Landscape ecology and behavioural responses of the Sunda pangolin (*Manis javanica*) to habitat fragmentation and degradation in Sabah, Malaysia

Elisa Panjang

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Abstract

This thesis investigates the habitat suitability and movement ecology of the Sunda pangolin (*Manis javanica*) in Sabah, Malaysian Borneo, a highly-threatened species due to illegal hunting, poaching and habitat loss and fragmentation. Using MaxEnt, suitable areas for Sunda pangolins were identified, with nearly all suitable habitats found within protected forests. The study recommends establishing and properly managing protected areas and conserving modified habitats to promote pangolin conservation. A radio telemetry study was conducted to estimate pangolin home ranges using various methods such as Minimum Convex Polygon, Kernel Density Estimation, Local Convex Polygon and Generalised Additive Models. Movement behaviour was also investigated using Expectation Maximization Binary Clustering. Results showed that resident pangolins have small home ranges restricted to forested areas, while translocated pangolins have larger exploratory ranges as they explore new and larger areas. Additionally, translocated pangolins were more active and exploratory than resident pangolins. The study emphasises the significance of microhabitat preferences, with tall, large, living trees with hollows and abundant vine coverage being the preferred sleeping sites for Sunda pangolins. These habitats are predominantly found in old and mature forests, emphasising the importance of protecting and maintaining natural forests for Sunda pangolin survival. This study provides important insights into the consequences of human-induced disturbances and their potential impacts on Sunda pangolin populations in fragmented and degraded landscapes. It underscores the need for effective conservation strategies, such as managing protected areas, conserving modified habitats and engaging with local communities. The results of this study can be used to assist in the protection of this critically endangered species and the management of fragmented and degraded landscapes.

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m	metre (unit)
ha	hectare (unit)
km	kilometre (unit)
cm	centimetre (unit)
Mm	millimetre (unit)
%	percent
asl	above sea level
ca.	approximately
°	degree
km/h	kilometre per hour
°C	degree Celsius
~	approximately

Chapter 1: General introduction

1.1 Pangolins of the world

Pangolins, also known as scaly anteaters, are members of the placental mammal order Pholidota and are one of the most distinctive orders of mammals in terms of their unusual morphology. The "scaly anteater" has been given a variety of colloquial names including "walking pinecones" and "perambulating artichoke" (Gaudin et al., 2019), because of its external armour, which is made up of overlapping epidermal scales. Pangolins are the only mammals that possess such an armour. In contrast to armadillos *Dasypus* spp (order: Xenarthra), which also have covering epidermal scales, the scales of pangolins are strongly connected with the bony osteoderms and, as a result, are arranged in a very different way from those of armadillos (Grasse, 1955a; Vikaryous and Hall, 2006). Pangolins use this armour to protect their bodies by rolling up into a ball, so that the hard and sharp scales protect them from their natural predators. This is where the term pangolin comes from, which is taken from the Malay word "pengguling", which literally translates as "one who rolls up" (Kingdon, 1997). As well as this defining characteristic, pangolins do not have teeth (Meredith et al., 2009), but instead have a long tongue (Kingdon, 1974; Chan, 1995), reflecting the taxon's ant and termite-based (myrmecophagous) diet (Heath, 2013) and it has evolved digging and climbing capabilities (Gaudin et al., 2009, 2016).

Pangolins belong to only one family (Manidae) in the order Pholidota and there are only eight extant species. This family is made up of three genera: *Manis*, *Phataginus* and *Smutsia*. *Manis* comprises four Asian pangolins; the Chinese pangolin (*Manis pentadactyla*), the Indian pangolin (*M. crassicaudata*), the Philippine pangolin (*M. culionensis*) and the Sunda pangolin (*M. javanica*). The African pangolins are classified into two genera, *Phataginus* and *Smutsia*, which each have two species: the black-bellied pangolin (*Phataginus tetradactyla*), the white-bellied pangolin (*P. tricuspis*), the giant pangolin (*Smutsia gigantea*) and the ground pangolin (*S. temminckii*). In addition to the extant species, fossil records of extinct genera in the order Pholidota have been discovered. The earliest known fossil record of a pangolin is from the genus *Eomanis*, which lived roughly 45 million years ago. More recent genera include *Necomanis*, *Patriomanis* and *Cryptomanis* (Gaudin and Wible, 1999; Gaudin et al., 2006). From the early to mid-1900s, a collection of bones (later named *Manis paleojavanica*) was discovered from sites in South Asia and mainland Southeast Asia that were morphologically the most similar to the extant *M. javanica* but at least twice the length (Dubois, 1907). Sunda pangolin remains were discovered in the Niah Cave in Sarawak, Malaysia Borneo, together with the bones of a large- bodied *Manis* taxon that was radiocarbon-dated to roughly 40 thousand years ago (i.e. late Pleistocene/early Holocene). This suggests that the two species co-existed and were hunted by humans at some point (Piper et al., 2007). Although the smaller Sunda pangolin survives today, it is likely that hunting pressure on the larger-bodied *Manis* pangolin species may have resulted in its recent extinction.

The scientific community widely agrees that extinct species have characteristics that are more primitive compared to those of current species. Yet, there remains a lack of consensus in understanding the phylogenetic relationships among current species. This ongoing discussion highlights the complexity and difficulty in figuring out the evolutionary connections and ancestry among these species. Gaudin and Wible (1999) used cranial features to construct a phylogenetic tree that consisted of three main clades: 1) the Asian species *M. crassicaudata*, *M. javanica* and *M. pentadactyla*, 2) the arboreal African species *M. tricuspis* and *M. tetradactyla* and 3) the land-dwelling African pangolins *M. temminckii* and *M. gigantea*. Despite these findings, the phylogenetic relationships within Pholidota remain uncertain. This uncertainty may arise from the limited scope of cranial characters used in previous studies. Expanding the range of characters analysed, including genetic data and employing advanced phylogenetic analysis techniques could provide more definitive insights into whether the present Asian or African species represent more primitive members of the genus (Gaudin and Wible, 1999; Gaudin et al., 2006).

The lack of clarity surrounding the evolutionary history of pangolins highlights the need for further research into their taxonomy and genetics. Recent advances in sequencing technology may provide new insights into the phylogenetic relationships among pangolins and help to resolve the debate over whether Asian or African species are the more primitive members of the genus. Additionally, the use of integrative approaches, such as combining morphological and molecular data, may also be beneficial in elucidating the evolutionary relationships among these unique and threatened mammals (Rubinoff and Holland, 2005). Such research efforts could provide crucial information for the conservation and management of pangolins, which are among the most threatened groups of mammals in the world.

1.2 The Sunda pangolin (*Manis javanica*)

The Sunda pangolin (*Manis javanica*), also known as the Malayan pangolin or the Javan pangolin, is one of four extant Asian pangolin species. Previously, it was believed that pangolins living in the Philippines were a part of the Sunda pangolin species. However, according to studies by Feiler (1998) and Gaubert and Antunes (2005), the existence of distinct physical characteristics has allowed for the identification of two separate species: the Sunda pangolin and the Philippine pangolin (*M. culionensis*). The classification was supported by comprehensive genetic analysis conducted by Gaubert et al. (2018), who extracted and sequenced DNA not just from the Sunda and Philippine pangolins but the entire pangolin family and using complete mitochondrial genomes and nine nuclear genes constructed a detailed phylogenetic tree.

Gaubert et al. (2018)'s genetic analysis confirmed significant genetic divergence not only between the Asian and African pangolins but also within these regional groups. Specifically, for the Sunda and Philippine pangolins, their results provided robust molecular evidence that supported their classification as distinct species, as initially suggested by Feiler (1998) and Gaubert and Antunes (2005) based on physical characteristics. There has so far been relatively little research on Sunda pangolin taxonomy, but the study of Gaubert and Antunes (2005) clarified the differences between the Philippine and Sunda pangolins. Nash et al. (2018) discovered that three previously unrecognised genetic lineages of Sunda pangolins exist, possibly originating in Borneo, Java and Singapore/Sumatra. Given the wide geographic distribution of the species, it is possible that there is cryptic diversity across the species' distribution. Comprehensive genetic and morphological research would contribute to the understanding of the taxonomic structure.

