Safeguarding Asian tapir habitat in Sumatra, Indonesia

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Abstract The Asian tapir *Tapirus indicus* is the only tapir species in Southeast Asia. It is declining across its range and is categorized as Endangered on the IUCN Red List. The forests of Sumatra are critical to Asian tapir conservation as they contain some of the last remaining populations of the species, yet conservation efforts are hindered by a lack of information on habitat suitability. We collated camera-trap data from nine landscapes across 69,500 km² of Sumatran rainforest to help predict suitable habitat for Asian tapirs on the island. Predictions from Bayesian occupancy models demonstrated that tapir occupancy was greatest in forests below 600 m elevation and exclusively in forests with high aboveground biomass. Forests around the Barisan Mountains on the west of Sumatra provide the most suitable habitat for the species. Only 36% of the most critical habitat (i.e. 80th percentile of predicted occupancy values, or above) for tapirs is formally protected for conservation, with much of the remainder found in forests allocated to watershed protection (35%) or logging (23%). We highlight several key areas in Sumatra where tapir conservation could be bolstered, such as by leveraging existing conservation efforts for other charismatic flagships species on the island.

Keywords Asian tapir, camera-trapping, conservation areas, habitat suitability, Indonesia, mammals, occupancy modelling, *Tapirus indicus*

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Introduction

Biodiversity continues to decline globally (IUCN, 2023). Although extinctions have occurred for centuries, human encroachment into forests and overexploitation have increased species extinction risk, particularly in tropical regions (Osuri et al., 2020). Deforestation, habitat fragmentation and degradation are major drivers of defaunation (Alroy, 2017), exacerbated by hunting, which can occur in intact and degraded forests alike (Canale et al., 2012).

Defaunation has disproportionately affected forest specialists, particularly large mammals (Bogoni et al., 2019). Southeast Asia harbours numerous large-bodied mammal species (Ripple et al., 2016), with Indonesia considered a centre of biodiversity and a priority country for conservation (Myers et al., 2000). Indonesia supports 29 large mammal species, many of which are endemic and found on the western islands of Borneo and Sumatra (Maryanto et al., 2019). Sumatra is the only place where the Sumatran rhinoceros *Dicerorhinus sumatrensis*, Sumatran tiger *Panthera tigris sumatrae*, Sumatran elephant *Elephas maximus sumatranus* and orangutan (Sumatran orangutan *Pongo abelii* and/or Tapanuli orangutan *Pongo tapanuliensis*) coexist, all of which are categorized as Critically Endangered on the IUCN Red List (2023). Sumatra is also home to an important population of the Asian tapir *Tapirus indicus*, which is one of only four tapir species and the only one occurring beyond South and Central America (García et al., 2012). By 2016 the remaining Asian tapir population was estimated to be c. 2,500 individuals in the wild, and the species is categorized as Endangered on the IUCN Red List (Traeholt et al., 2016). Habitat conversion and infrastructure development are major causes of Asian tapir population decline (Samantha et al., 2020). Although hunting and consumption also hinder tapir conservation in some areas, these threats are thought to have lesser impacts overall (Meijaard & van Strien, 2003). Habitat disturbances also exacerbate conflicts with people (e.g. through foraging in crops; Novarino, 2005) and can lead to indiscriminate snaring by poachers (Campbell et al., 2019).

Although tapirs contribute to important ecosystem processes through seed dispersal (Holden et al., 2003), the species is one of the least studied large mammals in Southeast Asia, receiving less conservation attention than other high-profile Sumatran species such as the tiger or elephant (Ardiantiono et al., 2024). A previous assessment across the species' range highlighted that Sumatra remained a stronghold for tapirs, with the island supporting relatively high species occupancy compared to other parts of Southeast Asia (Linkie et al., 2013).

In this study, we utilize bycatch data from a network of camera-trap surveys to predict the extent of suitable tapir habitat across Sumatra and to identify priority areas for conservation. We apply an occupancy modelling framework to identify key ecological and anthropogenic drivers associated with tapir occurrence and predict the distribution of the species across the island. Based on these predictions we estimate the status of tapir populations in various forest land uses and highlight the most important areas to safeguard tapir habitat across Sumatra. As many of these areas also support sizeable populations of other large mammal species, we discuss ways in which tapir conservation could be coupled with the management and monitoring of other high-profile taxa to maximize the long-term prospects for this charismatic yet understudied mammal species.

Study area

We conducted our study across the known geographical extent of the Asian tapir in Sumatra, encompassing the area south of Lake Toba in North Sumatra province to Lampung province in the south (Fig. 1; Traeholt et al., 2016). We compiled camera-trap data spanning nine landscapes within this extent, comprising conservation areas and neighbouring forests: Batang Toru, Bukit Rimbang Bukit Baling, Tesso Nilo, Bukit Tigapuluh, Kerinci Seblat, Berbak Sembilang, Dangku, Bukit Barisan Selatan and Way Kambas (Table 1; Supplementary Table 1). All landscapes are protected for conservation purposes except Batang Toru, which comprises a mosaic of protected and unprotected areas. Across landscapes, surveys encompassed an elevational range of 2–1,798 m, representing a mix of forest habitats from mountainous forest on the west coast to lowland and peat swamp forest near the east coast.

