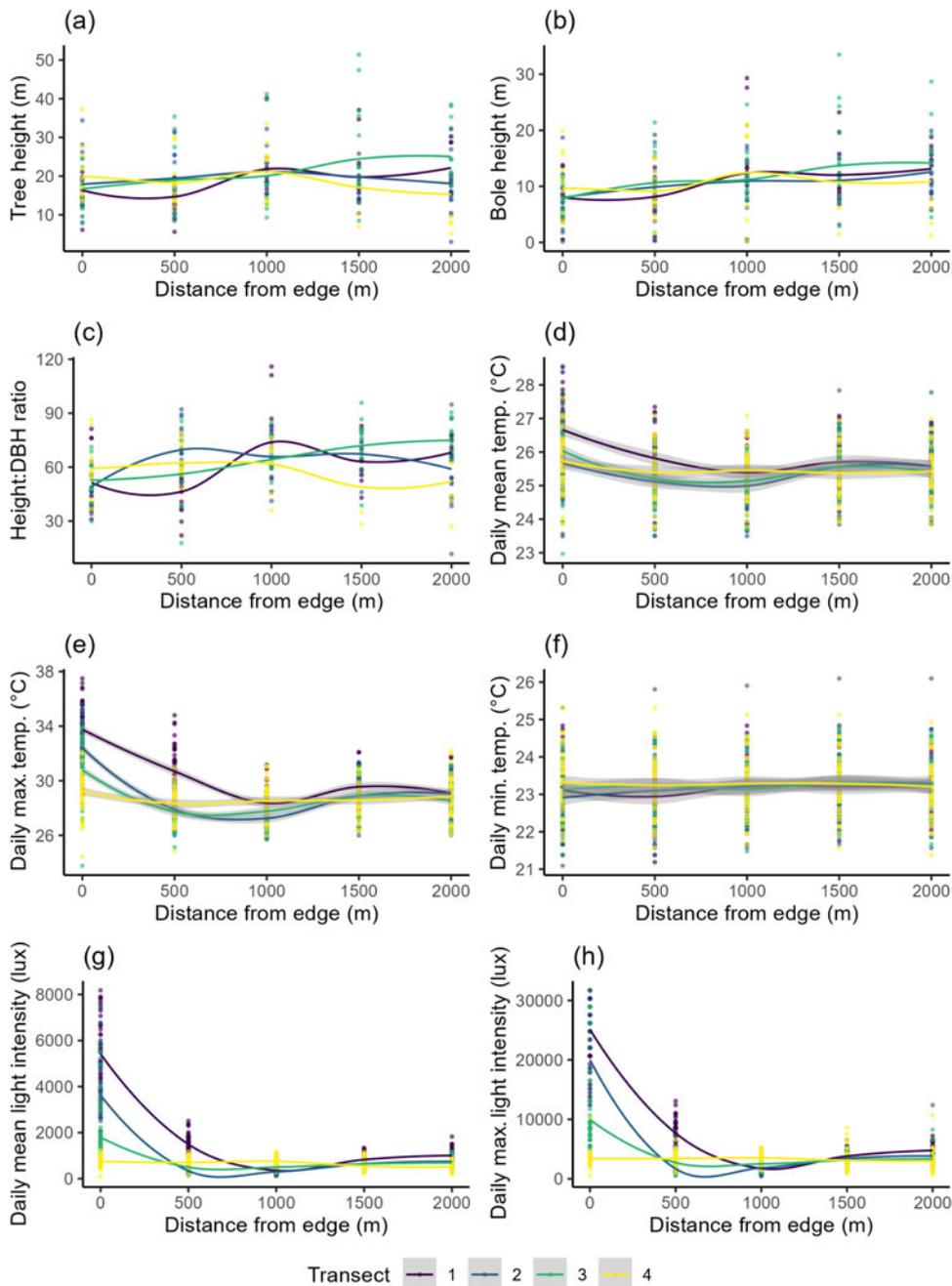


FIG. 2 Generalized linear mixed model predictions (lines) with 95% CIs (grey shading) and observed microclimate and forest structure with distance from the forest edge along transects at Aras Napal, Indonesia (Tables 2 & 3): (a) tree height; (b) bole height; (c) height:diameter at breast height (cm) ratio; (d) daily mean temperature; (e) daily maximum temperature; (f) daily minimum temperature; (g) daily mean light intensity; and (h) daily maximum light intensity. (Readers of the printed journal are referred to the online article for a colour version of this figure.)

Fig. 2a), as did bole height ($P < 0.01$; Table 1, Fig. 2b) and height:diameter at breast height ratio ($P < 0.05$; Table 1, Fig. 2c). Diameter at breast height, basal area, crown area and canopy connectivity did not change with distance from the forest edge (Table 1). The forest structure data are summarized in Supplementary Table 2 and Supplementary Fig. 1.

Microclimate There was a significant negative effect ($P < 0.01$) of distance from the forest edge on both temperature and light intensity (Table 2); daily mean and maximum temperatures and light intensities significantly decreased with increasing distance from the forest edge ($P < 0.01$; Table 3). Effect sizes were larger for daily maximums

compared with daily means for both temperature and light intensity (Table 3, Fig. 2d–h). These relationships were non-linear, with the gradient being steeper closer to the edge and levelling off at c. 1 km from the forest edge (Fig. 2d–h). The daily minimum temperature increased with distance from the forest edge ($P < 0.01$; Table 3, Fig. 2f). The microclimate data are summarized in Supplementary Table 3 and Supplementary Fig. 2.