Recently, a study conducted by Sitam et al. (2023) found evidence of a distinct mtDNA lineage in north Borneo, which diverged from lineages in West/South Borneo and the mainland. The estimated divergence time of this lineage is around 1.6 million years, comparable to the divergence time of the Philippine pangolin. This finding supports the 'out of Borneo hypothesis', which suggests that the Sunda pangolins diversified in Borneo before migrating throughout Sundaland. However, the study also opens up the possibility of a 'secondary contact scenario' between the mainland and Borneo pangolins. The evidence presented by Sitam et al. (2023) suggests a partial replacement of mtDNA haplotypes in West/South Borneo, indicative of a secondary contact, suggesting a gradual change of haplotype frequencies across Borneo. This scenario implies that individuals from the mainland might have dispersed more readily into Borneo, leading to increased genetic admixture. Based on the findings of Sitam et al. (2023), it appears that both hypotheses receive some level of support, with evidence strongly supporting the ‘out of Borneo hypothesis’. The 'out of Borneo hypothesis' is supported by the divergence times and distinct mtDNA lineage, suggesting an initial diversification in Borneo. Meanwhile, the secondary contact scenario is also plausible, given the evidence of haplotype replacement and potential gene flow from the mainland to Borneo. It seems that the evolutionary history of the Sunda pangolins is likely shaped by both an initial diversification in Borneo and subsequent interactions with mainland populations. The evidence from Sitam et al. (2023) points to a complex evolutionary pattern that potentially incorporates elements of both hypotheses.

Sundaland is a biogeographic region in Southeast Asia that encompasses the Malay Peninsula, Sumatra, Borneo, Java and surrounding islands. It was named after the ancient Sunda Shelf, which emerged during the last glacial period when sea levels were lower (Inger and Voris, 2008; den Tex et al., 2010). Sitam et al. (2023) further reported that the analysis of nuclear single nucleotide polymorphisms (SNPs) did not reveal any apparent genetic structure across Borneo, indicating potential mitonuclear discordance. Mitonuclear discordance is the lack of genetic structure revealed by mitochondrial and nuclear DNA. This phenomenon might be influenced by recent divergence among populations, where nuclear DNA has not had sufficient time to accumulate significant genetic differences, despite mtDNA indicating divergence (Dupont et al., 2022). Additionally, the different resolutions of mtDNA and nuclear

SNPs, with mtDNA having a higher mutation rate and nuclear SNPs providing a more comprehensive genetic picture due to their abundance and bi-parental inheritance, can offer varying insights into the genetic diversity and structure of a species (Fischer et al., 2017; Niemiller et al., 2022). Such discordance may have significant taxonomic implications as it may indicate the presence of cryptic species or unrecognised genetic diversity (Papakostas et al., 2016; Toth et al., 2017). These results have important taxonomic implications for the Sunda/Philippine pangolin complex, emphasising the need for additional samples to accurately classify the range-wide genetic variation and inform conservation efforts for this critically endangered species.

The Sunda pangolin is a medium-sized mammal that can typically grow to weigh between 4 and 7 kg and measure up to 140 cm in total length (Chong et al., 2020). Larger individuals are occasionally documented; in addition to a 13.5 kg male documented by Sulaiman et al. (2017), records from the logbooks of a trafficking syndicate in Sabah imply that the species can grow to a weight of up to 21 kg (Pantel and Anak, 2010). The species' diet consists primarily of ants and termites, with ants being the preferred prey (Lim, 2007). Male pangolins are larger and heavier than females, which may be linked to the fact that males are territorial. All pangolins are solitary species, though females have been observed with dependent young on occasion (Lim and Ng, 2008). Scent marks left by urine and secretions serve as a basis for social interaction. In the wild, the species is predominantly nocturnal, sleeping during the day and active at night (Lim and Ng, 2008); in captivity, a similar diel pattern of activity can be observed (Challender et al., 2012; Nguyen et al., 2014).

In comparison to other mammals and other species, pangolins have received relatively little research attention. The Sunda pangolin is semi-arboreal and wild individuals appear to have stable home ranges. Lim (2007) tracked five adult pangolins on an island in Singapore and using Minimum Convex Polygon (MCP) home range estimator, estimated that four males had an average home range of 41 ha and a single female had a 7-ha home range (100% MCPs). These estimates may be influenced, however, by the fact that the female gave birth to a baby. The tracking of the female pangolin was discontinued to avoid causing further stress to the female and potential harm to the newborn baby. The Sunda pangolins use a variety of structures as shelters, also known as sleeping sites, including tree hollows (which can be found in either standing or fallen trees, and can be either live or dead), burrows (which can be newly dug or modified existing structures) and among tall grasses (e.g., *Imperata cylindrica*) (Lim and Ng, 2008). Entrances to structures in tree hollows are typically one or more in number (Lim and Ng, 2008). Burrows are dug by the species when kept in captivity (Nguyen et al., 2014). Sunda pangolins can sometimes make use of similar artificial structures; for example, individuals have been discovered sleeping in large pipes in a city in Singapore (Lim and Ng, 2008). Lim and Ng (2008) reported that male pangolins were observed to remain in the same sleeping site for one to two nights, while female pangolins with young stayed for a longer period of time.

Reports show that the Sunda pangolin is widely distributed throughout Southeast Asia and is native to Brunei, Cambodia, Indonesia, Laos, Malaysia, Myanmar, Singapore, Thailand, and Vietnam (Challender et al., 2019) (**Fig 1.1**). Sunda pangolin is not reported from the Philippines (Corbet and Hill, 1992). The Sunda pangolin can be found in primary and secondary tropical forest (which includes dipterocarp forest), evergreen and hill forest, peat swamp forest, grasslands, monoculture (e.g., oil palm and rubber plantations), gardens, and urban areas, as well as a variety of other habitat types (Payne et al., 1985; Lim and Ng, 2008; Ketol et al., 2009; Azhar et al., 2013; Wearn, 2015). The presence of the species in artificial landscapes e.g., oil palm *(Elaeis guineensis)* plantations and degraded forest (e.g., in Singapore), as well as evidence of breeding, suggests that the species can adapt to modified habitats if there is sufficient prey and if the species is not threatened by human actions. Kwaja et al. (2019) reported that Sunda pangolins are more likely to be found in unprotected areas than in protected areas, though there is also the possibility that frequent sightings in modified habitats are due to higher observer effort in these areas. Despite the Sunda pangolin’s widespread distribution, no extensive research has been conducted on its population levels, ecology, or life cycle. More ecological research is needed to understand this, as well as the species' ability to persist and breed in these habitats.

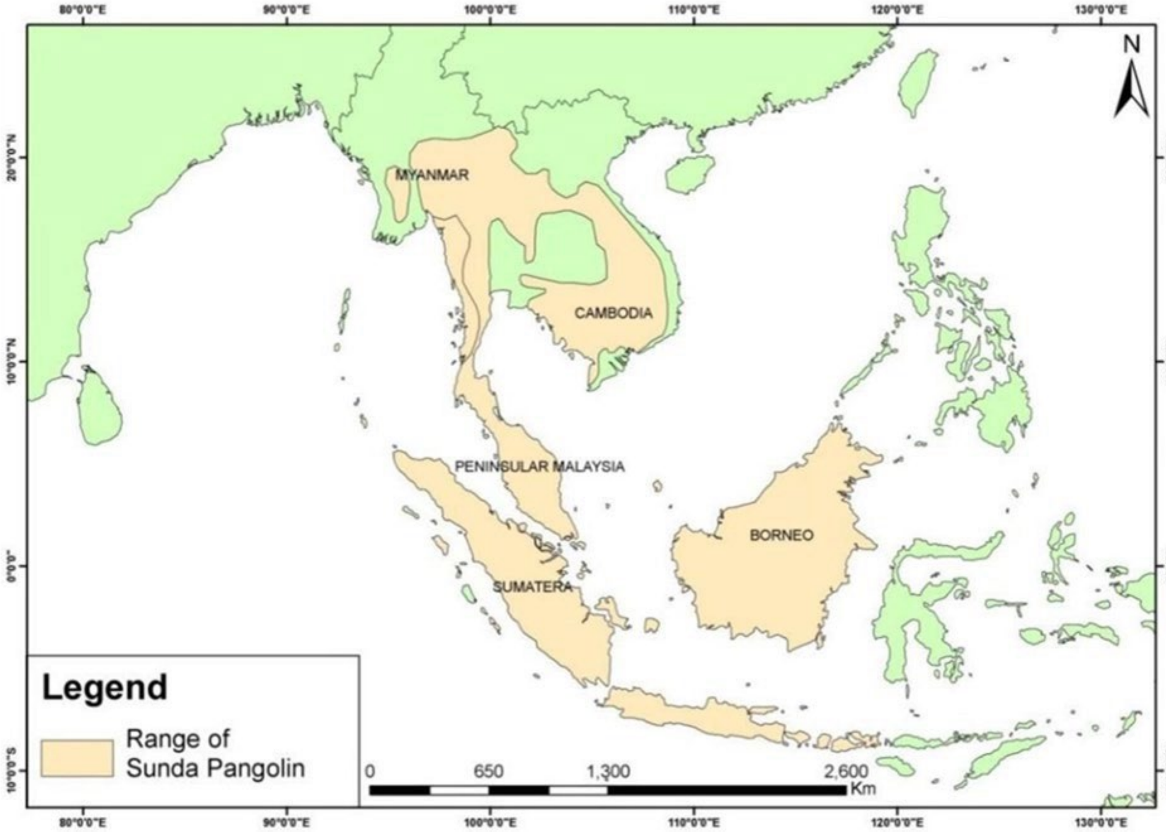

Fig. 1.1: Sunda pangolin distribution (Challender et al., 2019)

