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Original research article

Mapping the distribution of the Sunda pangolin *(Manis javanica)* within natural forest in Sabah, Malaysian Borneo

Elisa Panjang [a,b,*], Hong Ye Lim [c], Robert J. Thomas [a], Benoit Goossens [a,b,d,*], Andrew J. Hearn [e], David W. Macdonald [e], Joanna Ross [e], Seth Timothy Wong [f], Roshan Guharajan [f], Azlan Mohamed [f], Penny C. Gardner [a,b,g], Sharon Koh [h], Cheryl Cheah [h], Marc Ancrenaz [i], Isabelle Lackman [i], Robert Ong [j], Reuben Nilus [j], Alex Hastie [j], Jedediah F. Brodie [k,l], Alys Granados [m], Olga Helmy [k], Olivia Magritta Lapis [h], Donna Simon [h], Glyn Davies [f,h], Siew Te Wong [n], Mark Rampangajouw [o], Hisashi Matsubayashi [p], Chihiro Sano [p], Rebecca K. Runting [q], Symphorosa Sipangkui [d], Nicola K. Abram [c,**]

[a] *Organisms and Environment Division, Cardiff School of Biosciences, Cardiff University, Sir Martin Evans Building, Museum Avenue, Cardiff CF10 3AX, UK*
[b] *Danau Girang Field Centre, c/o Sabah Wildlife Department, 5th Floor, Block B, Wisma MUIS, Kota Kinabalu, Sabah 88100, Malaysia*
[c] *Forever Sabah, H30 Gaya Park, Lorong Muntahan 1C, Penampang Road, Kota Kinabalu, Sabah 88300, Malaysia*
[d] *Sabah Wildlife Department, 5th Floor, Block B, Wisma Muis, Kota Kinabalu, Sabah 88100, Malaysia*
[e] *Wildlife Conservation Research Unit (WildCRU), Department of Biology, University of Oxford, Recanati-Kaplan Centre, Tubney House, Tubney OX13 5QL, UK*
[f] *Leibniz Institute for Zoo and Wildlife Research, Berlin 10315, Germany*
[g] *RSPB Centre for Conservation Science, The Royal Society for the Protection of Birds, The Lodge, Sandy SG19 2DI, UK*
[h] *WWF-Malaysia, Centre Point Complex, Kota Kinabalu, Malaysia*
[i] *HUTAN/Kinabatangan Orangutan Conservation Programme, Kota Kinabalu, Sabah 88874, Malaysia*
[j] *Forest Research Centre, Sabah Forestry Department, Sandakan, Sabah, Malaysia*
[k] *Division of Biological Sciences and Wildlife Biology Program, University of Montana, Missoula, MT 59812, USA*
[l] *Institute for Biodiversity and Environmental Conservation, Universiti Malaysia Sarawak, Kota Samarahan, Sarawak, Malaysia*
[m] *Biodiversity Research Centre, University of British Columbia, Vancouver, Canada*
[n] *Bornean Sun Bear Conservation Centre, Sandakan, Sabah 90000, Malaysia*
[o] *Acacia Forest Industries (AFI), Unit 1, 2nd Floor, Block L, Metro Town, Jalan Lintas, Kota Kinabalu, Sabah 88300, Malaysia*
[p] *Tokyo University of Agriculture, 1737 Funako, Atsugi, Kanagawa 243-0034, Japan*
[q] *School of Geography, Earth and Atmospheric Sciences, The University of Melbourne, Parkville 3010, Australia*

A R T I C L E I N F O

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A B S T R A C T

Pangolins are the most trafficked mammals in the world and are severely threatened by poaching the loss, degradation, and fragmentation of habitat. In Malaysian Borneo, conservation initiatives for the Sunda pangolin (*Manis javanica*) are hindered by a paucity of data on their distribution and population size. Using MaxEnt niche modelling and consolidated species location data, we

* Corresponding authors at: Organisms and Environment Division, Cardiff School of Biosciences, Cardiff University, Sir Martin Evans Building, Museum Avenue, Cardiff CF10 3AX, UK.
** Corresponding author.
E-mail addresses: elisa_panjang@yahoo.com, panjange@cardiff.ac.uk (E. Panjang), goossensbr@cardiff.ac.uk (B. Goossens), nicola_abram@hotmail.com (N.K. Abram).

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projected the distribution of Sunda pangolins in Sabah. Additionally, we assessed the accessibility of their forest habitats to humans to understand potential threats. Our model indicated that, as of 2015, approximately half of Sabah's land area (39,530 km^2) is suitable for pangolins, with 43% in protected forests, 38% in production forests, and 19% outside of these areas. Alarmingly, our data suggest that nearly all (91%) of these suitable habitats are relatively easily accessible to poachers. Our findings provide a state-level baseline understanding of Sunda pangolin distribution and assess potential threats in Sabah. These can inform short- and long-term conservation management plans for pangolin to safeguard this critically endangered species.

1. Introduction

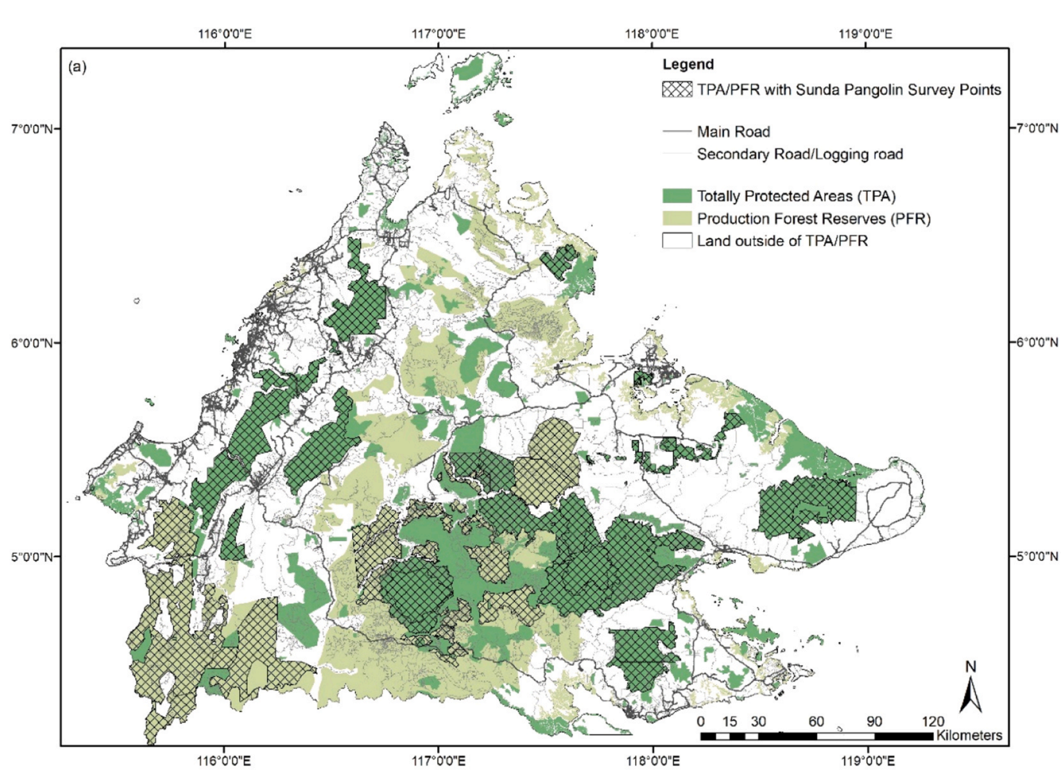
Deforestation, driven primarily by logging and agricultural land conversion activities, has resulted in significant habitat loss, drastically impacting biodiversity (Jackson and Fahrig, 2013). This loss of habitat can be so profound that it weakens wildlife populations and threatens to push entire species toward extinction (Harrison et al., 2016). On the island of Borneo, for example, a staggering 168,498 km^2 of primary forest disappeared between 1973 and 2010, amounting to 30.2% of its original forest cover, primarily due to oil palm (*Elaeis guineensis*) and other agricultural expansions (Gaveau et al., 2014). Amplifying this threat, the rapid expansion of roads and logging trails is worsening the threats of poaching to the island's endangered species (Wong and Linkie, 2013; Brodie et al., 2015). The Sunda pangolin (*Manis javanica*) is one such species facing these threats. Consequently, understanding the habitat needs of such species and the factors influencing their habitat suitability is crucial for their continued survival (Adhikari et al., 2012).