Methods

Camera-trap surveys

Camera-trap data were collected by various agencies through local and international partners during July 2013–February 2017, with most fieldwork undertaken during 2015–2016 (Supplementary Table 1). These surveys primarily targeted tigers and their ungulate prey, but survey designs were also appropriate for tapirs (Linkie et al., 2013). The setup comprised 584 unbaited camera-trap stations, with 801–14,178 camera-trap days per site. The placement and use of automatic cameras allowed other species to be detected but only tapir detection data were made available to us for analysis.

We constructed tapir detection histories for each study landscape and restricted sampling to the first 90 days of each survey to adhere to assumptions of population closure in occupancy modelling (Rota et al., 2009) and to reduce the bias of occupancy estimation (Kéry & Royle, 2016). We collapsed each 90-day period into 7-day sampling events to increase temporal independence (Deere et al., 2017), providing 8–13 temporal replicates across sites. Camera-trap spacing was 0.50–82.81 km. We discarded stations within 1 km of any neighbouring cameras to avoid pseudo-replication (Linkie et al., 2013).

Potential predictors of tapir occurrence

We selected site and detection covariates based on their potential influence on tapir distribution. We considered six environmental and human disturbance covariates as occurrence predictors for tapir: elevation (elev), distance from cameras to roads (road), rivers (river), human settlements (dpop) and forest edges (dedge), and aboveground live biomass in the forest as a proxy for habitat quality (e.g. high values reflect more larger trees; biom; Table 2). We calculated all proximity-based covariates using the Euclidian distances from source features using layers from the closest year available to the camera survey (e.g. we used a forest layer from 2014 to calculate distances to forest edge for a survey undertaken in 2014). We resampled non-distance covariates to 1 km resolution and we extracted each predictor layer as mean values aggregated across 1 km-radius buffers around each camera location. We standardized covariates (mean centred and scaled to one-unit standard deviation) to place them on a comparable scale and improve model convergence.

We tested all covariates for collinearity using Pearson's correlation coefficient and discarded variables if they were strongly correlated (Pearson's $r > |0.7|$; McCarthy et al.,