1.3 Landscape ecology and habitat fragmentation in Sabah: implications for biodiversity and conservation

Landscape ecology examines the relationship between spatial patterns and ecological processes across diverse scales and ecosystems (Wu, 2013). This field of study is essential for understanding the impact of land use changes and habitat structure on biodiversity and ecosystem functions (Clark, 2010; Gokyer, 2012). It emphasises the importance of spatial heterogeneity, habitat connectivity and ecological flows in shaping wildlife populations and their environments (Wu, 2013). For example, riparian forest corridors in fragmented oil palm landscapes in Sabah maintain gene flow and movement of species such as Bornean orangutans *(Pongo pygmaeus morio)* and elephants *(Elephas maximus borneensis)*, reducing the isolating effects of agricultural expansion (Alfred et al., 2012; Ancrenaz et al. 2014). Similarly, heterogeneous mosaic habitats that combine natural forest patches, regenerating secondary growth and mixed-use agroforestry support seasonal migrations and dispersal of hornbills and frugivorous bats, facilitating seed dispersal across landscapes (Struebig et al., 2008; Kitamura, 2011).

In the context of biodiversity-rich countries like Malaysia, landscape ecology provides insights into the interaction between anthropogenic activities and natural processes and how this interaction shapes the landscape, ultimately affecting the survival and distribution of species. The principles of landscape ecology are especially relevant in assessing the impacts of human-induced changes, such as deforestation and land-use conversion (Teng et al., 2020). This has been shown to be the case for a range of forest dwelling species such as Bornean orangutans (Goossens et al., 2006), Bornean elephants (Evans et al., 2018) or large carnivores like Sunda clouded leopards (*Neofelis diardi*) (Hearn et al., 2018). For smaller species like the Sunda pangolin, such fragmentation is particularly relevant, as this species is already critically threatened by habitat degradation and land use changes for agriculture.

Habitat loss and fragmentation compound these threats, not only disrupting their natural environment but also inadvertently providing greater opportunities for poachers, further jeopardising their survival (Chong et al., 2020). Understanding these dynamics is crucial for developing effective conservation strategies that address the complex interplay between ecological processes and human activities (Farina, 2022).

Habitat loss and fragmentation are significant threats to global biodiversity and this issue is particularly critical in countries with rich biodiversity, such as Malaysia (NRECC, 2006; Wilson et al., 2016). Such habitat loss can profoundly weaken wildlife populations and threaten to push entire species toward extinction (Harrison et al., 2016). Malaysia, a developing country in Southeast Asia, covers an area of 328,550 km^2 and is characterised by a diverse landscape, including tropical rainforests, mountainous regions, coastal ecosystems and extensive river systems (Khalifah and Tahir, 1997; PEMSEA et al., 2017; Aik et al., 2021; NRECC, 2023; World Bank, 2023). The country is geographically divided into two main regions: Peninsular Malaysia, referred to as West Malaysia and East Malaysia, which includes the states of Sabah and Sarawak, along with the federal territory of Labuan, located off the coast of Borneo. In Malaysia, the pace of economic development and population growth has led to extensive land-use changes, resulting in significant habitat changes and loss.

Peninsular Malaysia, with its long history of plantation agriculture (e.g., rubber and rattan), has primarily been a resource-based economy, characterised by expanding plantations that increasingly replace natural forests (Shevade and Loboda, 2019). Accessibility to existing plantations is a major driver of oil palm expansion, a pattern that has remained significant over time (Shevade and Loboda, 2019). This finding aligns with observations by Gunarso et al. (2013), who noted that in Peninsular Malaysia, the expansion of oil palm plantations primarily involves the conversion of other land uses, particularly existing plantation crops like rubber. These studies collectively highlight the ongoing transition in land use, where established agricultural lands are being reused for the growing oil palm industry. In East Malaysia, particularly in Sabah and Sarawak, the transformation of forests into oil palm plantations has been a significant trend (Shevade and Loboda, 2019). This extensive conversion is reflected in the high deforestation rates, contributing to a systematic reduction of natural habitats (Bryan et al., 2013). The extent of natural forest cover in Malaysia and the rate of recent forest loss can be seen in the data published by Global Forest Watch (Hansen et al., 2013; Harris et al., 2021; Gibbs and Harris, 2023). In 2010, Malaysia's natural forests covered 20.3 million hectares (mha), which accounted for 87% of the country's total land area, clearly indicating the substantial extent of natural forests at that time. However, by 2022, Malaysia had lost 118 thousand hectares (kha) of its natural forest, marking a significant decrease in forest area over just a 12-year period (Hansen et al., 2013; Harris et al., 2021; Gibbs and Harris, 2023).

Over the past two decades, from 2001 to 2022, Malaysia has experienced a significant loss of tree cover, highlighting an alarming rate of habitat degradation in the region. According to data from Global Forest Watch, the country lost 8.92 mha of tree cover during this period, amounting to a 30% decrease since 2000 (Hansen et al., 2013; Harris et al., 2021; Gibbs and Harris, 2023). This significant decrease in tree cover represents more than just changes in land use; it indicates a major environmental transformation with serious implications for the country’s biodiversity. Such decrease in tree cover can be detrimental to species dependent on forested habitats, like the Sunda pangolin (Lim and Ng, 2008; Chong et al., 2020). The loss of these habitats may lead to a decline in populations (Scotson et al., 2017). Moreover, the decrease in tree cover worsens habitat fragmentation. This results in more isolated wildlife populations, increasing their vulnerability to threats such as poaching and genetic bottlenecks (Wong and Linkie, 2013; Brodie et al., 2015; Frankham et al., 2017; Pinto et al., 2023).

Furthermore, fragmentation not only causes the loss of many trees but also impacts the growth of young, regenerating trees (Nunes et al., 2023). These trees often develop unusual shapes, becoming shorter, thicker and with heavier branches. Such changes in tree morphology, observed in fragmented Amazon rainforests, have led to significant reductions in forest biomass and carbon (Nunes et al., 2023). These changes can impact both the trees and the ecosystems they form part of. Trees exhibiting abnormal growth patterns may not support the same level of biodiversity as those that grow normally, as they may offer fewer resources and habitats for various species. Additionally, such abnormal growth may be sign of stress in trees, making them less resilient to environmental changes, diseases or pests (Nunes et al., 2023).

This situation poses potential concerns for the Sunda pangolin, which is primarily semi-arboreal and dependent on hollows within larger, mature trees for their survival (Lim and Ng, 2008). While the direct effects of these morphological changes in trees on Sunda pangolins in fragmented habitats are not yet fully understood, there is a possibility that such changes could interfere with their essential living and breeding habitats. Further research is needed to understand the extent to which these environmental changes impact the Sunda pangolin and similar species.

Sabah boasts a diverse ecological landscape due to its wide range of land cover types. This diverse region encompasses dense tropical rainforests, agricultural lands, coastal mangroves, mountainous terrains, transitional zones and urban and semi-urban areas (Bryan et al., 2013; Ancrenaz and Abram, 2017; Tangah, 2017). These diverse landscapes contribute not only to Sabah's unique biodiversity but also support many ecological functions and services essential for the survival of both wildlife and human populations. The tropical rainforest of Sabah, covering a significant portion of the state, is home to a diverse range of species, making them some of the world's most biodiverse ecosystems. This contributes to the region's status as a hotspot of species endemism and biological diversity (Whitten et al., 2012; Ancrenaz and Abram, 2017). These forests are crucial for carbon sequestration and serve as natural water reservoirs (NRO, 1994; Besar et al., 2020). Large areas of Sabah have been converted into agricultural lands, primarily for oil palm plantations (Gaveau et al., 2014; Ancrenaz and Abram, 2017). As of 2022, Sabah accounted for 26.6 per cent (%) of the total area of Malaysia planted with palm oil (Onn, 2021), 26% of Malaysia's total oil palm plantations, and contributes 24% of the country's total palm oil output (Statista, 2023).