Pangolins are now considered the world's most trafficked mammals, drawing significant global concern. All eight extant species are listed as Vulnerable, Endangered, or Critically Endangered on the IUCN Red List of Threatened Species and on CITES Appendix I (Challender and Waterman, 2017). Listed as Critically Endangered, the Sunda pangolin is the only pangolin species present in Malaysia, populating both Peninsular Malaysia and Malaysian Borneo, encompassing Sabah and Sarawak (Chong et al., 2020). In Sabah, the species holds the highest protection status, listed as "totally protected" under Schedule 1 of the Wildlife Conservation Enactment 1997 (Panjang and Goossens, 2022). However, this protection status contrasts sharply with the dire reality on the ground. The Sunda pangolin is under severe threat from poaching, fuelling both local and international markets, and also faces challenges from habitat degradation and fragmentation (Chong et al., 2020). An alarming indication of the scale of poaching was evident in 2019 in Sabah, when enforcement authorities confiscated over 30 tonnes of pangolin products, including live animals, scales, and meat (The Straits Times, 2019). This seizure shed light on the complex illicit trade networks, underscoring Sabah's crucial role in this illegal trade, having been linked to the smuggling over 40 tonnes of pangolins since August 2017 (TRAFFIC, 2019).

The Sunda pangolin is known to inhabit a diverse range of habitats, including primary and secondary forests, evergreen and hill forests to peat swamp forests, wetland and riverine ecosystems such as mangroves, and even grasslands (Payne et al., 1985; Lim and Ng, 2008; Ketol et al., 2009; Azhar et al., 2013; Willcox et al., 2017; Chong et al., 2020). Reports indicate their presence at elevations up to 1700 m asl on Mount Kinabalu, although their precise altitude limits need to be determined (Payne and Francis, 2007). Notably, they also inhabit monoculture plantations, including oil palm and rubber estates, as well as gardens, and urban areas (Wearn et al., 2017; Sompud et al., 2019; Chong et al., 2020). However, it is unclear how well the species can sustain and reproduce in these altered habitats over extended periods and if viable populations can be maintained long-term (Chong et al., 2020).

The rarity and elusive behaviour of the primarily nocturnal Sunda pangolin make data collection challenging, leading to gaps in knowledge about where they occur and hindering the development of effective conservation efforts. This lack of understanding of the species' ecology and population dynamics is evident in the data inadequacies highlighted by Chong et al. (2020). Population estimates for the Sunda pangolin, not only in Sabah but across Southeast Asia, still need to be made available. An exception is Singapore, where an estimated 1046 Sunda pangolins were reported within the country (Nash et al., 2020). The lack of standardised survey techniques complicates efforts to monitor pangolin populations across the species range (Khwaja et al., 2019). Past research efforts have employed a variety of methods, including sign surveys (footprints and claw marks), nocturnal spotlighting, burrow counting, camera trapping, interviews with local communities, GPS tracking, radio telemetry, and the use of detection dogs (Willcox et al., 2019; Chong et al., 2020). In the context of Sabah, all these methods have been employed except for the use of detection dogs (Panjang, 2015; Sompud et al., 2019; Panjang, 2023). Despite these efforts, our knowledge about the Sunda pangolin's distribution in Sabah is still limited.

In our current study, we employed the Maximum Entropy (MaxEnt) method, a species distribution modelling approach optimised for presence-only data, to predict the potential distribution of Sunda pangolins in Sabah (Elith et al., 2010). The MaxEnt approach is known for its ability to model species distributions, particularly when working with endangered species where data are often limited (Phillips and Dudík, 2008; Phillips et al., 2009). Notably, its efficacy has been supported in predicting global pangolin distributions, including for *M. pentadactyla and M. crassicaudata* in regions such as China and India (Suwal et al., 2020; Sharma et al., 2020; Waseem et al., 2020; Xian et al., 2022). The objectives of our study were: 1) to determine the habitat suitability of Sunda pangolins within Sabah's natural forests; and 2) identify the environmental variables associated with pangolin occurrence in Sabah.



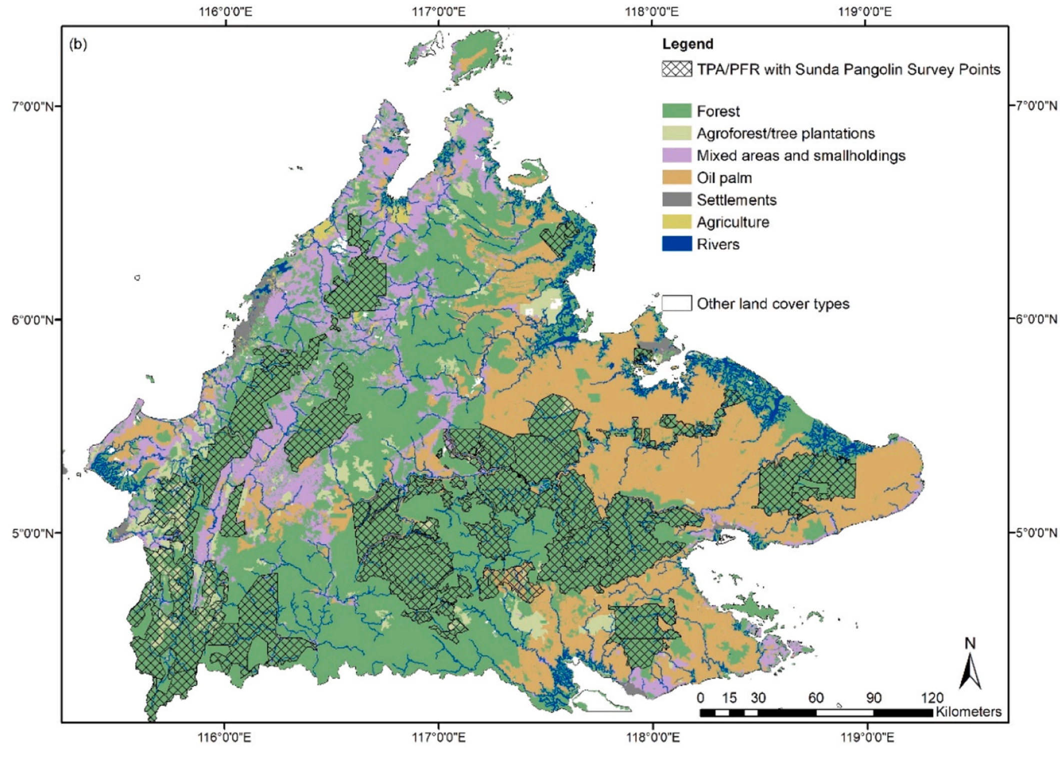


Fig. 1. Map showing Sabah's Totally Protected Areas (TPA) in dark green and Production Forest Reserves (PFR) in light green, with areas of black crosshatch showing TPAs/PFRs that have Sunda pangolin presence points (a); and a map showing land use and land cover for 2014/15, with black crosshatch showing TPAs/PFRs with Sunda pangolin presence points (b).

2. Materials and methods

2.1. Data collection and processing

This study is part of a wider assessment framework of High Conservation Value (HCV) areas within the Sabah state. It involved compiling a large dataset for terrestrial species categorised as Rare, Threatened and Endangered (RTE), following the guidelines provided by the Common Guidance for the Identification of HCVs (Brown et al., 2013). As part of the collaborative effort, existing location data for mammal species were provided by a network of 11 different researchers and organisations with location data covering various regions within Sabah and spanning from the years 2000–2018. These data were obtained through various survey methods, including camera trap surveys, ground, aerial and boat surveys, and opportunistic observations.