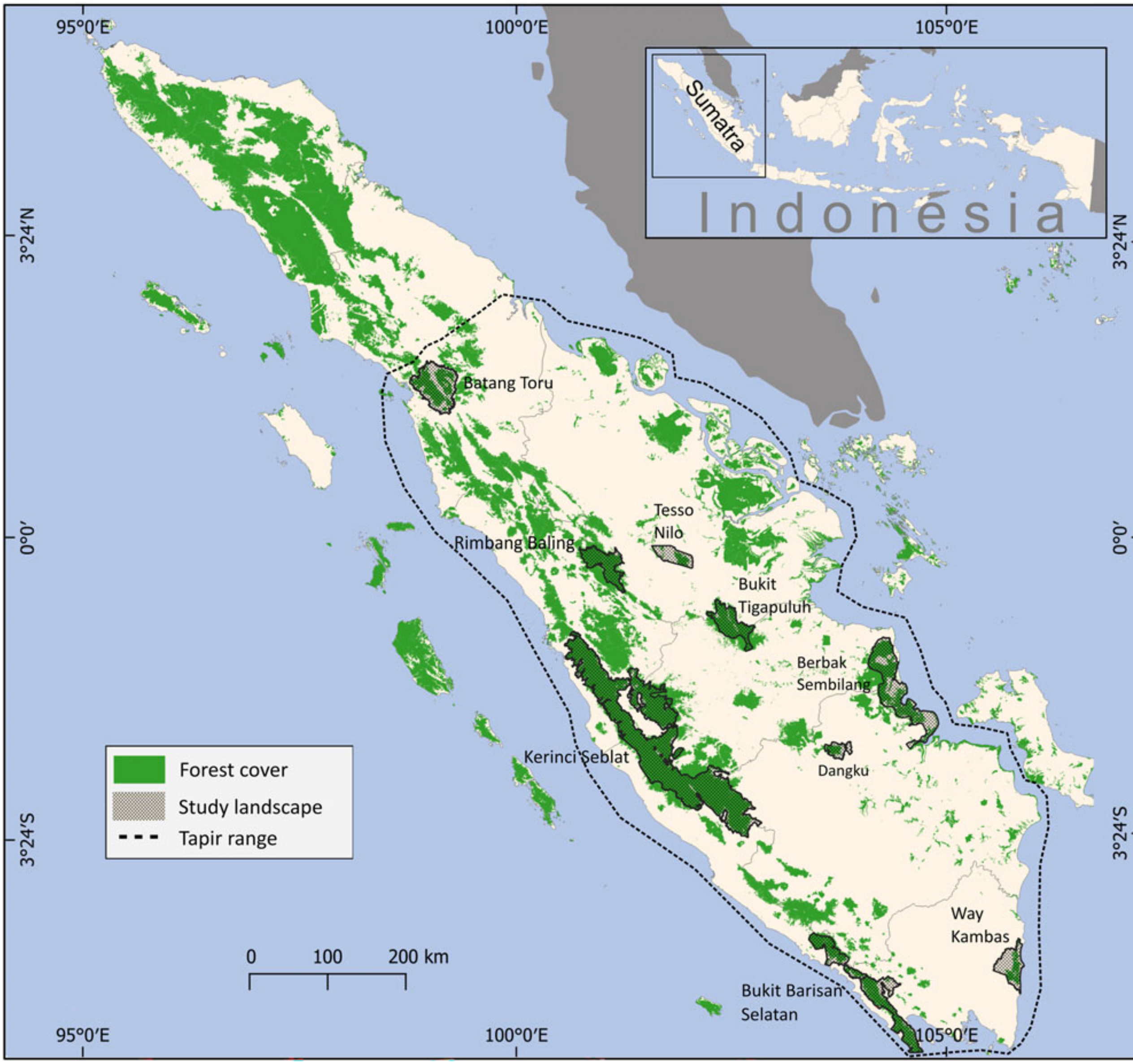

FIG. 1 Study region in Sumatra, Indonesia, comprising nine landscapes (Table 1) across the range of the Asian tapir *Tapirus indicus*. Intact forest cover is from MoEF (2015).

2015). We incorporated survey effort, sampling periods and habitat types in each landscape to account for their influence on detection. We included the following forest habitat types (hab_type): dipterocarp forest, peat swamp forest and mangrove forest, all at primary (i.e. old growth, little disturbed) and secondary (i.e. disturbed) levels (Table 2). We generated and extracted all site covariates in *QGIS 3.22* (QGIS Development Team, 2022) and we performed standardization and collinearity analyses in *R 4.3* (R Core Team, 2022).

Estimation of the area occupied by tapir

We estimated the probability of an area being occupied by the Asian tapir using occupancy (ψ) modelling to account for imperfect detection ($p < 1$; Mackenzie et al., 2002). We applied a single-species, single-season model modified to account for multiple study landscapes, in which landscape-specific parameters were drawn as random effects from a common distribution defined by calculable hyperparameters. Accordingly, hyperparameters reflect the aggregated response of tapirs to covariate effects across all study landscapes and are representative of range-wide trends across Sumatra. This approach provided improved estimation precision for landscapes in which tapirs were infrequently encountered whilst allowing statistical inference at two geographical scales (i.e. landscape-specific effects and Sumatra-wide trends).

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Table 1 Summary of camera-trap studies used to generate occupancy models for the Asian tapir *Tapirus indicus* in Sumatra, Indonesia (Fig. 1), and the model results (intercept of occupancy, ψ, and probability of detection, p, with Bayesian credible interval, BCI) and predictors in each landscape and for all nine landscapes (Fig. 1).

Study landscape	Top three habitat classes	Mean (range) elevation (m)	Number of camera-trap stations	Number of camera-trap days	Number of tapir records	ψ (95% BCI)	p (95% BCI)
Batang Toru	Secondary dipterocarp, primary dipterocarp & production/industrial forests	535 (337–719)	10	456	2	0.26 (0.07–0.53)	0.47 (0.34–0.65)
Bukit Rimbang Bukit Baling	Primary dipterocarp & secondary dipterocarp forests, agriculture	430 (175–764)	72	6,438	38	0.31 (0.16–0.48)	0.43 (0.25–0.57)
Tesso Nilo	Savannah, secondary dipterocarp forest, open land	79 (43–103)	23	2,009	5	0.30 (0.09–0.64)	0.42 (0.22–0.58)
Bukit Tigapuluh	Secondary dipterocarp, primary dipterocarp & production/industrial forests	174 (91–512)	61	4,447	16	0.32 (0.12–0.65)	0.46 (0.36–0.59)
Kerinci Seblat	Primary dipterocarp forest, savannah, shrub	914 (223–1,676)	64	3,948	51	0.31 (0.16–0.50)	0.49 (0.41–0.61)
Berbak Sembilang	Primary swamp & primary mangrove forests, swamp shrub	20 (4–32)	93	7,447	9	0.26 (0.07–0.50)	0.43 (0.24–0.60)
Dangku	Secondary dipterocarp forest, agriculture, shrub	57 (47–68)	10	747	1	0.32 (0.12–0.65)	0.45 (0.31–0.61)
Bukit Barisan Selatan	Primary dipterocarp & secondary dipterocarp forests, agriculture	505 (169–855)	63	5,520	58	0.33 (0.16–0.63)	0.39 (0.24–0.51)
Way Kambas	Secondary mangrove forest, savannah, swamp shrub	25 (7–40)	56	4,583	27	0.30 (0.11–0.62)	0.44 (0.26–0.61)
All nine landscapes (intercept)		316 (4–1,676)	452	35,595	207	0.30 (0.16–0.49)	0.44 (0.34–0.54)

TABLE 2 Details of covariates used in occupancy modelling and habitat prediction for the Asian tapir for the nine landscapes studied and combined for the Sumatra-wide model (Fig. 2). Scale indicates whether resampling of non-distance covariates used mean values across 1 km-radius buffers around each camera-trap station.