While these contribute to the state’s economy, they also impact natural habitats and biodiversity (Ancrenaz and Abram, 2017). The coastal mangroves of Sabah play a critical role in protecting shorelines from erosion, serving as nurseries for marine life, and acting as buffers against tidal surges (Saleh et al., 2011; Spalding et al., 2014). The mountainous landscapes are rich in endemic species, and these regions have distinct microclimates and ecological niches (Majuakim and Anthony, 2019). In Sabah, transitional zones where rainforests meet plantations or urban areas create unique ecological interfaces. These areas are often rich in biodiversity but can be vulnerable to human activities (SBS, 2012; Ancrenaz and Abram, 2017). Urban and semi-urban areas in Sabah, encompassing towns, cities and villages, represent another significant land cover type. These areas are characterised by infrastructure development, residential zones and commercial activities. While they are essential for human habitation and economic activities, these human-dominated landscapes often encroach upon natural habitats, leading to various environmental challenges such as human wildlife conflict and infectious disease transmission (Othman et al., 2013; Stark et al., 2019).

Sabah categorises its forests into various classes, each serving distinct ecological and socio-economic functions. The classification system is essential to preserve the ecological integrity of the region and support sustainable resource management. Within this framework, Sabah encompasses a variety of protected areas, including forest reserves and wildlife sanctuaries that are crucial for maintaining ecological processes and protecting diverse species. The Protection Forest Reserve, classified as Class 1, established a considerable part of Sabah's forested landscape, dedicated to preserve forests, watersheds, soil and other essential environmental elements (SFD, 2023). Timber harvesting is strictly prohibited within this reserve to uphold ecological stability and safeguard environmental services (Lim et al., 2021; SFD, 2023). The Commercial Forest Reserves, classified as Class 2, crucial to the state's forestry sector, are designated for regulated timber production, significantly contributing to Sabah's economy. Adhering to Sustainable Forest Management principles, these reserves implement strict harvesting guidelines to balance economic benefits with ecological stewardship (SFD, 2023). Similarly, the Domestic Forest Reserves, classified as Class 3, address the subsistence needs of local communities, providing a source of non-timber forest products under strict regulatory guidelines to ensure sustainability (SFD, 2023). Amenity Forest Reserves, classified as Class 4, focus on recreational infrastructure development and Mangrove Forest Reserves, classified as Class 5, are key to coastal ecosystem services. They further illustrate Sabah's commitment to harmonising environmental conservation with community welfare and commercial interests (SFD, 2023).

Continuing with Sabah's forest classifications, the Virgin Jungle Reserves, classified as Class 6, are untouched sanctuaries reserved exclusively for conservation science and ecological research. These relatively unmodified areas are invaluable for studies on ecological baselines, biodiversity conservation and genetic diversity, with timber harvesting strictly prohibited to maintain their integrity (SFD, 2023). The Wildlife Forest Reserves, classified as Class 7, aimed at the protection and conservation of wildlife, are especially crucial for safeguarding large mammals and avifauna. These reserves not only contribute to the overall ecological balance but also offer opportunities for scientific research that can inform future conservation practices (SFD, 2023). For a visual representation of Sabah's diverse forest classifications and their distribution across the state, refer to **Fig. 1.2**.

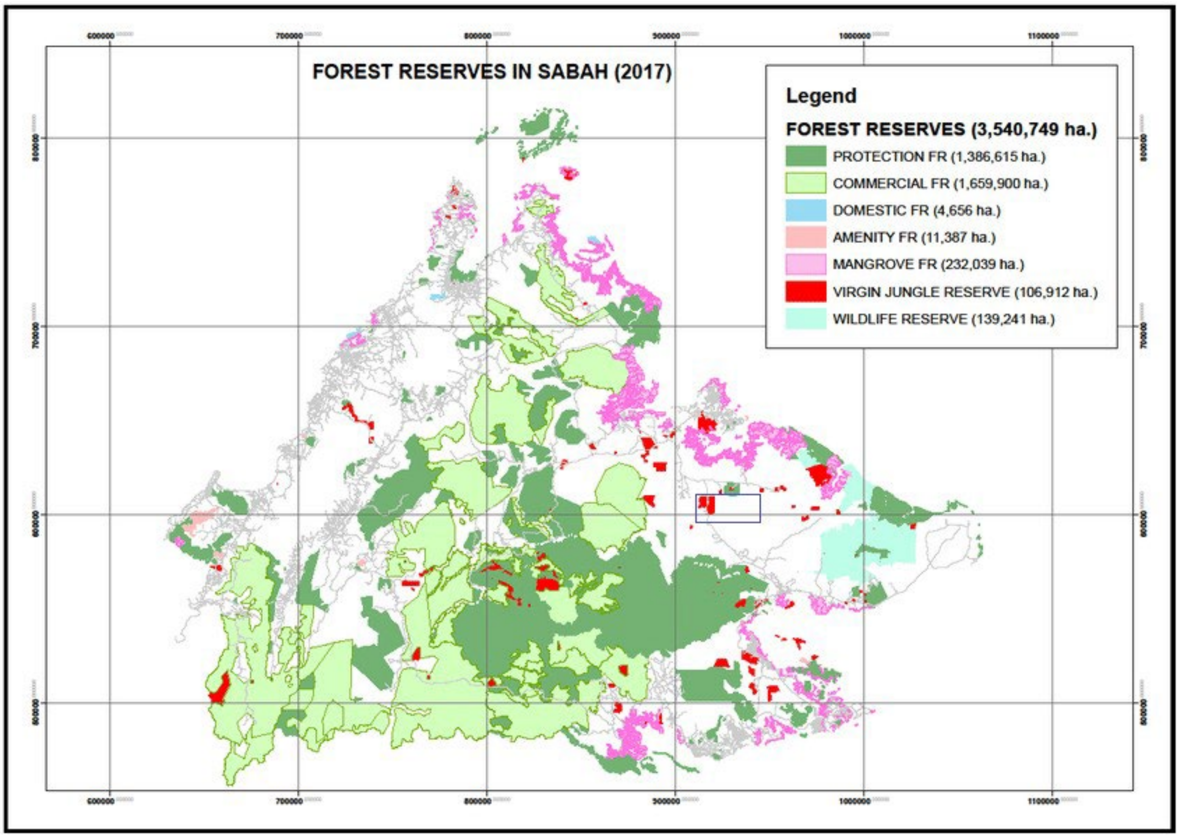

Fig. 1.2: Classification of Forest Reserves (FR) in Sabah as of 2017 (Tangah et al., 2019). The study area for this research is outlined in the blue-lined box.

High conservation value (HCV) areas and industrial timber plantations (ITP) in Sabah's landscape ecology

High Conservation Value (HCV) areas are a critical component in the landscape ecology of Sabah, playing a crucial role in conserving biodiversity and maintaining ecological processes (SFD 2023; Sahana et al., 2023). These areas are designated based on their importance for environmental, social or cultural values. Key aspects include biodiversity conservation, which involves providing habitat for diverse species, including those that are endangered and endemic to the region. Additionally, HCV areas contribute to vital ecosystem services such as natural flood control and carbon sequestration. Encompassing diverse ecosystems, from rainforests to mangroves, they are crucial in maintaining these ecological services. Furthermore, these areas hold cultural value for local communities, often being sites of historical, cultural or spiritual importance (SFD, 2023). The Sabah Forestry Department (SFD) plays a leading role in the monitoring and evaluation of these areas, ensuring their continued protection and management.

In contrast to HCV areas, Industrial Timber Plantations (ITP) in Sabah present a contrasting land use which focuses on the production of timber as a commercial resource. In Sabah, 400,000 ha are dedicated to ITP, but only 160,000 ha have been planted to date (Daily Express, 2021). While these plantations contribute to the economy, they can have significant ecological impacts, which include habitat changes, where the establishment of ITPs often involves converting natural forests into managed plantations, which can lead to habitat loss and reduced biodiversity (Pawson et al., 2013; Rodriguez et al., 2014; McEwan et al., 2019). This land use change poses challenges for endangered species like the Sunda pangolin, which depend on specific habitat conditions. Therefore, a key challenge in Sabah is to implement sustainable practices in ITPs to balance economic growth with ecological preservation (Daily Express, 2021; Malay Mail, 2022). The interaction between HCV areas and ITPs in Sabah represents the complex balance between conservation and development. Understanding this dynamic is crucial for effective landscape management and the conservation of endangered species like the Sunda pangolin.