From this meta-dataset, we extracted records for the Sunda pangolin. This collection of pangolin presence data is the most comprehensive compilation of occurrence data for this species in Sabah. We standardised the format of the geographical coordinates and removed any duplicated records (i.e., multiple records of the same species at the same location on the same date). We then visualised the location dataset and applied a filter to ensure that the location dataset contained only one data point within a 1 km circular buffer to minimise the effect of spatial autocorrelation (following Fourcade et al., 2014). The final set of records used for this study was 201 points collected from 2007 to 2017, with most of the data (62%) recorded from 2012 to 2016.

Presence data were principally collected within forest habitats (98%) including Sabah's Totally Protected Areas (TPAs) and Production Forest Reserves (PFRs) (Fig. 1**a**). Although this data set is limiting the distribution assessment within forested environments, this data is extremely useful for the States HCV assessment that aims to identity important forest no-go areas for new oil palm development (Brown et al., 2013).

In this study, we refrain from showing precise location of presence points due to the extreme vulnerability of this species to poaching in Sabah (FMT, 2019; The Star, 2022). Indeed, the documented ease of access by poachers to Sabah's TPAs and PFRs, led to various calls for a cautious approach to presenting data to safeguard pangolins while continuing to contribute valuable scientific insights (TRAFFIC, 2011; Lindenmayer and Scheele, 2017; Chapman, 2020; Bernama, 2020).

2.2. Bias grid

To minimise sampling bias, a "bias grid" was created to represent survey effort. This study is part of a broader assessment of HCV areas in Sabah and included data from multiple species using various survey methods. As such, presence data (of all mammal species) were categorised based on the survey methods used. These were then divided into survey method sub-datasets so that appropriate data for different species could be used to develop a survey effort bias grid. For Sunda pangolins, survey methods that could, theoretically, see or capture this species included camera traps (representing the majority of these data), ground surveys and opportunistic sightings. All species data from these survey methods were combined into a shapefile and converted to a raster grid (at 91 m resolution). The grid cells that contained species presence points were assigned a value of 1 (to represent surveyed cells) and 'un-surveyed' cells were assigned a value of 0.1. The bias grid was then created using focal descriptive statistics by summing three-by-three cells within a neighbourhood around each focal cell (following Kramer-Schadt et al., 2013). This bias grid approach was deemed appropriate due to the lack of more in-depth, comprehensive and consistent survey effort information collated from the array of data providers.

2.3. Spatial predictor variables

Sixteen predictor variables were developed to model habitat suitability (Table 1). These spatial variables encompass various land use and land cover types, forest quality variables, soil, proximity to rivers and roads, densities of roads and settlements, climatic and

Table 1
List of the 16 spatial predictor variables developed and used within the modelling process.

Category	Spatial predictor variable layers	Data type
Land use and land cover	Distance to forest (meters)	Continuous
	Distance to agroforestry (meters)	Continuous
	Distance to mixed areas and smallholdings (meters)	Continuous
	Distance to oil palm (meters)	Continuous
	Forest heterogeneity (500 m radius)	Categorical
	Forest majority (500 m radius)	Categorical
Soil	Soil association (51 classes)	Categorical
Anthropogenic	Distance to main roads (meters)	Continuous
	Road density	Continuous
	Settlement kernel density	Continuous
Hydrology	Distance to main rivers (meters)	Continuous
Climate	Annual temperature range (Bio 7)	Continuous
	Precipitation seasonality (Bio 15)	Continuous
	Precipitation during driest quarter (Bio 17)	Continuous
Topographical	Elevation (meters)	Continuous
	Slope degrees	Continuous

topographical data. The spatial data framework was prepared at a 91 m grid resolution for the entire extent of Sabah, then converted into. ascii files for use in MaxEnt.

For the land use and land cover variables, we generated these spatial data from on-screen digitising (in ArcGIS 10.6.1) of high resolution (1.5 m) true colour SPOT 5 satellite imagery. These images were available for the years 2014 and 2015. This time-frame was deemed appropriate, as it was within the species presence data period (from 2007 to 2017) and because most data were recorded between 2012 and 2016. Further, data collection being primarily done within TPAs and PFRs, the risk of forest conversion was minimum, and at least 98% of the pangolin data was still located within the 2014/15 mapped forest extent. Land use and land cover categories mapped included: forest (of various types and quality), oil palm (both estates and smallholdings), agroforest areas (i.e., monocrops of industrial tree plantations such as acacia or eucalyptus), and mosaic rural areas that contained homesteads and smallholdings of various crops (e.g., rubber, oil palm, fruit trees, rice paddy, and other types of agriculture) (Fig. 1**b**).

We also digitised Sabah's main rivers (i.e., those identifiable in the SPOT 5 satellite imagery, see Fig. 1**b**) and much of Sabah's public roads (Fig. 1**a**), including roads to settlements and forested areas. We defined the roads according to two categories: public main roads (asphalt) and secondary roads, i.e., public roads of gravel/earth and some roads within protected areas and Forest Reserves (e.g., logging roads). Settlement data on villages, towns, and oil palm cultivation settlements were initially derived from the Sabah Lands and Surveys Department online platform (http://www.jtuwma.net/, accessed 17th January 2017). These data were then checked against the SPOT 5 satellite imagery and amendments were conducted by removing dubious points, adding additional (unmarked) settlements and improving the settlement locations where needed.

For land use and land cover categories, rivers, and main roads (asphalt) variables, we created a "distance to" layer for each using the Euclidian distance tool in ArcGIS 10.6.1, thereby creating a continuous raster layer of distance in meters, from each feature. For the entire roads dataset (main and secondary/logging roads) and the settlements dataset, we generated a road density layer using the kernel density function in ArcGIS 10.6.1.

A forest condition (quality) layer was derived from the data provided by von Hase and Parham (2018). We aggregated this layer into four, more simplified categories: (1) open areas within forest, (2) degraded forest, (3) low to moderate quality forest, and (4) moderate to high quality forest; we further restricted these classes to the extent of our generic forest layer. Areas outside the forest were classified as "areas outside of forest". To capture the heterogeneity of forest conditions in surrounding areas, we used the focal statistics in ArcGIS 10.6.1 to create (1) a forest heterogeneity layer that showed the number of classes detected within a 500 m radius of a given grid cell and (2) a majority of forest condition layer that shows the dominant forest condition type within a 500 m radius of any given grid cell, classified into five categories (1= low, 2= moderate, 3 = moderate-high, 4 = high and 5 = very high). In addition, we used a digitised soil map generated by the State Department of Agriculture (Acres, 1975) containing 51 soil associations for Sabah, as soil is a strong influential factor in determining forest types.

Nineteen bioclimatic data layers (1950–2000) were downloaded from the WorldClim, ver. 1.4 dataset (http://www.worldclim.org/), at 30 arc-seconds resolution (Hijmans et al., 2005). To avoid issues with the multicollinearity of these 19 layers that could result in over fitting of the model (Pearson et al., 2007; Raes et al., 2009), we used three variables anticipated to limit pangolins principal food resources (Lim, 2007). These variables included annual temperature range, precipitation seasonality, and precipitation during the driest quarter-year period.

Sunda pangolins strongly prefer sleeping sites such as tree hollows and underground burrows that provide a stable thermal environment, essential for rest, mating, reproduction, and caring for their pups (Chong et al., 2020). These sites are likely selected for their ability to buffer temperature variations, highlighting the importance of the annual temperature range in determining habitat suitability. Additionally, the availability and abundance of their primary food source, soil-dwelling insects (specifically ants and termites), are influenced by temperature and precipitation patterns. This includes their abundance, diversity, and behavioural patterns (Pratiknyo et al., 2018; Uhey et al., 2020; Roeder et al., 2022). Seasonal precipitation levels rainfalls during drought influence insect availability, potentially impacting pangolin foraging behaviour and nutritional intake (Goldman et al., 2020; Jasrotia et al., 2022). Thus, these variables are crucial in understanding the pangolin's habitat preferences, linking their survival and reproductive success to the climatic conditions of their environment.