Covariate name (abbreviation)	Description	Source	Scale
Elevation (elev)	Mean elevation (m)	USGS Shuttle Radar Topography Mission 1 Arc-Second (30 m) (NGA, 2000)	Yes
River (river)	Distance to river (km)	Indonesia Geospatial Agency (2017)	No
Forest edge (dedge)	Distance to forest edge (km)	MoEF (2015)	No
Biomass (biom)	Aboveground live biomass (Mg/ha)	Santoro et al. (2018)	Yes
Human settlements (dpop)	Distance to settlements (defined as areas with a human population density ≥ 100 people/km2, in 2010) (km)	CIESIN (2018)	Yes
Roads (road)	Distance to road (km)	Indonesia Geospatial Agency (2017)	No
Habitat type (hab_type)	Habitat classification (primary dipterocarp, secondary dipterocarp, primary mangrove, secondary mangrove & primary swamp forests, swamp shrub)	MoEF (2015)	No

To investigate the factors underpinning the distribution of the Asian tapir we modelled occurrence as a function of six spatial covariates:

$$\begin{aligned}\log\text{it}(\psi_{j,i}) = \alpha_\psi &+ \beta_{\psi 1} \times \text{river}_i + \beta_{\psi 2} \times \text{road}\\ &+ \beta_{\psi 3} \times \text{dedge} + \beta_{\psi 4} \times \text{dpop}\\ &+ \beta_{\psi 5} \times \text{elev} + \beta_{\psi 7} \times \text{biom}\end{aligned}$$

We specified detection probability as a function of the habitat type and survey effort, which represents the ecological and sampling processes that affect the ability to detect the species given that it occupies an area. The model was:

$$\log\text{it}(p_{ij}) = \alpha_\text{p} \times \text{hab\_type} + \beta_i \times \text{trap\_effort}$$

We specified occupancy models within a Bayesian framework using *JAGS* in *R* using the *jagsUI* package (Kellner & Meredith, 2021).

Identifying priority areas for tapir conservation

To develop a distribution map of potentially suitable tapir habitat we applied landscape-specific parameters and hyperparameters to predict habitat suitability for each landscape independently and across the Sumatran range, respectively, whilst accounting for imperfect detection. We estimated habitat suitability as a function of all covariates included in the occupancy model. Prior to interpolation we weighted each value to represent the mean of all surrounding cells within a 1 km circular radius to maintain consistency with the scale used to extract predictor variables. We constrained predictions to within the range of observed values in variables to avoid under- or overestimation.

To investigate the contribution of various land-use designations and identify ways to conserve the tapir ex situ, critical habitat is defined by predicted occupancy values in the 80th percentile or above (i.e. the top 20% of the values) and suitable habitat area as values between the 40th and 80th percentiles. We overlaid this reclassified occupancy layer with a map of land-use designation, and categorized the areas into conservation or non-conservation areas. Conservation areas fell into five designation categories: national park, wildlife reserve, nature reserve, grand forest park and nature recreational park. Non-conservation areas were watershed-protection forest, production forest, limited production forest, non-forest and convertible production forest. We constrained the prediction map to the extent of occurrence according to the IUCN Red List assessment (Traeholt et al., 2016).

Results

Asian tapirs were recorded in 143 of 456 camera-trap stations across the nine landscapes over a total survey period of 35,595 camera trap-days. The highest number of tapir detections were in Bukit Barisan Selatan and Kerinci Seblat (58 and 51, respectively), and the lowest number in Dangku and Batang Toru (one and two, respectively; Table 1). Generally, tapir detections were concentrated < 7 km from major rivers (66% of 273 total detections), < 12 km from the nearest road (94%), < 3 km from the forest edge (77%) and < 50 km from human population centres (81%). Tapirs also occurred at elevations > 1,500 m (4%), although most detections were observed at < 600 m (74%) and were exclusively recorded in forests with high aboveground biomass (95%; 160–210 Mg C per ha; Supplementary Fig. 1).

We estimated occupancy across Sumatra to be 0.30 (95% Bayesian credible interval (BCI) 0.16–0.49), with a detection probability of 0.44 (95% BCI 0.34–0.54). Landscape-level occupancy and detection were broadly consistent with Sumatra-wide trends, ranging from 0.26 (95% BCI 0.07–0.53) in Batang Toru to 0.33 (95% BCI 0.16–0.63) in Bukit