Impact of oil palm plantations on Sabah's ecology and Sunda pangolin conservation

In recent decades, Sabah has witnessed a significant increase in the development of oil palm plantations. This expansion, driven by global demand for oil palm, has positioned Sabah as a key player in the international oil palm industry (UNDP, 2023; NST, 2023). The shift of extensive areas of land in Sabah into oil palm plantations has notably boosted the region's economy, particularly in its agriculture and export sectors (Bernama, 2023; UNDP, 2023). This economic development, however, has come with a significant change in land use patterns. The region has witnessed the clearing of vast forested areas to accommodate the expanding cultivation of oil palms. This has a major impact at a landscape scale, particularly in terms of biodiversity conservation and ecosystem health (Naidu and Moorthy, 2021). Sabah's rich and diverse ecosystems are home to many endangered species; among these is the Sunda pangolin, a species that has become symbolic of the region's conservation challenges. The expansion of oil palm plantations has resulted in substantial habitat changes, posing a direct threat to the survival of Sunda pangolin and other species (Naidu and Moorthy, 2021). The subsequent habitat loss and fragmentation have disrupted ecological processes, leading to a decline in biodiversity and changes in species composition (Wilson et al., 2015; Liu et al., 2018).

Sabah, covering 73,965 km^2 has experienced significant deforestation, primarily for agricultural expansion, particularly oil palm plantations, and logging activities (Gaveau et al., 2014; Abram and Ancrenaz, 2017). Between 1973 and 2010, Borneo lost 168,498 km^2 of its primary forests, amounting to 30.2% of its original forest cover (Gaveau et al., 2014), a critical habitat for many species, including the Sunda pangolin. The loss of these forests not only diminishes the available habitat for these pangolins but also fragments their living spaces, creating isolated populations (Daskalova et al., 2020). In 2022, Malaysia's total oil palm cultivation covered 5.67 mha. Within this, Sabah was the second-largest contributor, accounting for 1.51 mha of the country's oil palm plantations. As of 2021, the production of crude oil was 4.29 million tonnes (MPOB, 2022). For a visual representation of oil palm plantation distribution across Sabah, refer to **Fig. 1.3**.

In 2022, Sabah's GDP grew by 3.7% to Malaysian Ringgit (RM) 81.9 billion (USD18.84 billion) from RM79 billion (USD18.17 billion) in 2021, and the oil palm sub-sector dominates the agricultural sector in Sabah with a contribution of 9.6% to overall Sabah GDP (Malay Mail, 2023). In 2021, the gross domestic product from palm oil was estimated to be RM34.79 billion (USD8 billion) (Statista, 2023). The palm oil industry is a significant contributor to the Malaysian agricultural sector and is its fourth-largest contributor, employing nearly a million people (Statista, 2023). The extent of habitat loss and fragmentation in Malaysia, and specifically in Sabah, presents an alarming challenge to the conservation of the Sunda pangolin. The critical loss of natural habitats due to human activities requires urgent and effective conservation measures to halt and reverse this trend. While the expansion of oil palm plantations and consequent habitat loss pose significant threats to Sabah's biodiversity, these environmental changes also worsen another critical challenge: the rampant poaching and illegal wildlife trade further endangers species like the Sunda pangolin.

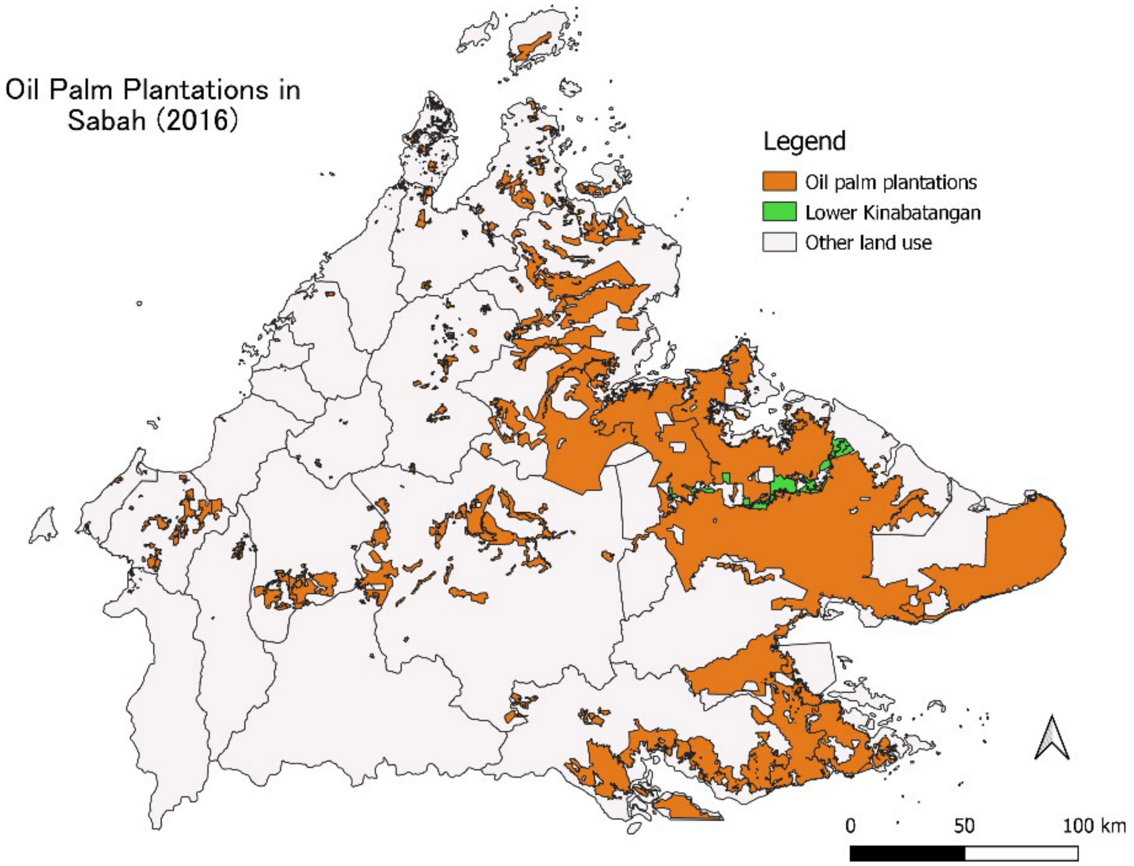

Fig. 1.3: Distribution of oil palm plantations in Sabah as of 2016 with Lower Kinabatangan shown as the study area. Map was created using data from SFD (2016).

Intersecting threats: Poaching, illegal wildlife trade and habitat fragmentation

Habitat loss and fragmentation are significant threats to many mammal species around the world, including the Sunda pangolin, resulting in the loss and fragmentation of many natural habitats (Brooks et al., 2002; Crooks et al., 2017; Chong et al., 2020). For the Sunda pangolin, habitat loss is an indirect but significant threat, resulting from activities such as road building, mining, dam construction, logging concessions, and the expansion of oil palm plantations (Chong et al., 2020). The increasing crisis of poaching and illegal wildlife trade in Sabah represents another dire consequence of environmental degradation. As habitats become fragmented and species like the Sunda pangolin are pushed into smaller, isolated areas, they become more accessible and vulnerable to poachers. This illegal activity not only threatens the survival of individual species but also disrupts the ecological balance and undermines conservation efforts. A comparative study is needed to evaluate the densities of Sunda pangolin populations in their natural habitats and in modified landscapes, such as oil palm plantations (Davies and Payne, 1982). This would help to understand the impact of habitat modifications and the effectiveness of conservation strategies to mitigate these impacts.

The Sunda pangolin is classified as “Critically Endangered” on the International Union for Conservation of Nature's Red List of Threatened Species because of past, ongoing and inferred future population declines, primarily as a result of overexploitation (Challender et al., 2019). In 2016, the Convention on International Trade in Endangered Species (CITES) up-listed all eight pangolin species to Appendix I, which means that international trade for commercial purposes is prohibited by law. The Sunda pangolins are protected by national legislation across their range of states, typically prohibiting exploitation for personal or commercial gain. If hunting were to be allowed, it would require a government-issued hunting license. Such licenses are, however, not issued. In Malaysia, pangolins are protected under three different legal frameworks. Pangolins are listed as “totally protected species” under the Wildlife Conservation Act (2010) in Peninsular Malaysia. In Sabah, the species is also listed as a “totally protected species” under the Wildlife Conservation Enactment (1997). Meanwhile, pangolins are listed as “protected species” in Sarawak under the Wildlife Protection Ordinance (1998). The penalties for breaking all these three laws include imprisonment and fines.