These variables were reclassified from 30 arc-second resolution (approx. 1 km) to our 91 m resolution grid. To generate elevation and slope topographical variables, a contour vector file (at 10 m intervals) was used to generate a Digital Elevation Model and slope variable using ArcGIS 10.6.1.

2.4. Habitat suitability modelling

We used MaxEnt software v.3.4.1 to model the habitat suitability of the Sunda pangolin (Elith et al., 2006; Phillips and Dudík, 2008). MaxEnt software is a robust tool for niche modelling, especially when species absence records are unavailable (Elith et al., 2011). Specifications used in MaxEnt included logistic output, 500 iterations, 10,000 background points, a regularisation multiplier of 1.0, and "auto-features". The Jackknife test was performed to measure the relative contribution of each of the 16 spatial variables to the overall model performance. The model was evaluated by measuring the area under the receiver-operator curve (AUC). The AUC score indicates the model's ability to discriminate between presence and absence, where an AUC score <0.5 denotes poor model performance, 0.5–0.7 denotes low performance but better than chance, 0.7–0.9 denotes moderately useful model performance, and >0.9 indicates excellent model performance (Manel et al., 2002).

2.5. Post-processing, review, and revision

The MaxEnt output comprises scores displayed in a grid format across the study area. We used the average value of Minimum Training Presence (MTP) and Maximum Training Sensitivity and Specificity (MTSS) to convert the output into a categorical map to define moderate and high suitability areas, respectively. MTP threshold predicts a more liberal extent of suitable areas with zero omission of training data, whereas MTSS threshold estimates a more conservative extent (Liu et al., 2005; 2013).

To refine the distribution map, an expert review process was undertaken during a workshop in Kota Kinabalu, Sabah, Malaysia on December 13th, 2018, and via email for wider participation from the contributing researchers. During this process, experts annotated the map and provided feedback in written format, identifying areas where the species was not known to occur and additional areas where the species was observed. The map was then revised based on the inputs from the experts.

To understand the degree of protection of the Sunda pangolin's habitat, we obtained data on Sabah's Totally Protected Area network for 2017, which included Wildlife Sanctuary, Class I Protection Forest Reserve, Class VI Virgin Jungle Reserve, Class VII Wildlife Reserve, Parks, and Wildlife Conservation Area. We also acquired data on Production Forest Reserves (Class II Commercial, Class III Domestic, Class IV Amenity, and Class V Mangrove Forest Reserves), which allow various land uses. Thirdly, we used cadastral data (acquired from www.jtuwma.net on the 2nd February 2017) from the Sabah Lands and Surveys Department's online platform. These data were used to identify alienated lands under differing granted land titles i.e., provisional lease or country lease titles, field register or native titles, and town lands. Lands outside of Protection and Production Forests, and alienated lands were considered State lands.

2.6. Accessibility

To better understand the potential level of poaching, hunting, and capture of animals for the live wildlife trade in pangolin habitat, associated threats, we generated an accessibility layer using a time-distance-surface approach, which accounts for travel time, distance and slope to calculate accessibility from settlements. This approach integrates multiple modes of travel, roads of different types, river travel, and walking, and categorises them based on specific criteria such as speed, and slope.

We first generated data for public roads of either asphalt or secondary gravel/earth roads, and non-public roads within protected

Table 2
Presence records used within the distribution model for the Sunda pangolin in Sabah from 2007 to 2016 and their surveyed areas and sampling methods.

Surveyed areas	Years	Sampling method(s)	No. of presence records used
Alienated lands (Kalabakan)	2014	Camera trapping	1
Bengkoka FR (Mixed areas)	2015	Camera trapping	1
Crocker Range NP	2011, 2012	Camera trapping	11
Danum Valley (Oil palm)	2009	Camera trapping	2
Danum Valley CA	2007 – 2014	Camera trapping	40
Deramakot FR	2008 – 2017	Camera trapping, Opportunistic sighting	36
Gomantong FR	2007	Ground survey	1
Gunung Rara FR	2012, 2013	Camera trapping	3
Kinabalu NP	2007	Ground survey	1
Kinabatangan W*R*	Unknown 2010	Camera trapping, Opportunistic sighting	4
Kuamut FR	2016	Camera trapping	7
Maliau Basin CA & Buffer Zone	2010, 2013	Camera trapping	4
Malua FR	2008 – 2013	Camera trapping, Opportunistic sighting	8
Mt. Louisa FR	2007	Ground survey	1
Mt. Mandalom FR	2007	Ground survey	1
Nurod Urod FR	2012, 2013	Camera trapping	2
Pin-Supu FR	2010	Camera trapping	1
Segaliud-Lokan FR	2010 – 2015	Camera trapping	7
Sepilok FR	2011	Camera trapping	2
Sungai Tagul FR	2007	Ground survey	1
Sipitang FR	2010 – 2013	Camera trapping	4
Sugut FR	2007	Ground survey	1
Sungai Pinangah FR	2015	Camera trapping	1
Sungai Talibu FR	2015	Camera trapping	3
Tabin W*R*	2009 – 2011	Camera trapping	6
Tangkulap FR	2009 – 2015	Camera trapping, Ground survey	18
Tawau Hill Park	2009 – 2013	Camera trapping	22
Tenompok FR	Unknown	Opportunistic sighting	1
Trus Madi FR	2007	Ground survey	1
Ulu Kalumpang FR	2012	Camera trapping	1
Ulu Segama FR	2007, 2010	Camera trapping	8
Ulu Sungai Padas FR	2007, 2010	Ground survey	1
Total number of point locations			201

* FR = Forest Reserve, NP = National Park, CA = Conservation Area, Mt. = Mountain, W*R*=Wildlife Reserve

areas and production forest reserves by on-screen digitising methods and using SPOT 5 1.5 m images for 2015. Roads were categorised as relatively flat (0–7 degree slope), moderate slopes (8–17 degree slopes), or steep areas (>18 degree slope). To factor in the time to traverse across a section of road according to road type and slope, we assigned the following: main/asphalt roads in flat areas as 90 km/hr, moderate slope areas 70 km/hr, and steep areas 50 km/hr. For secondary/gravel roads, we assigned flat areas as 60 km/hr, moderate slope areas 40 km/hr, steep areas 20 km/hr. As people can also access areas via river, we used a main rivers shapefile and assigned a boat travel speed at 15 km/hr.

For areas that did not have roads or rivers, walking speeds were allocated for 3 km/hr in flat areas (0–7 degree slope), 2 km/hr in moderately steep areas (8–17 degree slopes), and 1 km/hr for steep areas (>18 degree slopes). These times were indicative and were then combined with settlement data (a point shapefile) to model a raster time-distance-surface for Sabah at 91 m resolution that estimates how accessible each raster cell is from any given settlement factoring time and ruggedness of the landscape.

The model output had continuous values. For ease of viewing, we classified into three natural breaks (Jenks) and then extracted for areas that had Sunda pangolin habitat within natural forested areas.

3. Results

In total, 201 unique presence records were used in the MaxEnt model (Table 2). The model performance was highly discriminative, with an average test AUC score for the 10 replicate runs being 0.903, with a standard deviation of 0.026.

The final model's MTP threshold value was 0.0678 (representing moderately suitable habitat) and for MTSS it was 0.4238 (representing highly suitable habitat). The model was clipped to natural forest areas and estimated 39,530 km^2 of suitable areas for Sunda pangolins, of which 29,165 km^2 were moderately suitable areas, and 10,365 km^2 were highly suitable areas (Table 3; Fig. 2).

The occurrence of the Sunda pangolin was strongly correlated with areas where forests are the dominant habitat within a 500 m radius, contributing 39.9% to the model's gain. The next most important variable was soil association (21.2%), followed by distance to main roads (7.3%), distance to mixed areas and smallholdings (6%), elevation (5.8%), and distance to forest (4.6%) (Fig. 3).

Specifically, Sunda pangolin's natural habitat was associated with areas that had moderate to high quality forest, as the dominant forest condition class (Fig. 4**a**). For soil classes, Bang (class 2), Dagat (class 9), Lokan (class 23), Sipitang (class 38), and Wullersdorf (class 51) were the most influential in determining habitat suitability for the Sunda pangolin (Fig. 4**b**).