Mammal occurrence across a disturbance gradient

We removed one location from the analysis because the camera malfunctioned; the remaining 19 cameras yielded

TABLE 2 Coefficient estimates for the generalized linear mixed model with Gaussian distribution testing the effects of distance from the forest edge on hourly temperature and light intensity (N = 21,071) recorded over 49 days during August–October 2019 at Aras Napal, Indonesia (Fig. 2).

	Dependent variable	
	Temperature \pm SE ($^{\circ}$ C)	Light intensity \pm SE (lux)
Distance from forest edge (m)	−0.0002*** \pm 0.00001	−0.91*** \pm 0.02
Intercept	25.80*** \pm 0.41	2,025.94*** \pm 392.20
Random effects¹		
σ^2	1.23	5,881,034.02
τ_{00}	0.36 _{Day of year}	22,637.55 _{Day of year}
	3.58 _{Hour}	2,015,972.65 _{Hour}
	0.04 _{Transect}	273,899.88 _{Transect}
AIC	64,557.59	388,437.70

*P < 0.1; **P < 0.05; ***P < 0.01.

¹ σ^2 , residual variance; τ_{00} , random intercept variance.

1,079 sampling days (after accounting for days lost because of camera malfunctions), 1,384 images and 300 mammal detection events. We identified 16 mammal species across 14 families and six orders (Table 4). It was not possible to identify animals in the families Muridae (mice and rats) and Sciuridae (squirrels) to species level. The mean number of detected species was lowest at the forest edge ($\mu = 3.00 \pm$ SE 1.00) and highest at 1 km from the forest edge ($\mu = 7.00 \pm$ SE 3.56). Three families had fewer than five detections, and five families had more than 20 detections. The species accumulation curve (Fig. 3) shows that after c. 200 total sampling days, 12 out of 14 families had been detected, indicating that the sampling effort was adequate to capture all present and detectable families.

The number of detection events of each mammal order differed between distances from the forest edge ($\chi^2 = 75.324$, df = 20, $P < 0.01$; Fig. 4). Primate detection rates were higher towards the National Park boundary and elephants were detected only within 1 km from the forest edge and not farther into the forest. Moonrats were only detected at distances > 1 km from the forest edge and carnivores were not detected at the edge. Ungulates and rodents were detected at all distances but had a higher detection rate at 1 km from the forest edge than at any other distance (Fig. 4).

Environmental predictors of mammal abundance

All temperature and light intensity variables except for minimum temperature were highly correlated ($r > 0.7$); accordingly, only maximum and minimum temperature were used in the models. We selected maximum temperature as the variable to be included in the analysis as it varied the most between locations and is likely to restrict the occurrence of diurnal terrestrial mammals more than mean temperature. Total tree height and bole height were also strongly correlated ($r > 0.7$); consequently, we included only total tree height in the analysis.

Overall mammal detections The best performing model was that with the variables maximum and minimum temperature, tree height and diameter at breast height (Table 5). The deviance explained by this model was 28%. The number of detections decreased with increasing minimum and maximum temperatures, and tree height (Table 5, Fig. 5a–c), and increased with increasing diameter at breast height (Table 5, Fig. 5d).

Detections by mammal order The mixed model with the best performance included maximum temperature, tree height and diameter at breast height (Table 6, Fig. 6). For all mammal orders, maximum temperature and tree height were negatively correlated with the number of detections (Table 6, Fig. 6a,b). Diameter at breast height was positively correlated with number of detections (Table 6, Fig. 6c).

Discussion

Edge effects on abiotic forest conditions

Mean and maximum temperatures and light intensity were higher at the forest edge, whereas minimum temperatures increased towards the forest interior. Elevated temperatures occurred up to 0.5–1.0 km into the forest (Fig. 2d,e). Smaller forest fragments are subject to more extreme diurnal variation than larger fragments. Open-access climate datasets are usually only available at scales much larger than the body size of a species or even its mean home range. Many climate envelope models only incorporate annual means and do not account for fine-scale temporal variations such as daily maximums, which can be much higher than the mean (Bennie et al., 2014). We recorded daily maximum temperatures of up to 37.5 $^{\circ}$ C, which is considerably higher than the overall mean of 25.5 $^{\circ}$ C.

TABLE 3 Coefficient estimates with standard errors in parentheses for the generalized linear mixed model with Gaussian distribution testing the effects of distance from the forest edge on daily values of forest microclimate (N = 908 days) at Aras Napal, Indonesia (Fig. 2).

Dependent variables		Daily mean temperature ± SE (°C)	Daily maximum temperature ± SE (°C)	Daily minimum temperature ± SE (°C)	Daily mean light intensity ± SE (lux)	Daily maximum light intensity ± SE (lux)
Distance from forest edge (m)		-0.0002*** ± 0.00	-0.001*** ± 0.00	0.0001*** ± 0.00	-0.876*** ± 0.05	-4.434*** ± 0.26
Intercept		25.71*** ± 0.13	30.18*** ± 0.39	23.11*** ± 0.11	1,982.21*** ± 264.35	10,031.03*** ± 1,205.12
Random effects¹						
σ ²	0.2		2.11	0.1	1,258,641.48	29,722,948.87
τ ₀₀	0.47 _{Day of year}		1.26 _{Day of year}	0.47 _{Day of year}	0.00 _{Day of year}	0.00 _{Day of year}
	0.03 _{Transect}		0.48 _{Transect}	0.01 _{Transect}	262,871.95 _{Transect}	5,415,830.38 _{Transect}
AIC	1,335.38		3,412.66	734.99	15,344.76	18,209.03

*P < 0.1; **P < 0.05; ***P < 0.01. ¹σ², residual variance; τ₀₀, random intercept variance.