While overexploitation is a major threat to Sunda pangolin populations in their range states, including Sabah, habitat loss and degradation also pose significant challenges. The synergy of these factors, overexploitation, and habitat destruction, worsen the risk to these populations, highlighting the need for comprehensive conservation strategies that address both issues to effectively protect this critically endangered species. Overexploitation is primarily driven by demand in China and Vietnam for pangolin body parts for use in traditional medicine, as well as for luxury products in high-end urban restaurants and more locally as “bush-meat” (e.g., in villages near protected forests). In the study by Corlett (2007), it was reported that indigenous people and local communities have traditionally consumed the Sunda pangolin for subsistence purposes, as a source of protein. Additionally, the scales of pangolins have been used for various applications, as reported by Hafiz and Chong (2016); for example, the scales are used for traditional medicine, as they are believed to have medicinal properties among Orang Asli in Peninsular Malaysia and in some cultures in Sarawak and Sabah (Chong et al., 2020). In some parts of Sabah, commercial hunting of pangolins has been reported, and the animals are sold to generate income (Pantel and Anak, 2010).

The interplay between overexploitation and habitat loss and degradation creates a complex challenge for Sunda pangolin conservation. Habitat degradation, often resulting from deforestation for agriculture, urban expansion and infrastructure development (Wong and Linkie, 2013; Brodie et al., 2015) not only diminishes the natural habitats vital for pangolins but also makes them more susceptible to exploitation (Chong et al., 2020). As their habitats shrink and fragment, pangolins are forced into closer proximity with human settlements, increasing their vulnerability to poaching and illegal trade and this situation is compounded by the existing high demand for pangolins in traditional medicine and luxury markets (Chong et al., 2020). The loss of habitat thus directly feeds into the cycle of overexploitation, as reduced and fragmented landscapes facilitate easier access for poachers.

In addition to pressures to the species because of environmental factors, there are also cultural issues that play a role in pangolin extinction threats. For instance, research is needed to determine the specific uses of pangolin scales in different cultural contexts. In some cultures, Sunda pangolins are considered a delicacy (Chong et al., 2020) and their meat is consumed as a form of traditional cuisine or for medicinal purposes. However, the high prices pangolins command in the market, driven by demand in illegal markets, lead many individuals to sell them for profit rather than consume them (MacMillan and Nguyen, 2014; Chong et al., 2020). This practice has contributed to the decline of pangolin populations in many regions and is a major driver of their threatened status. For instance, in parts of Southeast Asia, like Sabah, selling a pangolin can be highly profitable. As an example, consider a scenario where a seller captures an adult pangolin weighing 7 kg. In 2021, the price for pangolin was about RM250 (USD53) per kilogram, as per unpublished data from the Sabah Wildlife Department. Therefore, a single sale of such a pangolin could fetch approximately RM1,750 (USD374). This amount exceeds the typical minimum monthly salary in

Malaysia, which is RM1,500 (USD320). This comparison highlights the substantial economic incentive for individuals engaged in this illegal trade.

Throughout the early and mid-20th Century, commercial and international trade in the Sunda pangolin was undertaken. This trade continued even after it was made illegal, with reports of pangolin trafficking persisting into the 21st Century. In fact, between 2001 and 2019, the Sunda pangolin was the most frequently seized or confiscated pangolin species in the world (Challender et al., 2020). This highlights the continued demand for pangolin products and the need for greater efforts to combat illegal trade and protect these threatened animals. Approximately 22,000 Sunda pangolins from Sabah were reportedly exported between 2007 and 2009 (Pantel and Anak, 2010). In 2019 alone, authorities in Sabah seized 30 tonnes of pangolins, which involved a mix of live pangolins, frozen carcasses and scales (The Strait Times, 2019; TRAFFIC 2019). Currently, it is believed that hunters and traders might be focusing on pangolin populations in areas that have been relatively protected from hunting pressure. This could be regions with stricter conservation measures or less human intrusion. For example, in Sabah, there is evidence of active poaching within protected areas, involving local individuals and organised syndicates, who often use large vehicles and operate in groups, targeting protected species such as Bornean elephants and bantengs (*Bos javanicus*) (FMT, 2019; The Borneo Post, 2021b).

This information has been corroborated by camera trap data collected by field researchers and reports from roadblocks and vehicle checks conducted by the authorities such as Sabah Wildlife Department and Sabah Forestry Department in districts of Sandakan and Lahad Datu (Borneo Today, 2020; Borneo Post, 2021; New Strait Times, 2022). This approach might explain why, several decades after commercial exploitation began, large numbers of individuals are still involved in the illegal trade (Chong et al., 2020). However, it is important to note that this is a hypothesis and not a definitive statement. The actual situation might vary, and the specific locations where pangolins are being targeted for illegal trade can be diverse and not limited to protected areas alone. Enforcement of conservation laws and the effectiveness of protection measures can also significantly influence whether protected areas are targeted by hunters and traders. These findings indicate that even protected areas are vulnerable to illegal hunting activities, emphasising the complexity of wildlife conservation challenges in the region. Overexploitation is worsened by inadequately resourced and ineffective law enforcement in range countries (Challender and Waterman, 2017). Additionally, while there have been efforts to reduce demand for pangolin products, there is limited evidence to suggest that these measures have been effective in curbing the illegal trade of pangolins (Veríssimo and Wan, 2019). This may be due to various factors, including inadequate implementation of policies and a lack of awareness among consumers. Further research and improved strategies are needed to address this issue and protect the survival of Sunda pangolins.

At the start of 2019, a Coronavirus disease (Covid-19) caused by the severe acute respiratory syndrome coronavirus 2 (SARS-CoV-2) negatively impacted human communities all over the world. SARS-CoV-2-related coronaviruses have been discovered in bats, and evidence suggests that pangolins may have served as an intermediate host, allowing humans to become infected with the virus (Lam et al., 2020, Wacharapluesadee et al., 2021). Since the onset of the pandemic, the scientific and conservation community has called for an end to the bushmeat trade and consumption of pangolins, according to reports (France 24, 2020; Nyasa Times, 2020). As a result, there has been a decrease in the demand for pangolins for bushmeat in several countries (Phys.org, 2020, Deemie et al., 2021). The trade and trafficking of pangolins continue in some countries, despite the threat of coronavirus infection (TRAFFIC, 2021). Further investigation would be beneficial, to better understand the impact of the Covid-19 pandemic on pangolin trade and trafficking.

While there has been a growing focus and funding for pangolin conservation in recent years, successful conservation initiatives require coordination and cooperation among different stakeholders within range states. This includes governments, law enforcement agencies, conservation organisations, local communities and other key actors. Furthermore, there needs to be agreement on priority conservation actions that can effectively address the threats faced by pangolins. These actions may include increased protection and enforcement efforts, habitat restoration, and demand reduction programs (Khatiwada et al., 2020; Nash et al., 2020). A lack of coordination and cooperation among stakeholders at the local level, as well as challenges in implementing agreed-upon priority conservation actions, pose significant barriers to the success of pangolin conservation efforts. While the Global Action Plan and specific action plans on Sunda pangolin such as those by Challender et al. (2014) and the IUCN SSC Pangolin Specialist Group et al. (2018), do provide a structured approach to conservation at a broader scale, the effective translation of these frameworks into local contexts remains a challenging issue. This highlights the need for stronger alignment and integration of global conservation strategies with local efforts to ensure the effective protection of pangolins.

To strengthen these conservation initiatives, a deeper understanding of the Sunda pangolin's habitat and distribution in Sabah is crucial. This understanding is crucial for tailoring conservation efforts to the specific needs and threats in different areas. In Chapter 2, this thesis aims to fill this knowledge gap. This study hypothesises that habitat changes in Sabah may have contributed to a decline in pangolin populations, and spatial analysis is employed to explore this further. Using spatial analysis tools and predictive models, this chapter will map the current distribution of the Sunda pangolin, highlighting areas of dense primary forest alongside those impacted by human activities, such as oil palm plantations and urban development. Simultaneously, the study will evaluate how accessible these habitats are to poachers. This aspect acknowledges that even suitable habitats for wildlife can be vulnerable to human intrusion, potentially increasing the risk of poaching and illegal wildlife trade.