Three of these soil classes (Bang, Dagat and Lokan) are associated with mudstone/sandstone parent rocks in moderate to hilly areas **(SI)**, whereas Wullersdorf is associated with intermediate and acid igneous parent rock in mountain areas, and Sipitang is associated with peat and alluvium parent soil in swamp-like landforms **(SI)**. Habitat suitability increased with distance from: main roads (Fig. 4**c**), and mixed areas with small holdings (Fig. 4**d**). Habitat suitability decreased in areas over 200 asl (Fig. 4**e**), and with distance from forest (Fig. 4**e**).

43% of Sunda pangolin's distribution within natural forest areas was within Totally Protected Areas and 38% in Production Forest Reserves (Table 3; Fig. 2). Of the 38% in Production Forest Reserves, Alienated lands, in total, harbored around 7% of the Sunda pangolin's total distribution with 2% being within commercial land titles (i.e., Provisional lease/Country lease titles), 2% within smallholdings or Native titles, and around 3% was within unknown land title types. The remaining 12% of the Sunda pangolin distribution was potentially on State land (Table 3; Fig. 5**a**).

Of the estimated 39,530 km^2 of areas suitable for Sunda pangolins, we found that 53% was very accessible to humans, 38% was

Table 3
Areas suitable and unsuitable for the Sunda pangolin in Sabah, areas protected and unprotected, and accessibility of areas.

	Area (km²)	%
Suitability		
Suitable Area	39,530	53
High suitability	(10,365)	(26)
Moderate suitability	(29,165)	(74)
Unsuitable Area	34,070	47
Total	*73,600*	*100*
Protection/Management Status		
Totally Protected Areas (TPAs) *(these included: Class I Protection Forest Reserve, Class VI Virgin Jungle Reserve, Class VII Wildlife Reserve Parks, Wildlife Conservation Area & Wildlife Sanctuary)*	16,998	43
Production Forest Reserves (PFRs) - Class II Commercial, Class III Domestic, Class IV Amenity & Class V Mangrove Forest	15,021	38
Outside Protected Area - State Land	4744	12
Unknown land title	(142)	(3)
Commercial land titles (Provisional lease/Country lease titles)	(95)	(2)
Small holdings or Native titles	(95)	(2)
Outside Protected Area - Alienated Land	2767	7
Total	*39,530*	*100*
Accessibility		
Very accessible	20,951	53
Moderately accessible	15,021	38
Less accessible	3558	9
Total	*39,530*	*100*

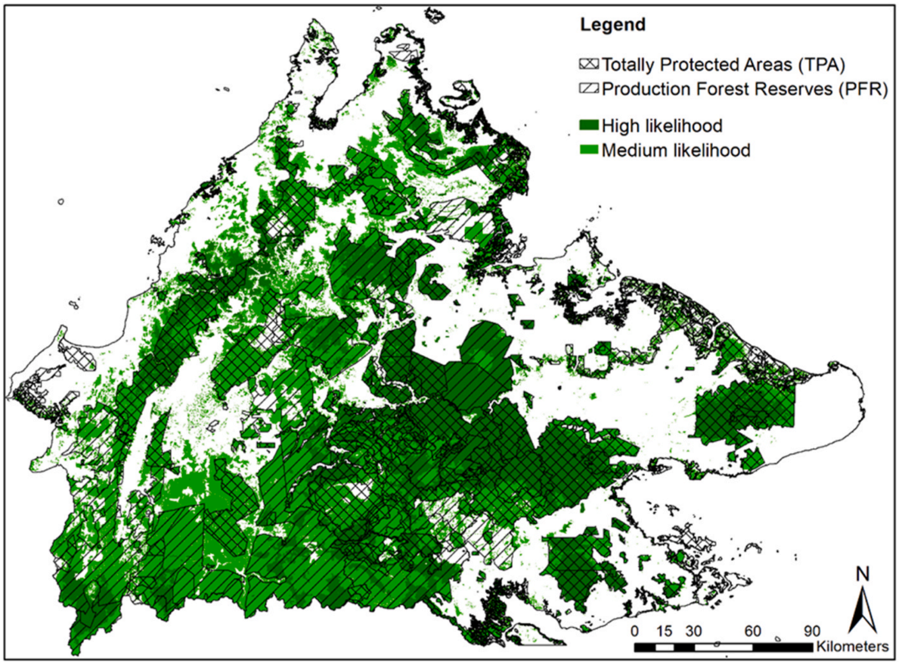


Fig. 2. Map showing areas of high and medium likelihood of suitable habitat for the Sunda pangolin within natural forests (as of 2014/2015), overlaid with Totally Protected Areas (crosshatch) and Production Forest Reserves (diagonal line).

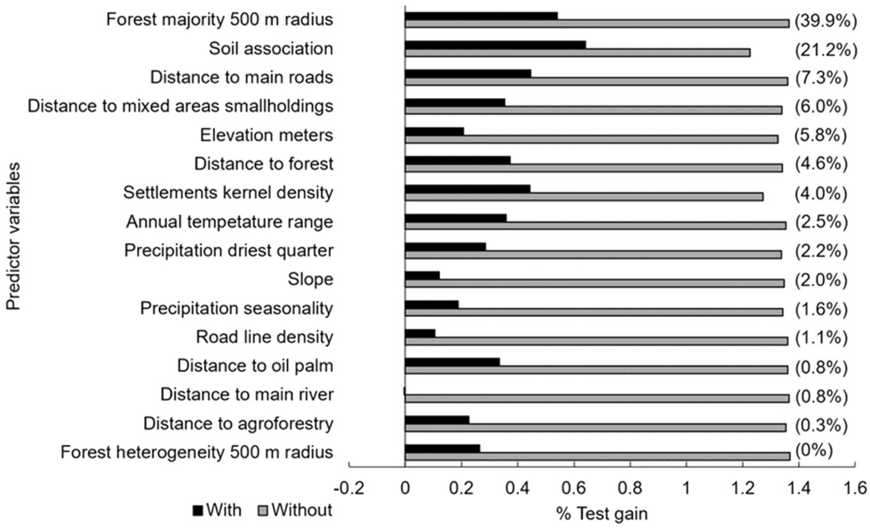


Fig. 3. A Jackknife test of the importance of predictor variables in the habitat suitability model of the Sunda pangolin. An estimate of the relative contribution of each variable to the overall model is shown in parentheses (%). Variables are ranked in descending order of importance. Grey bars represent the performance of the overall model (or % test gain) without each variable; and black bars indicate the contribution of each variable in isolation.

within moderately accessible areas, and only 9% was in less accessible areas **(**Table 3**;** Fig. 5**b**).

4. Discussion

4.1. Habitat suitability

Our study aimed to bridge the knowledge gap on the distribution of the Sunda pangolin in Sabah. Using the MaxEnt model, we determined that as of 2015, the Sunda pangolin's forested habitat spanned roughly half of Sabah's land area (Fig. 2). Of this habitat,