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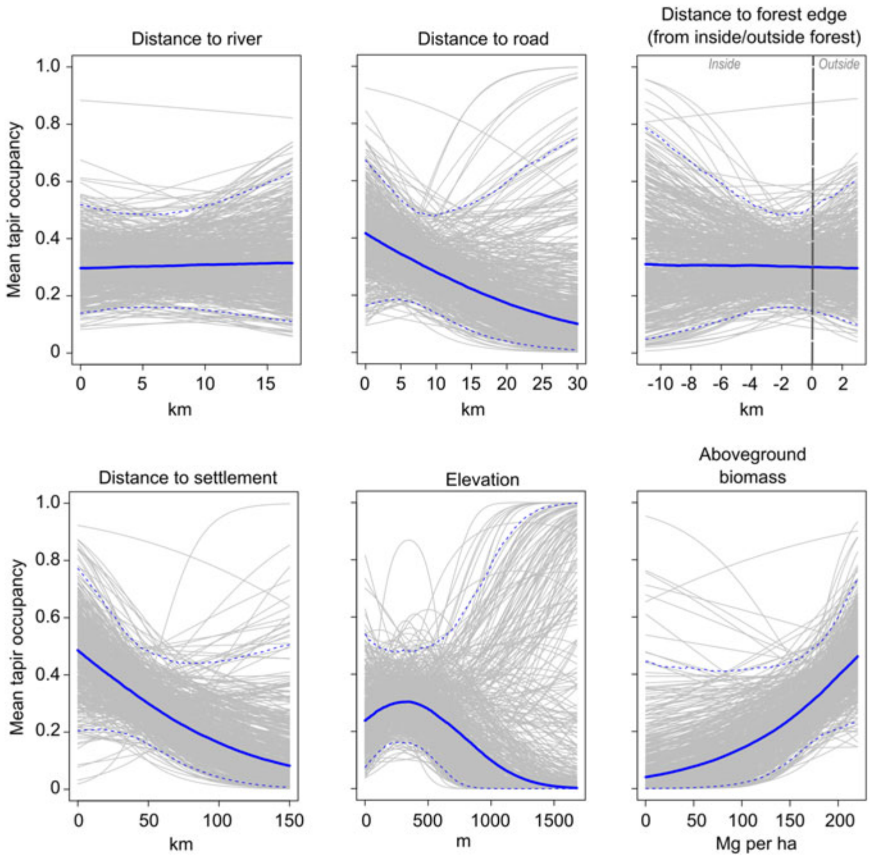

Fig. 2 Tapir occupancy responses to each covariate at the level of Sumatra (i.e. combining data from all nine landscapes, with the mean (thick line), 95% quantile (dotted lines) and 500 random samples (thin lines); Table 2). Distance to forest edge is negative for cameras placed inside the forest and positive for those placed outside the forest.

Barisan Selatan, and 0.39 (95% BCI 0.24–0.51) in Bukit Barisan Selatan to 0.49 (95% BCI 0.41–0.61) in Kerinci Seblat, respectively (Table 1). At the island level tapirs occurred more frequently in areas characterized by high-biomass forest and lower elevation. Although occupancy tended to be higher close to the forest edge, this broadly reflected the sampling effort, and we found no discernible link between occupancy and the covariate distance to forest edge (Fig. 2).

All nine landscapes were deemed suitable habitats for tapir (i.e. within the 40–80th percentiles of predicted occupancy values), although not all contained critical habitat (i.e. above the 80th percentile). Four landscapes comprised the greatest extents (i.e. more than half the landscape area) of suitable or critical habitat: Kerinci Seblat (59% suitable, 31% critical), Bukit Rimbang Bukit Baling (64% suitable, 19% critical), Bukit Barisan Selatan (47% suitable, 31% critical) and Batang Toru (55% suitable, 15% critical). Three landscapes contained suitable but no critical habitat: Dangku (7% suitable), Tesso Nilo (5% suitable) and Bukit Tigapuluh (1% suitable; Table 3).

Island-wide model predictions revealed that suitable tapir habitat comprised all forest types within conservation and non-conservation areas, which totalled 43,888 km^2. Forests in the Barisan Mountains located along the west of Sumatra contained the most suitable habitat for tapir (Fig. 3). Almost 40% of the suitable and critical areas were formally protected in conservation areas, with five areas contributing the majority: Kerinci Seblat National Park (20%), Bukit Barisan Selatan National Park (4%), Bukit Rimbang Bukit Baling Wildlife Reserve (2%), Tarusan Arau Hilir Wildlife Sanctuary (2%) and Berbak Sembilang National Park (1%). The remaining suitable habitat was distributed across forests maintained for watershed protection (28%), limited production (i.e. low-intensity logging; 13%) and production (industrial logging or timber plantation;

Table 3 The amount of suitable (40–80th percentiles of predicted occupancy values) and critical (80th percentile of predicted occupancy values) Asian tapir habitat in each of the nine landscapes (Fig. 3).