1.4 Study area

Sabah, Malaysian Borneo

Sabah, in Southeast Asia, is known for its rich biodiversity, which includes many endemic species of flora and fauna (Whitten et al., 2012), as well as its significant and diverse tropical rainforests, such as the Danum Valley Conservation Area, Maliau Basin Conservation Area, Imbak Canyon Conservation Area, and the Lower Kinabatangan Wildlife Sanctuary (LKWS). Through the provision of timber, non-timber forest products, and ecosystem services, these forests play an important role in regulating the regional climate and supporting local communities. However, Sabah faces a slew of environmental challenges, including habitat loss, fragmentation, and degradation, all of which pose serious threats to the state's unique and valuable biodiversity (Abram and Ancrenaz, 2017).

The state has the most oil palm planted of the country's 13 states, accounting for more than 29% of national oil palm coverage and 10% of annual palm oil output in 2012 (MPOB, 2012). By 2022, its share of planted area had declined to 26% while its contribution to output had increased to 24% (Onn, 2021; Statista, 2023). Palm oil, by far Sabah's most important export, accounted for 40% of the state's revenue in 2010 (Sabah State Government, 2012). In 2011, oil palm covered 19.3% of Sabah's land mass. The state's economic development strategy stated that oil palm development could expand to 21,000 km² to help quadruple Sabah's GDP by 2025 (IDS, 2007; MPOB, 2012). Because oil palm can only thrive at elevations lower than 500 m asl, lowland forests have been particularly targeted for oil palm, resulting in the loss of 80% of Sabah's lowland mixed dipterocarp forest (Abram and Ancrenaz, 2017). With only 47% of natural forest remaining in Sabah in 2010 (Gaveau et al., 2014), habitat loss, along with poaching, is one of the state's major threats to biodiversity. To ensure the protection and preservation of Sabah's unique and valuable biodiversity for future generations, it is critical to address these challenges through effective conservation strategies and sustainable development practices.

The Lower Kinabatangan floodplain – highly fragmented and degraded landscape

The Lower Kinabatangan floodplain is located in the Kinabatangan District of Sabah at approximately 5º30'N and 118ºE (Appendix 2) (Abram and Ancrenaz, 2017). The Lower Kinabatangan is a vast floodplain characterised by small limestone hills, covering an area of about 4,000 km², the largest floodplain in Malaysia. The longest river in Sabah at 560 km, the Kinabatangan River flows through this region. The humidity and consequent rainfall from Central Sabah's mountainous region drain into the Kinabatangan River (Ancrenaz et al., 2004; Estes et al., 2012). Combined with an annual rainfall of 3,000 mm and temperatures ranging from 21-34°C (Ancrenaz et al., 2004), the floodplain creates a landscape that supports a diverse array of habitats, including riparian forest, swamps, dry dipterocarp forest and mangrove forests (Estes et al., 2012). The Lower Kinabatangan is regarded as one of the most productive wetlands in Sabah and is considered to be among the richest in terms of biodiversity and ecosystem services (Davison, 2006).

The entire Kinabatangan catchment area, spanning over 16,800 km², accounts for 23% of the state's total land area. Once, a continuous stretch of forest connected the coastal environment to the interior highlands, providing vital connectivity for various ecological and ecosystem processes. However, habitat loss and fragmentation, including converting forested areas to oil palm plantations and other human activities, have disrupted this connectivity (Lackman-Ancrenaz and Manokaran, 2008). Over the past few decades, the Lower Kinabatangan Forest ecosystem has undergone significant changes due to human activities such as timber extraction using heavy machinery, agricultural development, and large-scale oil palm production since the 1990s (Abram and Ancrenaz, 2017). These activities have resulted in a dramatic loss of forest cover and fragmentation of the landscape. Today, less than 1% of the Kinabatangan region's primary forest remains (Sabah State Government, 2012; Abram and Ancrenaz, 2017). Despite this, the region still holds considerable biodiversity value, supporting many rare and threatened species, though these species are now confined to smaller, fragmented habitats.

Despite the damage to its forest, the floodplain is a significant biodiversity hotspot. It is home to various animals and plants, including Bornean orangutans, Bornean elephants, proboscis monkeys (*Nasalis larvatus)* and other species (Sha et al., 2008; Lackman-Ancrenaz and Manokaran, 2008; Estes et al., 2012; Ancrenaz et al., 2014), including Sunda pangolins. The floodplain previously consisted of diverse forest types, ranging from beach forests near the coastline, to Nipah, and mangrove forests. Inland, the forest types transition into freshwater swamp forests and peat swamp forests in waterlogged areas. Riparian and mixed-lowland dipterocarp forests were also present in well- drained regions, along with limestone forests on karstic hills and escarpments. However, these forests have largely disappeared or become degraded due to the expansion of oil palm plantations, and some are at risk of being eliminated (Abram and Ancrenaz, 2017). The riparian corridor that exists between the Kinabatangan River and its tributaries, as well as the oil palm plantations, is recommended by best practices to be 100 m wide; however, this distance varies greatly along the river's course, and in some areas, the riparian corridor is entirely absent.

This variation can be attributed to human activities such as agricultural expansion, which encroach into the buffer zones, enforcement challenges, geographical constraints, and historical land use practices. Policing these boundaries involves several mechanisms, including the Roundtable on Sustainable Palm Oil (RSPO) Manual on Best Management Practices for the Management and Rehabilitation of Riparian Reserves, which, while not legally binding, provides guidelines to encourage sustainable practices. These practices include using aerial monitoring, on-the-ground inspections, community involvement, and the implementation of penalties promote compliance. Despite these efforts, maintaining a consistent buffer width remains a challenge due to the varying degrees of adherence and enforcement.

The LKWS and the Kinabatangan catchment are distinct in their scope and size. The LKWS is a protected area established in 2005, covering approximately 27,000 ha. It is divided into 10 blocks of forest, known as ‘lots’, which are connected by narrow corridors to an additional 10,000 ha of state and private forests and 15,000 ha of Virgin Jungle Reserves (VJR) (Ancrenaz et al., 2004). In contrast, the Kinabatangan catchment is a much larger area encompassing the entire watershed of the Kinabatangan River. It spans over 1,680,000 ha, making up 23% of Sabah's total land area (Global Water Partnership, 2013). The catchment includes a variety of land uses such as agricultural lands, plantations, settlements, and protected areas like the LKWS. Therefore, the LKWS is a specific protected area within the much larger Kinabatangan catchment. Nonetheless, connectivity between the LKWS patches and between them and other forested areas remains poor, with narrow strips of highly degraded forest and, in the worst cases, no connectivity (Abram et al., 2014).

The Lower Kinabatangan floodplain’s highly fragmented landscape provides an opportunity to learn about how habitat loss and fragmentation impact the wildlife community, as well as how species have adapted to survive in such a severely degraded environment. Concurrently, the development of such knowledge helps to influence state wildlife conservation policies (i.e., species action plans) by providing on-the-ground information to improve forest connectivity and decrease oil palm expansion (e.g., Ancrenaz et al., 2004; Estes et al., 2012; Abram et al., 2014; Goossens et al., 2016; Stark et al., 2017; Guharajan et al., 2017; Hearn et al., 2018).

1.5 Thesis overview

The overall aim of the PhD research was to obtain a more accurate understanding of the Sunda pangolin's habitat use and ranging patterns in a fragmented and degraded forest landscape. The Sunda pangolin, a critically endangered species that is heavily poached and hunted for the illegal wildlife trade, was used as an example species to study its ecological behaviour in a landscape that has been heavily modified by humans. The resulting habitat loss and fragmentation, as well as increased hunting pressure, are putting the remaining Sunda pangolin populations at risk (Challender et al., 2019). Because pangolins are elusive and rare, there is a significant gap in our understanding of their ecology, particularly in Sabah. This lack of comprehensive information hinders effective conservation efforts. This study is the first of its kind in Sabah, aiming to fill this knowledge gap and provide important data on the ecology of the Sunda pangolin.