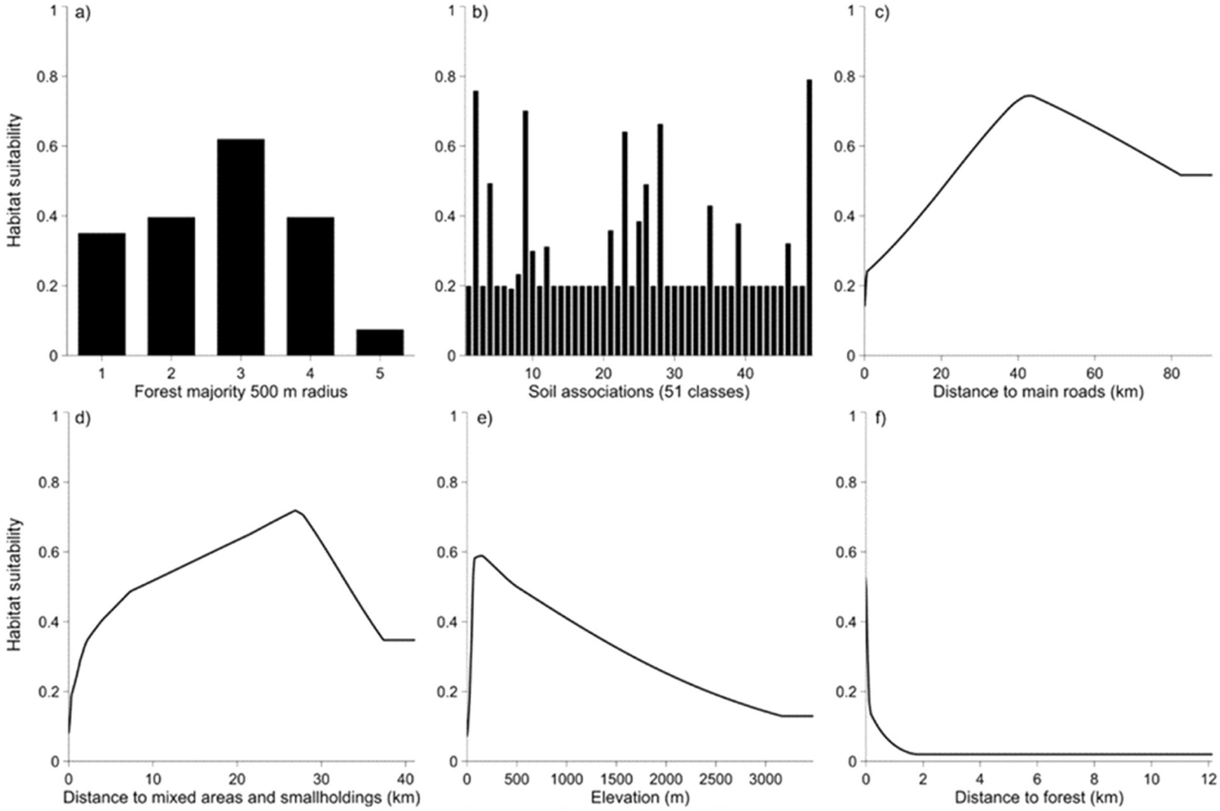


Fig. 4. Univariate response curves of the top 6 most influential predictor variables, in descending order, showing: (a) forest majority 500 m radius (contributing 39.9%) with moderate-high condition forest (class 3) being the most influential; (b) soil (21.2%) with Classes 2 (Bang soil type), 9 (Dagat), 23 (Lokan), 38 (Sipitang), and 51 (Wullersdorf) being the most influential in determining habitat suitability; (c) distance to main roads (7.3%) with habitat likelihood increasing further from main (asphalt) roads to around 40 km; (d) distance from mixed areas with an array of various smallholdings (6%) with habitat probability increasing further from these areas (to around 27 km); (e) elevation (5.8%) with a decrease in habitat suitability over 200 m asl; and, (f) distance to forest (4.6%) with habitat suitability decreasing dramatically from the forest edge to 2 km outside of forested areas.

43% (16,998 km²) was within Sabah's Totally Protected Areas (Table 3). Sabah's commitment to expand its TPAs from 26% (19,000 km²) to 30% (22,000 km²) by 2025 (Williams et al., 2020; The Borneo Post, 2021) aligns with the global '30 by 30' target of the Convention on Biological Diversity – Theme 1: Protecting biodiversity (Dinerstein et al., 2019). This expansion could secure approximately 50% (19,765 km²) of Sunda pangolin's habitat, boosting the existing conservation efforts for the species. In a complementary move, the Sabah State Cabinet pledged in 2015 to produce 100% (Roundtable for Sustainable Palm Oil) RSPO-certified sustainable palm oil by 2025 (Ng et al., 2022). This certification approach mandates the conservation of areas housing RTE species by prohibiting oil palm cultivation and ensuring habitat management supports the survival of RTE species (Senior et al., 2015; Sabah Forestry Department, 2021). These commitments collectively signify promising conservation strides in Sabah.

Despite the growing number of forest areas gaining protection or meeting sustainability standards, there is still a risk of forest loss for some of the current Sunda pangolin habitat. Our findings indicate that approximately 38% (15,021 km²) of the Sunda pangolin's forested habitat is located within Sabah's Production Forest Reserves (PFR) (Table 3). Presently, Sabah has established industrial tree plantations (ITP) that include monoculture tree crops among other plantation developments within its PFR (Ratnasingam et al., 2020; New Straits Times, 2022). Sabah is planning to expand its ITP areas, potentially to 6000 km² (up from 1600 km² as of 2021), which could significantly reduce the Sunda pangolin habitat (Daily Express, 2021). The development of infrastructure such as roads, highways, pipelines, railways (Sloan et al., 2019; Abram et al., 2022) as well as large hydroelectric dam projects (Alamgir et al., 2020; Chong et al., 2020), among other threats, further jeopardise the long-term survival prospects for this species in some parts of its range in the State.

The conservation of mature, old-growth forests is paramount for the Sunda pangolin, due to its semi-arboreal habits and reliance on tree hollows (Lim and Ng, 2008; Chong et al., 2020). Our results underscore the significance of forest type and condition in determining suitable habitats for this species. The 'majority of forest condition' metric emerged as the dominant predictor of these areas (Fig. 3), indicating a strong association between moderate to high forest conditions and pangolin presence (Fig. 4**a**). A study from Singapore highlighted the importance of tall, mature trees with cavities as critical sleeping and breeding sites for the Sunda pangolin (Lim and Ng, 2008). Similarly, research in Kinabatangan, east Sabah, demonstrated that while Sunda pangolins use various structures for sleeping