The frequency and duration of such hotter periods probably represent important constraints on the survival and fitness of wildlife species. These effects are not considered in models using annual means of coarse-scale data, which may underestimate local extinction risks.

Mammal–environment interactions

We found that mammals favour locations with wider trees, lower mean and maximum temperatures and higher minimum temperatures, conditions that are usually associated with less disturbed forests. Lower detections rates in more disturbed and warmer forest areas indicate that mammals are spending less time there. This is probably because avoiding such areas reduces the energy costs associated with elevated temperatures (Korstjens & Hillyer, 2016). Total tree height was negatively associated with mammal detections, probably because of the removal of tall trees during historical selective logging. Trees in most plots had a small diameter at breast height relative to the mean tree height, suggesting a higher proportion of young trees. Our findings indicate that mammals prefer areas with more mature trees. A camera-trap study conducted in Tanzania reported similar findings, with mammal abundance being negatively associated with stem density of small trees (diameter at breast height 5–10 cm) and positively associated with larger trees (diameter at breast height > 10 cm; Martin et al., 2015). The relationship between mammals and canopy height is probably more complex in secondary forests, which differ markedly in vegetation structure from primary forests.

The number of detected individuals varied amongst orders with the distance from the National Park edge. This is expected, given that some species tolerate forest edge conditions better and are known to utilize adjacent human-dominated landscapes (Segan et al., 2016). For many species, however, forest edges have a notable negative impact. The number of species detected was lower at the forest edge, with only five species being detected there compared to 8–13 species detected further away from the edge. Elephants, terrestrial primates and pigs were the groups most commonly detected at the forest edge, and they reportedly utilize agricultural lands to forage (Love et al., 2017; Castillo-Contreras et al., 2018; Ruppert et al., 2018). Deer, moonrats and carnivores were only detected in the forest interior, and are known to avoid human-dominated land (Brodie et al., 2015; Farris et al., 2017; Brozovic et al., 2018; Wynn-Grant et al., 2018). These results highlight the significant impacts of human disturbance on the species richness, abundance and composition of mammal communities.

Crop-foraging by pig-tailed macaques *Macaca nemestrina* and wild boars *Sus scrofa* in smallholder farms adjacent to the forest are reported daily; these species had the highest naïve occupancy (H.D. Slater, unpubl. data, 2019). Elephants were only detected within 1 km of the forest edge, and these

TABLE 4 Mammals detected at Aras Napal, Indonesia (Fig. 4), with the total number of detections and naïve occupancy (the proportion of sampling locations at which the family/species was detected).

Family (by Order)	Common name	Scientific name	IUCN status ¹	Population trend	Detection events	Naïve occupancy
Eulipotyphla						
Erinaceidae	Moonrat	<i>Echinosorex gymnura</i>	LC	Unknown	16	0.21
Primates						
Cercopithecidae	Long-tailed macaque	<i>Macaca fascicularis</i>	EN	Decreasing	1	0.05
Cercopithecidae	Pig-tailed macaque	<i>Macaca nemestrina</i>	VU	Decreasing	83	0.79
Cercopithecidae	Thomas’s langur	<i>Presbytis thomasi</i>	VU	Decreasing	2	0.05
Carnivora						
Ursidae	Sun bear	<i>Helarctos malayanus</i>	VU	Decreasing	2	0.11
Mustelidae	Asian small-clawed otter	<i>Amblonyx cinereus</i>	VU	Decreasing	1	0.05
Herpestidae	Collared mongoose	<i>Herpestes semitorquatus</i>	NT	Decreasing	1	0.05
Herpestidae	Short-tailed mongoose	<i>Herpestes brachyurus</i>	NT	Decreasing	5	0.11
Prionodontidae	Banded linsang	<i>Prionodon linsang</i>	LC	Decreasing	5	0.16
Felidae	Sumatran tiger	<i>Panthera tigris</i>	EN	Decreasing	1	0.05
Proboscidea						
Elephantidae	Sumatran elephant	<i>Elephas maximus sumatranus</i>	CR	Decreasing	11	0.21
Artiodactyla						
Suidae	Wild boar	<i>Sus scrofa</i>	LC	Unknown	23	0.53
Tragulidae	Lesser oriental chevrotain	<i>Tragulus kanchil</i>	LC	Unknown	48	0.47
Cervidae	Sambar	<i>Rusa unicolor</i>	VU	Decreasing	3	0.16
Cervidae	Southern red muntjac	<i>Muntiacus muntjak</i>	LC	Decreasing	37	0.26
Rodentia						
Muridae	Rat				9	0.26
Muridae	Mouse				44	0.16
Hystriidae	Malayan porcupine	<i>Hystrix brachyura</i>	LC	Decreasing	16	0.37
Sciuridae	Squirrel				17	0.37

¹LC, Least Concern; NT, Near Threatened; VU, Vulnerable; EN, Endangered; CR, Critically Endangered.