		Habitat (km^2)	
Name	Area (km^2)	Critical	Suitable
Batang Toru	2,493	390	1,741
Bukit Rimbang Bukit Baling	1,416	272	1,183
Tesso Nilo	816	0	41
Bukit Tigapuluh	1,441	0	9
Kerinci Seblat	13,562	4,226	12,241
Berbak Sembilang	3,689	2	210
Dangku	480	0	31
Bukit Barisan Selatan	3,154	1,009	2,521
Way Kambas	1,272	98	486
Nine landscapes combined	28,323	5,997	18,463

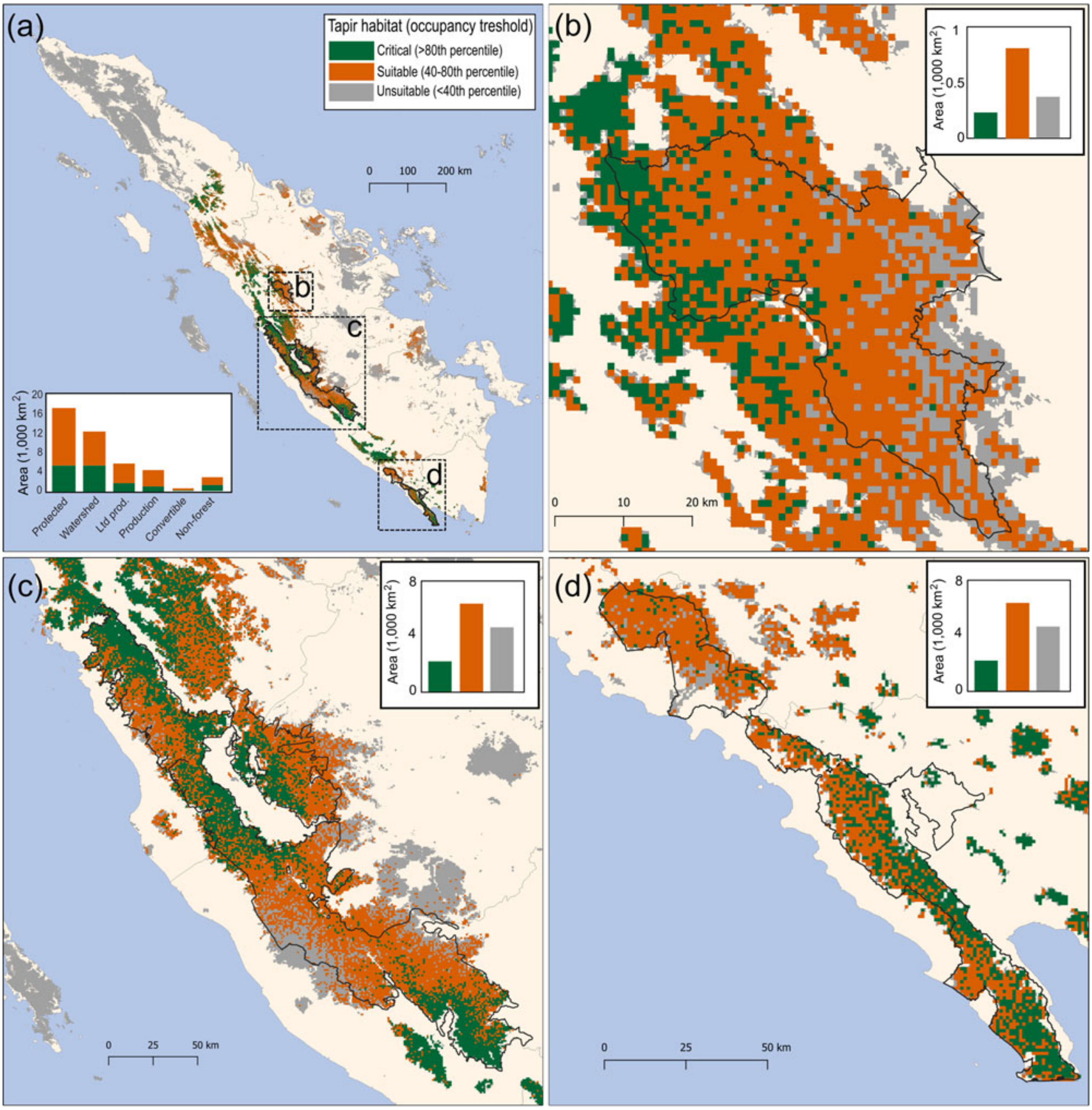

FIG. 3 (a) Predicted habitat suitable for the Asian tapir in Sumatra (Table 3). The bar charts indicate the amount of unsuitable (< 40th percentile of predicted occupancy values), suitable (40–80th percentiles) and critical (> 80th percentile) habitat in three example landscapes ((b) Rimbang Baling, (c) Kerinci Seblat, (d) Bukit Barisan Selatan) and the broader distribution across land-use classes in Sumatra.

10%), with smaller extents in forested areas not legally recognized as forest (7%) or in areas designated for conversion (i.e. plantations; 1%). Almost 35% (15,465 km²) of the suitable habitat was deemed critical for tapir. Of the total critical habitat extent, 35% (5,533 km²) was in conservation areas, with a further 36% in forest protected to maintain watersheds. The remaining consisted of forests designated for limited production (12%), production (8%) and convertible production (1%), and non-forest (8%). Five conservation areas contributed 26% of the critical habitat: Kerinci Seblat (14%, 2,209 km²), Bukit Barisan Selatan (5%, 715 km²), Tarusan Arau Hilir (4%, 612 km²), Bukit Rimbang Bukit Baling (1.5%, 241 km²) and Malampah Alahan Panjang (1%, 220 km²; Supplementary Table 2).