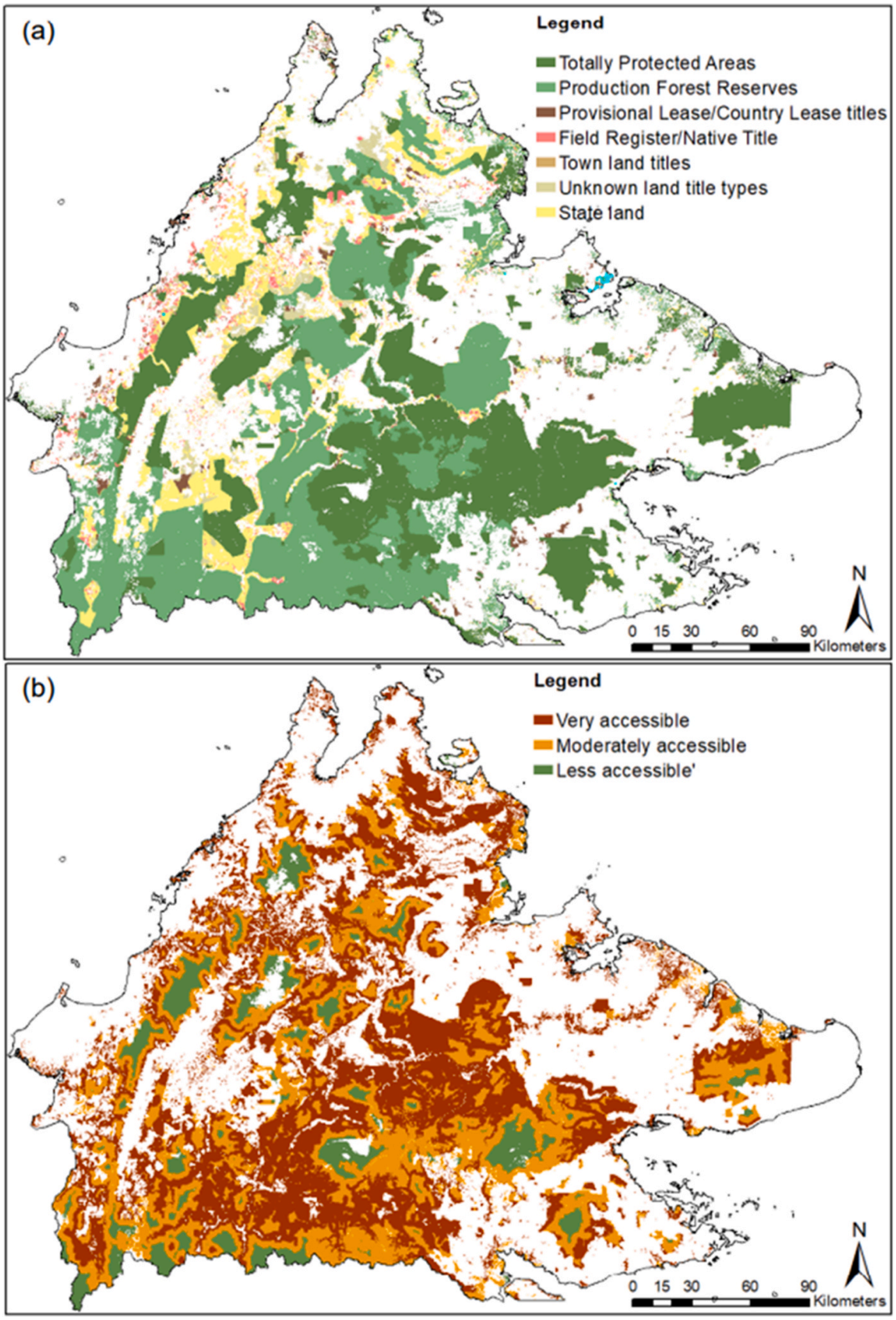


Fig. 5. (a) The distribution of suitable habitat for the Sunda pangolin across different land management categories - Totally Protected Areas (dark green), Production Forest Reserves (light green), Provisional Lease/Country Lease titles (dark brown), Field Register/Native Titles (pink), Town land titles (light brown), Unknown land title types (light green), and State lands (yellow); and, (b) the relative accessibility of these suitable habitats, with red indicating very accessible areas, orange indicating moderately accessible areas, and green indicating less accessible areas.

sites, they exhibit a preference for tall and large trees with hollows, especially those entwined by climbing plants. These are predominantly large, aged dipterocarp trees, serving as sleeping, breeding, and reproductive sites (Panjang, 2023). Tree hollows, which develop over extended time frames, are primarily found in large trees within old-growth forests (Haslem et al., 2012; McLean et al., 2015). The ongoing loss and fragmentation of habitat, along with certain practices labelled as 'sustainable logging', are diminishing the availability of trees with potential hollows. Such reductions limit vital habitats for hollow-dependent species, like the Sunda pangolin (Gibbons et al., 2008; Ranius et al., 2009; Lindenmayer et al., 2012).

In exploring the specifics of suitable habitats, our model highlighted potential correlations between Sunda pangolin habitat suitability and certain soil classes, specifically Classes 2 (Bang soil type), 9 (Dagat), 23 (Lokan), 38 (Sipitang), and 51 (Wullersdorf). Dipterocarp trees, fundamental to the dense rainforest ecosystems (Saw and Sam, 1999; Corlett and Primack, 2005) are closely linked with specific soil classes, especially Classes 2 (Bang), 9 (Dagat) and 23 (Lokan) (Paoli et al., 2008; Lim et al., 2021; Forest Research Centre, 2023). Many of these dipterocarp trees, being mature and towering, function as vital habitats for the Sunda pangolins (Panjang, 2023). Preliminary observations from Kinabatangan by Panjang (2023) indicate potential preferences of pangolins for freshwater swamp forests, particularly those with soils from Classes 9 (Dagat), 23 (Lokan), and 38 (Sipitang). This affinity suggests that the likelihood of pangolins selecting sleeping sites is significantly higher in these freshwater swamp forests. While these initial findings underscore the potential importance of these forests as habitats, a detailed exploration of pangolin behaviours within these habitats will be presented in subsequent studies. On the other hand, igneous soils from the Wullersdorf region (Class 51) hint at possible highland habitats for pangolins. However, the actual distribution of pangolins in such areas may be influenced by altitude constraints, indicating that while pangolins might inhabit highlands, they may be limited to specific elevation zones.

Building on the importance of soil classes, the altitude of these habitats plays a crucial role in Sunda pangolin distribution. The specific altitudinal range favourable for the species in Sabah has been somewhat ambiguous (Chong et al., 2020). However, our model suggests a diminishing presence of the species beyond 200 m asl (Fig. 4**e**). This observed trend stands in contrast to records showing that Sunda pangolins have been identified at altitudes up to 1700 m asl in regions such as Borneo and Laos (Duckworth et al., 1999; Payne and Francis, 2007; Kaicheen and Mohd-Azlan, 2018). Even though they exhibit adaptability across diverse altitudes (Chong et al., 2020), the specific requirements of their diet could limit their expansion in elevated habitats. As myrmecophagous species, pangolins rely solely on ants and termites for sustenance (Lim, 2007). Yet, the diversity and numbers of these insects dwindle with increased altitude, potentially due to factors such as soil compaction, shallower humus layers, and temperature shifts (Brühl et al., 1999; Jones and Eggleton, 2000; Malsch et al., 2008; Pratiknyo et al., 2018). The scarcity of food sources, and the pangolin's known sensitivity to cold, underscores their vulnerability at elevated terrains (Hua et al., 2015; Save Vietnam's Wildlife, unpubl. data). These findings highlight the significance of conserving lowland forest habitats, while still recognising the value and role of highland habitats, for the species.

4.2. Accessibility and poaching

The increased incidence of poaching, aggravated by the growing accessibility to the pangolin's habitats, presents a significant conservation challenge for their continued survival in Sabah. Our 2015 accessibility model revealed that 91% of their habitats were either highly or moderately accessible to humans (Fig. 5**b and** Table 3). The historical incorporation of pangolins and their by-products into international trade has led to significant trafficking since the early 21st century (Challender et al., 2020). Astonishingly, from 2000 to 2019, nearly 895,000 pangolins were trafficked globally with Sabah contributing over 22,000 individuals between 2007 and 2009 (Pantel and Anak, 2010; Challender et al., 2020). It is also alarming to note that protected species are often found in local markets across Sabah (The Star, 2013; 2016). However, the trade in pangolins tends to be clandestine, typically exposed through intelligence-led operations (Clean Malaysia, 2017; The Star, 2022). In light of this, authorities have intensified their efforts to combat poaching (Malay Mail, 2021). The high market prices for pangolins (Chong et al., 2020) combined with the accessibility of their habitats put them at increased risk. Specifically, employees in monoculture plantations have been found to exploit this resource, collecting pangolins for illegal trade (Azhar et al., 2013; Panjang et al., 2023).

Pangolins are increasingly venturing into multiple-use landscapes transformed by human activities, a shift attributed to habitat degradation, fragmentation, and increased pressures in their natural habitats (Chong et al., 2020). For example, Panjang et al. (2023) noted approximately 278 pangolin rescues in Sabah between 2019 and early 2023, with a significant proportion occurring in urban, suburban, and oil palm plantation areas. Ongoing infrastructural expansions in Sabah, including new settlements, roads, and plantations, will likely further exacerbate the vulnerability of this species to poaching, and requires robust conservation strategies (Wong and Linkie, 2013; Brodie et al., 2015).

4.3. Study limitations

Our modelling approach was dependent upon existing and available occurrence data. These data were combined to produce the largest meta-dataset for this species available thus far. High resolution imagery also allowed the development of various important spatial layers for our models. Our approach enabled the first Statewide habitat distribution model for the Sunda pangolin in Sabah. However, further research could fill additional knowledge gaps and some of the limitations in both the current data set and the approach.

One limitation in our current data set was its restriction to natural forest areas. This approach may not capture the pangolin's full potential distribution, given that the species is resilient and seem to adapt to a certain extent to human-modified landscapes. Incorporating data from surveys within differing land cover types, would improve future understanding of pangolin distribution, providing a more holistic and nuanced view of their environmental preferences or tolerances.