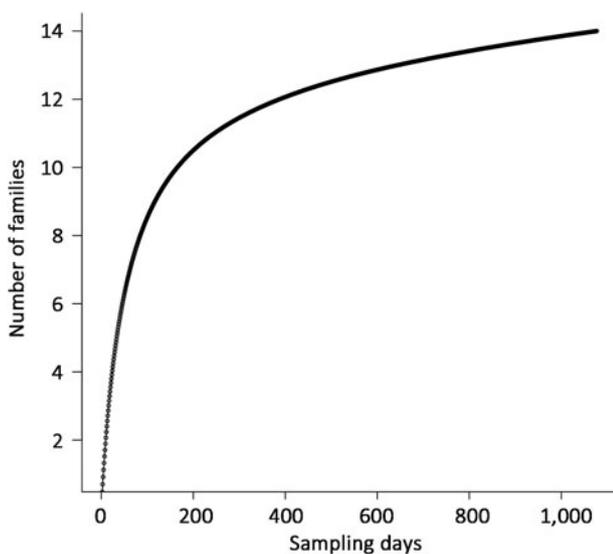


FIG. 3 Species accumulation curve showing the number of mammal families detected with increasing sampling effort in Aras Napal, Indonesia.

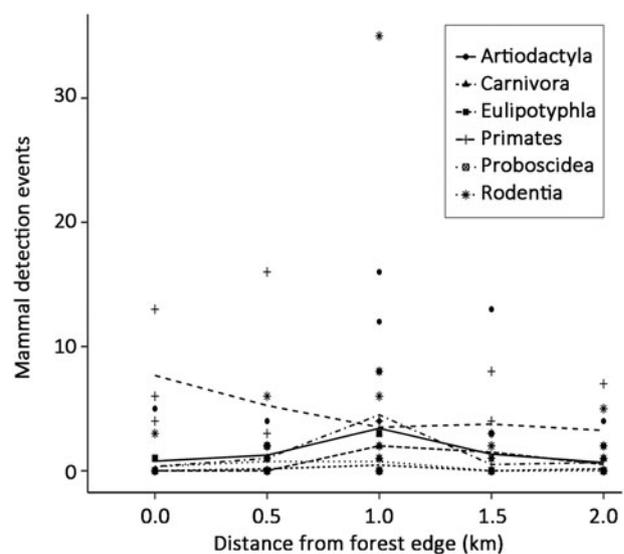


FIG. 4 Total number of detection events for each mammal order detected at different distances from the forest edge at Aras Napal, Indonesia (Table 4).

TABLE 5 Coefficient estimates for the generalized linear model with Poisson distribution testing the effects of environmental variables on the number of overall mammal detection events (N = 19 locations) at Aras Napal, Indonesia (Fig. 5).

	Model 1
Intercept ± SE	27.47* ± 10.72
Maximum temperature ± SE (°C)	−0.13*** ± 0.03
Minimum temperature ± SE (°C)	−1.14* ± 0.49
Tree height ± SE (m)	−0.11*** ± 0.02
Diameter at breast height ± SE (cm)	0.19*** ± 0.03
AIC	171.89

*P < 0.05; **P < 0.01; ***P < 0.001.

detection events were associated with reports of the elephants entering commercial plantations (H.D. Slater, unpubl. data, 2019). There is no evidence of elephants foraging in or damaging smallholder plantations, and residents of Aras Napal generally have a favourable attitude towards them. We found no evidence of large carnivores utilizing forest edges, and there are no reports of them

entering agricultural areas. Although reported human-wildlife interactions are relatively infrequent and local tolerance of wildlife remains high (H.D. Slater, unpubl. data, 2019), the situation warrants monitoring to ensure human-wildlife conflict remains low.

Although we found clear relationships between mammal detections and temperature, tree height and tree diameter, there are other factors that are probably important drivers of mammal occurrence. Higher human foot traffic and hunting risk lead to more vigilant animal behaviours or the avoidance of areas with high human impact (e.g. wolverines *Gulo gulo*; Stewart et al., 2016). Differences in species composition and food availability at the forest edge also influence the distribution of species, and the effects of abiotic changes at the forest edge could therefore be indirect. Deer, for example, are preferred prey for tigers (Allen et al., 2021) and were detected less frequently near the forest edge.

Because of our relatively small study area and the low population density of some mammal species, the sample sizes were too small to perform more detailed analyses.