Discussion

The Asian tapir is one of the most threatened large mammal species in Sumatra, yet there has been relatively little

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research on its population or conservation status compared to other threatened mammal fauna (Ardiantiono et al., 2024). We applied a Bayesian occupancy framework to a network of camera-trap data to address this gap and found tapir occupancy was highest in forests below 600 m and exclusively in areas with high aboveground biomass. These forests also tended to be nearer human settlements, road infrastructure and other human-dominated areas. However, the response of tapir occupancy to environmental and anthropogenic covariates varied amongst the nine landscapes surveyed, with aboveground biomass being important in all regions, distance to roads being important in Bukit Rimbang Bukit Baling, Berbak Sembilang, Bukit Barisan Selatan and Way Kambas and distance to settlements being important in all landscapes except Batang Toru. Approximately 43,888 km^2 of land were suitable for the Asian tapir, with 15,363 km^2 deemed critical habitat.

We utilized data for 2013–2017 as these represented the most up-to-date camera-trap information on tapirs available to us, although it is possible that forests and their tapir populations could have changed since then. The use of remote cameras has substantially increased as a non-invasive research tool to investigate and monitor wildlife populations in Sumatra (Pusparini et al., 2018). However, camera-trap surveys remain limited to a few high-profile species, and often not all species' information is recorded and shared. As measures of habitat quality are important factors influencing tapir occupancy, it is probable that changes to forests will have led to tapirs declining or being extirpated since the time of the surveys. However, we note that deforestation rates have greatly reduced in Sumatra since the tapir surveys were implemented (Gaveau et al., 2022), and forest cover has remained broadly consistent in the landscapes sampled since the study period. We also emphasize that although our modelling was based on data for 2013–2017, we applied the projections and spatial assessment using more recent covariate data. Therefore, assuming that the spatial predictors of tapir occupancy remain broadly the same as those from our survey period, we can still draw useful inferences from our analyses.

Tapir occupancy in the nine study landscapes

In a previous assessment of Asian tapirs that included data from across the Asian range it was found that Sumatra supported some of the highest occupancy estimates of Asian tapirs, of 0.12–0.90 amongst seven landscapes surveyed on the island during 2004–2010 (Linkie et al., 2013). Our occupancy values of 0.26–0.33, derived from subsequent data (2013–2017), are substantially lower. However, although occupancy modelling was applied in both studies, it was formulated in fundamentally different ways: the former assessment specified occupancy using maximum likelihood estimation, whereas we took a Bayesian approach. The two assessments are therefore not easily compared, and so we avoid drawing conclusions on whether our findings represent a population decline or not. The hierarchical nature of our model specification allowed us to integrate data more robustly from across the Sumatran range of the Asian tapir, to improve the precision of occupancy estimates whilst accounting for regional nuances. The framework provided the flexibility to identify scale-dependent population pressures that can be practically applied to inform conservation management at the island and landscape levels.

Across Sumatra, tapir occurrence is probably determined by a combination of bottom-up and top-down selection pressures. Amongst the four spatial covariates utilized, aboveground biomass in the forest had the strongest influence on Asian tapir occupancy in all landscapes. This could reflect the dietary preferences of Asian tapirs, which feed on a range of plant species in structurally intact rainforest (Samantha et al., 2020). We also found tapirs to be prevalent in the vicinity of human settlements, roads and other human-dominated areas, which suggests a degree of tolerance of human impacts (or lack of habitat choice), contradicting the findings from the previous range-wide assessment of the species (Linkie et al., 2013). Furthermore, this species is known to prefer evergreen forests, and ecotones between forest and non-forest lands result in varied plant composition that suits the habitat/foraging preferences of the species (Lynam et al., 2012). The situation in Sumatra, in which forest boundaries with non-forest lands are not always hard edges and in many areas follow transitions between habitats over several kilometres (Priatna, 2020), could explain the high occurrence of tapirs near forest edges.

Habitat suitability across the Sumatran range

Understanding characteristics of suitable habitat is vital for managing wildlife populations. In Sumatra, Asian tapirs occupy a broad suite of habitats, including forests on peat (Sasidhran et al., 2016), mineral soils in the lowlands (Traeholt & Sanusi bin Mohamed, 2009) and mountainous areas (Steinmetz et al., 2008). These suitable forest areas also overlap with the distributions of the big four mammal megafauna: orangutan in Batang Toru (Tapanuli species) and Bukit Tigapuluh (Sumatran species, reintroduced); elephant in Tesso Nilo, Kerinci Seblat, Bukit Tigapuluh, Bukit Barisan Selatan and Way Kambas; rhinoceros in Way Kambas and Bukit Barisan Selatan; and tiger in all regions. This coexistence between tapirs and other large mammals implies that efforts to safeguard the big four species in Sumatra could also benefit tapir conservation and vice versa (Sibarani et al., 2019). Additionally, the role of the Asian tapir as an important seed disperser (Campos-Arceiz et al., 2012) could be used to highlight this animal as a keystone species to help promote the protection of forests in Sumatra (Andelman & Fagan, 2000) and advocate for forest restoration (Paolucci et al., 2019).