Another limitation was the timeframe of presence data collection (over a ten-year period) and regional biases in locations. Surveys are resource-intensive, and few presence surveys have specifically targeted pangolins in Sabah yet. We suggest for future surveys to target areas not covered yet, to limit biases in presence locations and amplify the current meta-dataset. Further, as additional presence data is contributed to the meta-dataset, future analyses could model distributions across longer time frames, especially forest has been converted to other types of land-uses to understand the impacts of forest loss on pangolin distribution. As such, we also recommend to closely monitor changes in the landscape, utilising advanced remote sensing technologies such as LiDAR (Light Detection and Ranging) and high-resolution spatial data (Araujo et al., 2021; Massey et al., 2023). These methods hold the potential to enhance our understanding of how habitats impact the Sunda pangolin and can guide the development of informed and adaptable conservation strategies that can effectively navigate the rapidly changing environmental landscape.

4.4. Key conservation recommendations

4.4.1. Strengthening enforcement and policies

Poaching threatens the survival of viable pangolin population in Sabah. Targeted anti-poaching strategies, especially regular patrols in protected areas, bordering habitats, and intelligence-led operations are crucial to curb the rampant pangolin poaching (Cooney and Challender, 2020; Wilson-Holt and Roe, 2021; Alagesan, 2022). Given the thriving illegal wildlife trade in Sabah (The Star, 2019), including local hunters capitalising on the lucrative pangolin trade, boosting the operational capabilities of dedicated anti-poaching units in Sabah is paramount. As the frontline against wildlife crimes, these units require sustained support and resources for maximal effectiveness. Considering the international scope of the pangolin trade, a cross-boundary approach is essential for effective conservation. Collaborative efforts with neighbouring countries can help monitor and control the illegal trade routes, thereby reducing the demand and supply channels for pangolin and their products (Challender et al., 2020; Harrop, 2020). Tapping into the potential of Indigenous Peoples and Local Communities (IPLCs), who often reside near protected and production forests, could be game-changing. Their intimate knowledge of the terrain and activities can offer invaluable intelligence to counteract poaching (Cooney and Challender, 2020; Wilson-Holt and Roe, 2021). Embracing a community-based conservation model that actively involves IPLCs is critical for the sustainable conservation of Sunda pangolins in Sabah.

4.4.2. Expanding Totally Protected Areas (TPAs)

TPAs are paramount to curb poaching, preserve biodiversity, mitigate habitat loss and facilitate the recovery of wildlife populations (Geldmann et al., 2013; Steinmetz et al., 2014; Terraube and Llamazares, 2020; Nuttall et al., 2021). TPAs remain a cornerstone for conservating the Sunda pangolin to ensure its natural habitat is maintained or enhanced. Although the species can be found in non-forest habitats, most of the pangolin presence points collected during the study period were located within TPAs and areas of natural forest management over the study period. Sabah has pledge to increase its network of TPAs, which would contribute significantly to pangolin conservation. In addition, buffer areas, surrounding TPAs could also provide refuge for pangolins and especially if enforcement activities were effective in reducing potential threats in these areas.

4.4.3. Human-modified environmental management

To ensure the species' survival, it is critical to minimise habitat destruction and mitigate anthropogenic disturbances within these regions. However, the species shows an unexpected level of resilient and survival in non-forest habitat. Transitioning towards sustainable and responsible management of the extensive oil palm landscape in the State becomes paramount to secure viable populations of pangolin. Assigning a High Conservation Value Forest (HCVF) value to all forest fragments within plantations would require plantation managers to maintain and manage the ecological value of these forest patches, which could serve as potential refugia for Sunda pangolin so long as poaching is eradicated.

4.4.4. Education and public awareness

As pangolins are being highly exploited, strategic awareness efforts are required to guarantee sustained support for their conservation (Thomson and Fletcher, 2020). To address the root of the poaching crisis, it is necessary to confront the driving demand. Within Sabah, it is concerning that local consumption of pangolin meat persists alongside illegal trade (Panjang et al., 2023). Tailored awareness campaigns directed at individuals who hunt and those who consume and sell pangolins, encompassing both rural and urban communities, are crucial. By emphasising the ecological importance of pangolins and the consequences of their illegal trade, awareness campaigns can induce significant behaviour changes, thereby reducing demand and curbing the increase in pangolin poaching (Burgess et al., 2020).

4.4.5. Enhancement of rescue facilities

In light of the rising counts of rescued Sunda pangolins in Sabah, there is an urgent need to upgrade and adapt rescue facilities specifically tailored for pangolins. These enhanced facilities will ensure the well-being of pangolins during their captivity and prepare them for reintroduction into the wild (Wright and Jimerson, 2020). Release sites for rehabilitated pangolins must be carefully selected, prioritising locations that are free from poaching threats (Pietersen et al., 2016). These sites should also offer abundant food, appropriate habitats, and vital ecological structures such as tree hollows for sleeping (Wright and Jimerson, 2020). Through these facility improvements and targeted release strategies, the recovery of Sabah's Sunda pangolin population can be better supported.

5. Conclusion

This comprehensive and detailed study on the distribution of Sunda pangolins in Sabah has revealed the presence of substantial areas of suitable habitat across the State, emphasising the critical role of Sabah's natural forests as sanctuaries for the species' remaining wild populations. However, pangolins still face serious threats from poaching, aggravated by habitat fragmentation and the accessibility of these areas to humans. Addressing these challenges requires a multifaceted strategy: conserving natural forests, improving habitat quality in non-forest areas such as oil palm plantations, strengthening enforcement and policy frameworks, adopting a cross-boundary approach to combat international trade, engaging IPLCs in conservation efforts, the expansion of TPAs, intensifying public education and awareness initiatives, and enhancing rescue and rehabilitation facilities. With the dedicated effort to put these measures into action, we can hope for a better future for Sunda pangolins in Sabah. The insights derived from this study hold potential value for enriching the Sunda Pangolin State Action Plan, serving as a key basis for future conservation strategies.

CRediT authorship contribution statement

Hisashi Matsubayashi: Resources, Writing – review & editing. **Chihiro Sano:** Resources, Writing – review & editing. **Roshan Guharajan:** Resources, Writing – review & editing. **Azlan Mohamed:** Resources, Writing – review & editing. **Penny C. Gardner:** Resources, Writing – review & editing. **Sharon Koh:** Resources, Writing – review & editing. **Cheryl Cheah:** Resources, Writing – review & editing. **Marc Ancrenaz:** Resources, Writing – review & editing. **Isabelle Lackman:** Resources, Writing – review & editing. **Robert Ong:** Resources, Writing – review & editing. **Reuben Nilus:** Resources, Writing – review & editing. **Rebecca K. Runting:** Writing – review & editing, Formal analysis. **Alex Hastie:** Resources, Writing – review & editing. **Symphorosa Sipangkui:** Writing – review & editing. **Nicola K. Abram:** Data curation, Formal analysis, Funding acquisition, Writing – original draft, Writing – review & editing, Conceptualization, Visualization. **Elisa Panjang:** Writing – original draft, Writing – review & editing, Conceptualization, Visualization. **Hong Ye Lim:** Data curation, Formal analysis, Writing – review & editing, Writing – original draft, Conceptualization, Visualization. **Robert J. Thomas:** Writing – review & editing. **Benoit Goossens:** Resources, Writing – review & editing. **Andrew J. Hearn:** Resources, Writing – review & editing. **David W. Macdonald:** Resources, Writing – review & editing. **Joanna Ross:** Resources, Writing – review & editing. **Jedediah F. Brodie:** Resources, Writing – review & editing. **Seth Timothy Wong:** Resources, Writing – review & editing. **Alys Granados:** Resources, Writing – review & editing. **Olga Helmy:** Resources, Writing – review & editing. **Olivia Magritta Lapis:** Resources, Writing – review & editing. **Donna Simon:** Resources, Writing – review & editing. **Glyn Davies:** Resources, Writing – review & editing. **Siew Te Wong:** Resources, Writing – review & editing. **Mark Rampangajouw:** Resources, Writing – review & editing.

Declaration of Competing Interest

The authors declare there is no conflict of interest in this study.

Data availability

Data will be made available on request.

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