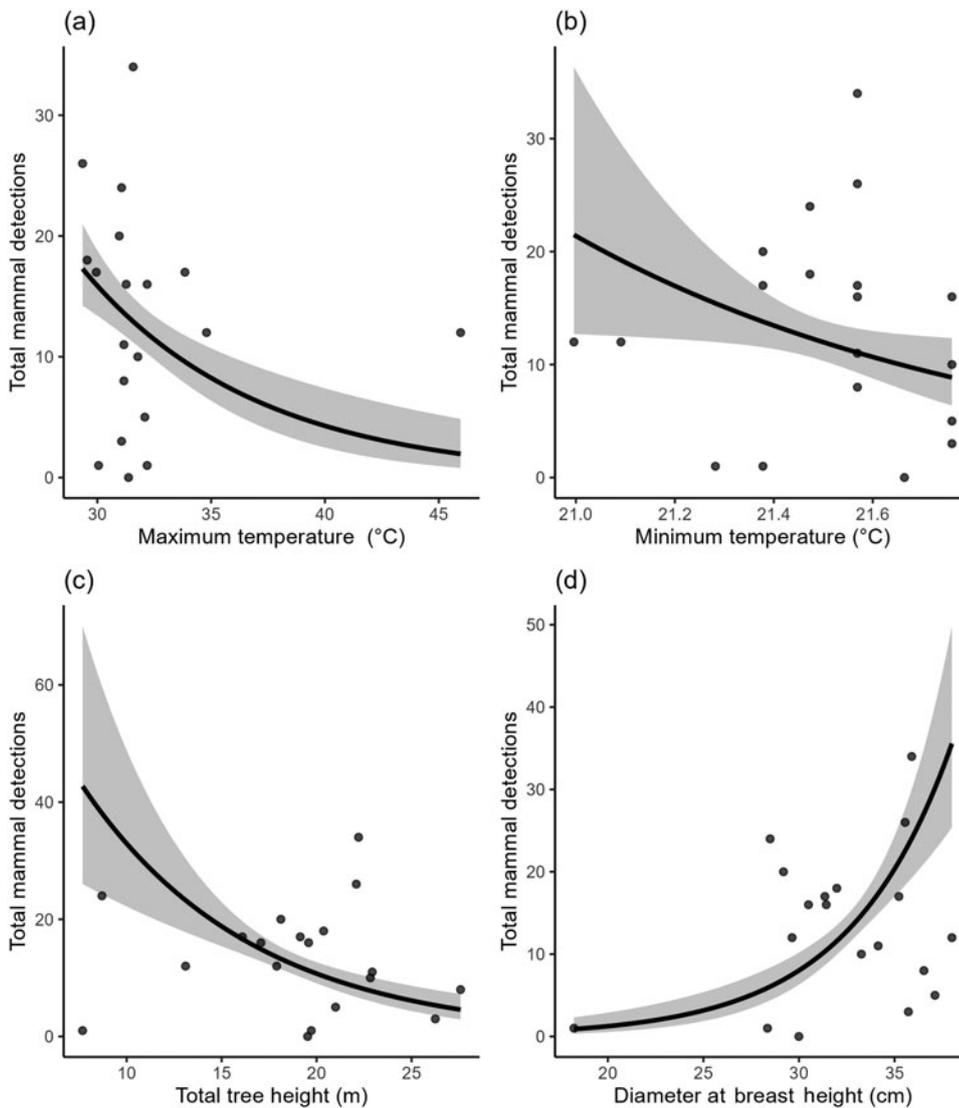


FIG. 5 Generalized linear model predictions (lines) with 95% CIs (grey shading) and observed numbers of mammal detections against (a) maximum temperature, (b) minimum temperature, (c) tree height and (d) diameter at breast height on the total number of mammal detection events at Aras Napal, Indonesia (Table 5).

TABLE 6 Generalized linear mixed model (negative binomial) fit by the Laplace approximation of total detection events of six mammal orders according to environmental variables at Aras Napal, Indonesia (Fig. 6). Significant effects ($\alpha = 0.05$) are highlighted in bold.

	Dependent variable
	Number of detections
Intercept \pm SE	-0.70 ± 0.05
Tree height \pm SE (m)	$-0.18^{***} \pm 0.06$
Diameter at breast height \pm SE (cm)	$0.29^{***} \pm 0.07$
Random effects ¹	
σ^2	1.13
$\tau_{00Order}$	0.93
AIC	429.44

^{*}P < 0.1; ^{**}P < 0.05; ^{***}P < 0.01.

¹ σ^2 = residual variance; τ_{00} = random intercept variance.

Future work that samples a larger area and includes different land-use types at the boundary (e.g. oil palm plantations, roads) would yield higher sample numbers and facilitate more sophisticated analyses and comparisons of edge effects between differing land uses. Inferential approaches such as occupancy modelling would allow for interspecies comparisons by accounting for imperfect detection (Martin et al., 2015). This would provide more detailed insights into how each species is affected by environmental disturbance and how such disturbance influences the community structure and functional diversity of forests. Such analyses are not possible with our current sampling design, as our intention was to monitor species preferences within their ranges and not to test for differences in occupancy between sites. This study does, however, provide a useful baseline regarding the species that are using the forest and those that appear to be more affected by the environmental changes caused by edge effects at the National Park boundary.

Conservation implications

Sikundur represents a key habitat for Indonesian mammals. Eight out of 17 detected species are threatened with extinction, and a further two are categorized as Near Threatened on the IUCN Red List (IUCN, 2021b). Apart from three species with unknown population trends, all identified species have decreasing population trends globally (IUCN, 2021b). Several species are endemic to Sumatra, with limited geographical ranges and low population sizes. The populations in Sikundur must be maintained to prevent the extinctions of these mammals. Data on these populations will be critical for tracking national progress towards biodiversity targets and informing adaptive conservation management for several species of national and global conservation importance in Indonesia (Steenweg et al., 2017).