We extended habitat suitability predictions beyond our study landscapes to identify priority tapir conservation areas across the range of the species. The predicted suitable habitat was 89% lower than estimated in the IUCN Red List estimate based on occurrence and area of extent (Traeholt et al., 2016). Our map of suitable habitat only overlaps with 28% of the IUCN Red List range map and covers 25% of the critical habitat when our prediction was based on occupancy results. Furthermore, our study indicates that non-conservation areas contribute c. 60% of the suitable habitat, with watershed protection forests (which are protected to some degree but not for the purpose of wildlife conservation) the largest area followed by forests allocated for logging.

Conservation areas alone are therefore insufficient to safeguard this Endangered species, which is also the case for other wide-ranging, large-bodied mammals in Sumatra (Moßbrucker et al., 2016). Watershed protection forests are designed to preserve ecological functioning, and our analysis demonstrates that these forests also play an important role in providing additional habitat for Asian tapirs. Production forest and non-forest areas (usually designated for logging) adjacent to conservation areas are also important for conservation. Batang Toru, for instance, is an extensive landscape that comprises protected forests and areas allocated for production (i.e. logging and non-forest uses), which collectively form a critical habitat for the remaining population of the Tapanuli orangutan (Wich et al., 2019) as well as for the tapir. Another example is the forest allocated to logging production on the northern and eastern coasts of Berbak Sembilang National Park, which is recognized as an important area for tigers (Ariyanto et al., 2020) and elephants (MoEF, 2020) whilst also supporting critical habitat for the Asian tapir. Thus, integrating the conservation and non-conservation areas for landscape-scale protection will be important for achieving species and habitat conservation objectives.

In general, the extent of suitable and critical tapir habitat defined by landscape-specific components in our model tended to be greater than that defined according to Sumatra-wide predictions. This disparity reflects geographical extent and habitat features, and so these results should be interpreted with this context in mind (Wyborn & Evans, 2021). At the landscape scale, our habitat suitability maps could support land managers in identifying priority areas for conservation and optimizing resource investments locally. At the island-wide scale the prediction map could be used to help allocate resources to the landscapes that could best contribute to Asian tapir conservation.

Future directions for Asian tapir conservation

An estimate of the area of suitable habitat does not necessarily indicate a species will be present in that habitat because other factors not accounted for in the models could influence suitability. Habitat disturbances could also influence the Asian tapir distribution temporarily or in the long term. For example, in the peat swamp forest of Kampar peninsula in Riau (an area deemed suitable in our assessment), Asian tapirs were reported by local people in 2000 (I.M.R. Pinondang, unpubl. data, 2020), but an intensive camera-trap survey in 2015 did not detect the species (Avriandy et al., 2016). Therefore, it is important to confirm the viability of forests deemed suitable or critical for Asian tapirs via sightings or other detection data.

To date, only two assessments have documented Asian tapir population density in Sumatra (Novarino, 2005, in West Sumatra; Asmita et al., 2014, in Riau) despite the species being a high conservation priority (Traeholt et al., 2016) and a national target for conservation (MoF, 2013). The lack of population information is challenging for designing a management strategy or conservation intervention. However, data-sharing amongst camera-trap campaigns could contribute to future management plans to help optimize the impacts and cost-effectiveness of activities and interventions. Encouraging researchers, practitioners and government stakeholders to collaborate in data analysis is a high priority for biodiversity research more broadly, especially in Indonesia (Ardiantiono et al., 2024). Our assessment of the Asian tapir demonstrates the value of documenting wildlife other than the target species in camera-trap images.

Safeguarding suitable Asian tapir habitats in non-conservation areas requires multi-stakeholder engagement. Promoting species conservation in community-managed forests and restoring forest habitat are potential options. Indonesia has pioneered a social forestry system in which local communities manage forests to achieve development and environmental goals; however, to date there are no systematic assessments of whether these schemes benefit biodiversity (Meijaard et al., 2020). Ecosystem restoration has also received renewed focus as part of the international commitments of Indonesia to tackling climate change. Government Regulation No. 23/2021 mandates the areas that are to remain as forests, and Ecosystem Restoration Concession licences are being used to allow private management of production forests to restore habitat (Harrison et al., 2020). Hutan Harapan, for instance, is a restoration programme that is focused on production forests in central Sumatra, and it aims to protect the forest and its biodiversity, including the Asian tapir (Gemita et al., 2007).

We conclude that conservation of the Asian tapir in Sumatra would benefit from being coupled with the management and monitoring of high-profile species such as the tiger and elephant, to maximize the long-term prospects for this species. Our study has refined the predicted extent of suitable habitat available to Asian tapirs across Sumatra and identified the main land uses within this area. Future research

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should focus on estimating Asian tapir population sizes and consider the ways that the species interacts with its habitat.

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Conflicts of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards.

Data availability The data that support the findings of this study are available from the Ministry of Environment and Forestry, Indonesia, with restrictions applying to their use. The data can be shared upon reasonable request to the authors if permission is granted by the Ministry.

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