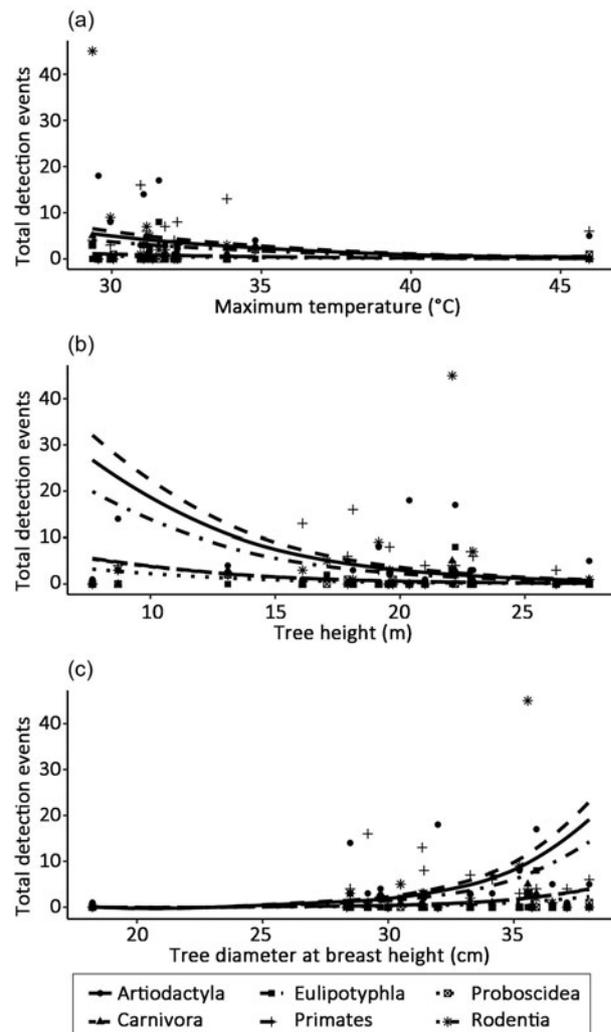


FIG. 6 Generalized linear mixed model predictions (lines) and observed values (points) of detection rates by mammal order against (a) maximum temperature, (b) tree height and (c) diameter at breast height (Table 6).

Conservation in secondary and fragmented forests requires an understanding of the impacts of edge effects on target species. Reserves and corridors will need to provide buffers of at least 1 km to protect threatened species (particularly large carnivores, deer and primate species with a low tolerance for human disturbance) from harmful edge effects. Many reserves in agricultural landscapes are not large enough to provide such buffers and will be unsuitable for these species in the long term without further action (Scriven et al., 2019). This work highlights the essential role of secondary as well as primary forests in preventing extinctions (Dent & Wright, 2009). Other secondary forest sites can support similar numbers of species to primary forests within 20 years of the cessation of logging activities (Dunn, 2004). Protecting primary forests should remain a priority, but secondary forest cover now exceeds primary forest cover in over 40 tropical countries (Dent & Wright,

2009). Conservation actions in human-modified forests will therefore be key to prevent extinctions in the tropics and sustain healthy, resilient mammal populations.

Acknowledgements We thank the Ministry of Research and Technology, RISTEK, Indonesia, the Nature Conservation Agency, BKSDA, Indonesia, and Gunung Leuser National Park for granting us permission to undertake this research; all staff from RISTEK, Taman Nasional Gunung Leuser, and Universitas Syiah Kuala for their in-country support; the Sumatran Orangutan Conservation Programme, the Aras Napal Community Group and Invisible Flock for their contributions at various stages; and the following people for their invaluable contributions: Matthew Nowak, Ucock, Supriadi, Suprayudi, Rusman and Nursal. Funding was provided by Bournemouth University. Climate data loggers were supplied by Tempcon Instrumentation Ltd., Ford, UK.

Author contributions Study conceptualization and design: HDS, PKG, AA, S, AHK; field data collection: HDS, VP, BE, SF, S; data analysis: HDS; writing: HDS; revision: HDS, PKG, AHK.

Conflicts of interest None.

Ethical standards All field research in Indonesia adhered to the legal requirements for foreign researchers in Indonesia, with the required research visa (permit numbers: 70/SIP/FRP/E5/Dit.KI/III/2018 and 6/E5/E5 4/SIP EXT/2019). We obtained an entry permit (Surat Izin Masuk Kawasan Konservasi, SIMAKSI) for Gunung Leuser National Park prior to starting the work, and permission to place cameras from landowners and Aras Napal residents. This study was approved by the Research Ethics Committee of Bournemouth University prior to commencement and adhered to the *Oryx* guidelines on ethical standards. This research was carried out in collaboration with researchers and conservationists from Syiah Kuala University in Banda Aceh, the Sumatran Orangutan Conservation Programme and the Aras Napal Community Group. This study used non-intrusive observatory methods only and great care was taken to prevent any potential disturbances to the forest and wildlife.

References

- ALLEN, M.L., SIBARANI, M.C. & KROFEL, M. (2021) Predicting preferred prey of Sumatran tigers *Panthera tigris sumatrae* via spatio-temporal overlap. *Oryx*, 55, 197–203.
- BARTON, K. (2020) *MuMIn: Multi-Model Inference*. R package version 1.43.17. CRAN.R-project.org/package=MuMIn [accessed March 2023].
- BENNIE, J., WILSON, R.J., MACLEAN, I.M.D. & SUGGITT, A.J. (2014) Seeing the woods for the trees – when is microclimate important in species distribution models? *Global Change Biology*, 20, 2699–2700.
- BRODIE, J.F., GIORDANO, A.J. & AMBU, L. (2015) Differential responses of large mammals to logging and edge effects. *Mammalian Biology*, 80, 7–13.
- BROOKS, M.E., KRISTENSEN, K., VAN BENTHEM, K.J., MAGNUSON, A., BERG, C.W., NIELSEN, A. et al. (2017) glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modelling. *R Journal*, 9, 378–400.
- BROZOVIC, R., ABRAMS, J.F., MOHAMED, A., WONG, S.T., NIEDEBALLA, J., BHAGWAT, T. et al. (2018) Effects of forest degradation on the moonrat *Echinosorex gymnura* in Sabah, Malaysian Borneo. *Mammalian Biology*, 93, 135–143.
- BUCKLEY, L.B., KHALIQ, I., SWANSON, D.L. & HOF, C. (2018) Does metabolism constrain bird and mammal ranges and predict shifts in response to climate change? *Ecology and Evolution*, 8, 12375–12385.
- BURIVALOVA, Z., MITEVA, D., SALAFSKY, N., BUTLER, R.A. & WILCOVE, D.S. (2019) Evidence types and trends in tropical forest conservation literature. *Trends in Ecology & Evolution*, 34, 669–679.
- CASTILLO-CONTRERAS, R., CARVALHO, J., SERRANO, E., MENTABERRE, G., FERNÁNDEZ-AGUILAR, X., COLOM, A. et al. (2018) Urban wild boars prefer fragmented areas with food resources near natural corridors. *Science of the Total Environment*, 615, 282–288.
- DENT, D.H. & WRIGHT, S.J. (2009) The future of tropical species in secondary forests: a quantitative review. *Biological Conservation*, 142, 2833–2843.
- DUNN, R.R. (2004) Recovery of faunal communities during tropical forest regeneration. *Conservation Biology*, 18, 302–309.
- ESRI (2010) *ArcGIS Pro 2D, 3D & 4D GIS Mapping Software*. esri.com/en-us/arcgis/products/arcgis-pro/overview [accessed 25 May 2021].
- FARRIS, Z.J., GERBER, B.D., VALENTA, K., RAFALIARISON, R., RAZAFIMAHAIMODISON, J.C., LARNEY, E. et al. (2017) Threats to a rainforest carnivore community: a multi-year assessment of occupancy and co-occurrence in Madagascar. *Biological Conservation*, 210, 116–124.
- HADDAD, N.M., BRUDVIG, L.A., CLOBERT, J., DAVIES, K.F., GONZALEZ, A., HOLT, R.D. et al. (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Science Advances*, 1, e1500052.
- HANKINSON, E.L., HILL, R.A., MARSH, C.D., NOWAK, M.G., ABDULLAH, A., PASARIBU, N. et al. (2021) Influences of forest structure on the density and habitat preference of two sympatric gibbons (*Symphalangus syndactylus* and *Hylobates lar*). *International Journal of Primatology*, 42, 237–261.
- HANKINSON, E., KORSTJENS, A.H., HILL, R.A., WICH, S.A., SLATER, H.D., ABDULLAH, A. et al. (2022) Effects of anthropogenic disturbance on group densities of Thomas' langurs (*Presbytis thomasi*) within a lowland tropical forest, north Sumatra. *Ecological Research*, 38, 293–305.
- HARRISON, N.J., HILL, R.A., ALEXANDER, C., MARSH, C.D., NOWAK, M.G., ABDULLAH, A. et al. (2020) Sleeping trees and sleep-related behaviours of the siamang (*Symphalangus syndactylus*) in a tropical lowland rainforest, Sumatra, Indonesia. *Primates*, 1, 3.
- HIJMANS, R.J., CAMERON, S. & PARRA, J. (2015) *WorldClim*. worldclim.org [accessed March 2023].
- ITIS (2021) *Integrated Taxonomic Information System (ITIS) Online Database*. itlis.gov [accessed May 2021].
- IUCN (2021a) *Mapping Standards and Data Quality for IUCN Red List Spatial Data*. IUCN, Gland, Switzerland. iucnredlist.org/resources/mappingstandards [accessed May 2021].
- IUCN (2021b) *The IUCN Red List of Threatened Species. Version 2021-3*. iucnredlist.org [accessed December 2021].
- KINNAIRD, M.F., SANDERSON, E.W., O'BRIEN, T.G., WIBISONO, H.T. & WOOLMER, G. (2003) Deforestation trends in a tropical landscape and implications for endangered large mammals. *Conservation Biology*, 17, 245–257.
- KORSTJENS, A.H. & HILLYER, A. P. (2016) Primates and climate change: a review of current knowledge. In *An Introduction to Primate Conservation* (eds S.A. Wich & A.J. Marshall), pp. 175–192. Oxford University Press, Oxford, UK.
- LAURANCE, W.F. (2004) Forest–climate interactions in fragmented tropical landscapes. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 359, 345–352.
- LOVE, K., KURZ, D.J., VAUGHAN, I.P., KE, A., EVANS, L.J. & GOOSSENS, B. (2017) Bearded pig (*Sus barbatus*) utilisation of a fragmented forest–oil palm landscape in Sabah, Malaysian Borneo. *Wildlife Research*, 44, 603.

- MARSH, C.D., HILL, R.A., NOWAK, M.G., HANKINSON, E., ABDULLAH, A., GILLINGHAM, P. & KORSTJENS, A.H. (2022) Measuring and modelling microclimatic air temperature in a historically degraded tropical forest. *International Journal of Biometeorology*, 66, 1283–1295.
- MARTIN, E.H., CAVADA, N., NDIBALEMA, V.G. & ROVERO, F. (2015) Modelling fine-scale habitat associations of medium-to-large forest mammals in the Udzungwa Mountains of Tanzania using camera trapping. *Tropical Zoology*, 28, 137–151.
- MATHEWSON, P.D., PORTER, W.P., BARRETT, L., FULLER, A., HENZI, S.P., HETEM, R.S. et al. (2020) Field data confirm the ability of a biophysical model to predict wild primate body temperature. *Journal of Thermal Biology*, 94, 102754.
- MCCAIN, C.M. & KING, S.R.B. (2014) Body size and activity times mediate mammalian responses to climate change. *Global Change Biology*, 20, 1760–1769.
- NIEBALLA, J., SOLLMANN, R., COURTIOL, A. & WILTING, A. (2016) camtrapR: an R package for efficient camera trap data management. *Methods in Ecology and Evolution*, 7, 1457–1462.
- OKSANEN, J., BLANCHET, F.G., FRIENDLY, M., KINDT, R., LEGENDRE, P., MCGLINN, D. et al. (2019) *vegan: Community Ecology Package*. R package version 2.5-6. cran.r-project.org/package=vegan [accessed March 2023].
- ORANGUTAN INFORMATION CENTRE (2009) The Gunung Leuser National Park. In *Guidebook to the Gunung Leuser National Park*. Orangutan Information Centre, Medan, Indonesia. miteco.gob.es/parques-nacionales-oapn/proyectos-de-cooperacion/guia_tcm30-287424.pdf [accessed March 2023].
- POHLMAN, C.L., TURTON, S.M. & GOOSEM, M. (2007) Edge effects of linear canopy openings on tropical rain forest understory microclimate. *Biotropica*, 39, 62–71.
- R CORE TEAM (2020) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. [r-project.org](https://www.R-project.org/) [accessed March 2023].
- ROTH, T.S., RIANTI, P., FREDRIKSSON, G.M., WICH, S.A. & NOWAK, M.G. (2020) Grouping behavior of Sumatran orangutans (*Pongo abelii*) and Tapanuli orangutans (*Pongo tapanuliensis*) living in forest with low fruit abundance. *American Journal of Primatology*, 82, e23123.
- RUPPERT, N., HOLZNER, A., SEE, K.W., GISBRECHT, A. & BECK, A. (2018) Activity budgets and habitat use of wild southern pig-tailed macaques (*Macaca nemestrina*) in oil palm plantation and forest. *International Journal of Primatology*, 39, 237–251.
- SCRIVEN, S.A., CARLSON, K.M., HODGSON, J.A., MCCLEAN, C.J., HEILMAYR, R., LUCEY, J.M. & HILL, J.K. (2019) Testing the benefits of conservation set-asides for improved habitat connectivity in tropical agricultural landscapes. *Journal of Applied Ecology*, 56, 2274–2285.
- SEGAN, D.B., MURRAY, K.A. & WATSON, J.E.M. (2016) A global assessment of current and future biodiversity vulnerability to habitat loss–climate change interactions. *Global Ecology and Conservation*, 5, 12–21.
- STEENWEG, R., HEBBLEWHITE, M., KAYS, R., AHUMADA, J., FISHER, J.T., BURTON, C. et al. (2017) Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. *Frontiers in Ecology and the Environment*, 15, 26–34.
- STEWART, F.E.C., HEIM, N.A., CLEVINGER, A.P., PACZKOWSKI, J., VOLPE, J.P. & FISHER, J.T. (2016) Wolverine behavior varies spatially with anthropogenic footprint: implications for conservation and inferences about declines. *Ecology and Evolution*, 6, 1493–1503.
- TAMIAN, A., VIBLANC, V.A., DOBSON, F.S., NEUHAUS, P., HAMMER, T.L., NESTEROVA, A.P. et al. (2022) Integrating microclimatic variation in phenological responses to climate change: a 28-year study in a hibernating mammal. *Ecosphere*, 13, e4059.
- TULLOCH, A.I.T., SUTCLIFFE, P., NAUJOKAITIS-LEWIS, I., TINGLEY, R., BROTONS, L., FERRAZ, K.M.P.M.B. et al. (2016) Conservation planners tend to ignore improved accuracy of modelled species distributions to focus on multiple threats and ecological processes. *Biological Conservation*, 199, 157–171.
- VARNER, J. & DEARING, M.D. (2014) The importance of biologically relevant microclimates in habitat suitability assessments. *PLOS ONE*, 9, e104648.
- VENABLES, W.N. & RIPLEY, D.B. (2002) *Modern Applied Statistics with S*, 4th edition. Springer, New York, USA.
- WEARN, O.R., ROWCLIFFE, J.M., CARBONE, C., PFEIFER, M., BERNARD, H. & EWERS, R.M. (2017) Mammalian species abundance across a gradient of tropical land-use intensity: a hierarchical multi-species modelling approach. *Biological Conservation*, 212, 162–171.
- WYNN-GRANT, R., GINSBERG, J.R., LACKEY, C.W., STERLING, E.J. & BECKMANN, J.P. (2018) Risky business: modeling mortality risk near the urban–wildland interface for a large carnivore. *Global Ecology and Conservation*, 16, e00443.