By evaluating the extent and quality of habitats suitable for the Sunda pangolin, it is possible to identify current constraints of the distribution of this species. This allows for the identification of important habitats and environmental variables that can then be investigated further, and conserved where relevant (Cayuela et al., 2009; Elith and Leathwick, 2009). Identifying suitable habitats for a species with statistical robustness is critical and methods such as the Maximum Entropy (MaxEnt) model, have been used to estimate habitat suitability and improve ecological understanding (Elith et al., 2006; Franklin and Miller, 2009). The MaxEnt model is particularly useful for this study as it allows for the identification of key environmental factors influencing habitat suitability for the Sunda pangolin, which is important given the lack of comprehensive ecological data on this species in Sabah. **Chapter 2** utilises the MaxEnt model's predictive performance to identify the most important environmental factors influencing habitat suitability for the Sunda pangolin in Sabah. As a result, potential suitable areas for the Sunda pangolin conservation effort have been identified.

Camera trapping is an effective non-invasive sampling method for gathering occurrence data necessary for modelling species distribution, in contrast to more invasive methods such as museum collections or less reliable methods like observations of animal signs (Elith and Leathwick, 2009; Kanagaraj et al., 2013). By providing robust occurrence data, camera traps enhance the accuracy and reliability of the MaxEnt model. This integration allows for a more precise assessment of habitat suitability, informing conservation strategies for the Sunda pangolin in Sabah. Thus, the combined use of camera trapping and the MaxEnt model is essential to achieve the study's objectives and improve our understanding of the Sunda pangolin's habitat use and ranging patterns.

The results of the first movement ecology assessment for the Sunda pangolin conducted using Very High Frequency (VHF) radio telemetry were presented in **Chapter 3** of this thesis. The use of GPS and VHF telemetry have been beneficial in gaining a greater understanding of how species behave in the LKWS landscape e.g., the monitor lizard *Varanus salvator* (generalist species) (Guerrero-Sanchez et al., 2021), Bornean elephant (Abram et al. 2022), Sunda clouded leopard (large carnivore) (Hearn et al., 2018), Malay civet *Viverra tangalunga* (small carnivore) (Evans et al., 2019) and proboscis monkey (primate) (Stark et al., 2017). VHF telemetry has not been widely applied to pangolins. In the few studies that have been carried out on pangolins' home ranges, VHF telemetry systems have been used on Chinese pangolins (Sun et al., 2019), ground pangolins (Pietersen et al., 2014) and Sunda pangolins (Lim and Ng, 2008; Gray et al., 2020). With the help of VHF tags and Global Positioning System (GPS) data, this chapter compares the home ranges of nine pangolins, which include both resident and translocated individuals. High-definition images provided by Light Detection and Ranging (LiDAR) was also used to describe habitat preferences.

It is believed that the Sunda pangolin's choice of sleeping site is critical to its survival (Lim and Ng, 2008). The species spends approximately half of its life at sleeping sites, and the choice of sleeping site may have an impact on individual fitness and survival. The Sunda pangolin's choice of sleeping site is expected to be influenced by a variety of factors, including the type of microhabitat structure, food proximity, thermoregulation, predation threat, and the need for shelter. "Comfort" in this context refers to the suitability of the sleeping site to meet the pangolin’s ecological needs, such as protection from predators, appropriate substrate for resting, and environmental conditions that reduce stress. This could include a location that is well-protected from predators, has a soft substrate for sleeping, or provides a familiar scent or visual cues that indicate safety. These factors were thought to be similar for both resident and translocated pangolins when it came to selecting a sleeping site. While detailed studies on micro-habitat selection for pangolins are limited, individual survival and reproductive success are greatly influenced by the ecology of the sleeping sites in many species, and it is reasonable to infer similar dynamics may be at play for Sunda pangolins based on what is known about other mammalian species. **Chapter 4** aims to describe the physical and spatial characteristics of the Sunda pangolin's sleeping sites, and to analyse sleeping site selection by Sunda pangolins in the fragmented and degraded landscape of the Lower Kinabatangan floodplain. The Sunda pangolin chooses the structure and location of its sleeping site. The use of multiple sleeping sites and the consequent infrequent use of the same site over consecutive nights may also be chosen by them to prevent predators from anticipating their location. In addition, high-definition images obtained through LiDAR were used to describe microhabitat selection.

Lastly, **Chapter 5** (the General Discussion) provides an overall synthesis of the findings from the previous chapters to explain the status of the Sunda pangolin population in the Lower Kinabatangan floodplain. One of the main aspects discussed in this chapter is the effect of oil palm plantations on the Sunda pangolin's population dynamics, which involves changes in the population's size and structure over time. However, this study did not specifically investigate the population size and structure of Sunda pangolins in the Lower Kinabatangan floodplain. Instead, the study focused on examining the habitat use and selection patterns of the species. The chapter explores how habitat loss and fragmentation caused by oil palm development may impact the pangolin's survival and reproductive abilities and discusses the potential consequences of these changes on the long-term viability of the population. The chapter emphasises the importance of long-term studies with a holistic perspective to understand how human-modified landscapes impact the ecology of both the species within the anthropogenic habitats as well as within the adjacent forest. Results of the thesis are discussed in terms of how they can be used to develop appropriate guidelines and inform conservation management plans. Aspects of future research are also discussed in detail.

Chapter 2: Mapping and predicting the distribution of the Sunda pangolin (*Manis javanica*) in Sabah, Malaysia

2.1 Introduction

The alarming rate of deforestation occurring right now is the direct cause of the loss of habitat, which has a continuous, significant, and negative effect on biodiversity (Jackson and Fahrig, 2013). The loss of available habitat devastates animal populations and ultimately leads to species extinction (Harrison et al., 2016). The logging rate and the landscape's conversion to monocultural plantations are highest in Borneo compared to other tropical regions worldwide (Gaveau et al., 2014). Gaveau et al. (2014) reported that in the year 1973, approximately 558,060 km² (75.7%) of Borneo was still covered in natural forest (mainly intact old-growth forest). Over the past four decades, approximately 30.2% (168,493 km²) of primary forest has already been lost, primarily due to deforestation and the expansion of oil palm plantations. In addition, habitat loss often has effects that interact with other conservation issues. For example, the rapid increase in roads and logging trails on Borneo has resulted in an alarming rise in poaching, which poses a significant risk to the island's endangered species (Wong and Linkie, 2013; Brodie et al., 2015). Therefore, it is vital to have a robust understanding of the habitat suitability requirements of species of conservation concern and the factors that influence habitat suitability to ensure that such species will continue to exist (Adhikari et al., 2012).

In recent years, pangolins have attracted significant attention as the most trafficked mammals in the world (Challender and Waterman, 2017). There are currently eight distinct species of pangolin, all listed on the IUCN Red List of Threatened Species as either “vulnerable,” “endangered” or “critically endangered” (IUCN, 2021). Additionally, these pangolin species are included in CITES Appendix I, which places an international ban on the commercial trade in wild-caught pangolins and their derivatives (Challender and Waterman, 2017). The Sunda pangolin is the only species of pangolin that can be found in Malaysia. This species is also called the Malayan or Javan pangolin and is found all over Peninsular Malaysia and in Malaysian Borneo (Sabah and Sarawak). In Sabah, the Sunda pangolin is listed in Schedule 1 of the Wildlife Conservation Enactment 1997 as “totally protected,” making hunting illegal

(Panjang and Goossens, 2022). Possessing a pangolin, including a live pangolin and its meat and body parts, is a crime that can result in a fine of up to RM250,000 (approximately USD57,800) and up to five years in prison. The population of Sunda pangolins in Sabah is most at risk from unsustainable hunting practices and poaching for both local and international use, which are worsen by the loss and fragmentation of their habitat. Habitat loss not only reduces the available living space for pangolins but also makes them more accessible and vulnerable to poachers (Chong et al., 2020).

Sunda pangolins have been found in Sabah's protected and non-protected areas (Wearn et al., 2017; Chong et al., 2020; Sompud et al., 2023). Their presence has also been reported in some of the larger islands surrounding Sabah (Sompud et al., 2019). In general, Sunda pangolins can inhabit a wide variety of environments, including primary and secondary forests, evergreen and hill forests, peat swamp forests (Payne et al., 1985; Ketol et al., 2009; Azhar et al., 2013), wetland and riverine ecosystems (Willcox et al., 2017), grasslands, monoculture plantations (such as oil palm and rubber) (Chong et al., 2020), as well as gardens in urban areas (Lim and Ng, 2008). In Sabah, they have been observed in diverse habitats ranging from lowland areas to higher elevations, such as Mount Kinabalu at an altitude of up to 1,700 m asl (Payne and Francis, 2007), although the precise altitude limits are unknown. Occurrences in artificial landscapes, like oil palm plantations, indicate the pangolin adaptability to modified habitats; however, the species’ ability to thrive and reproduce in these environments over the long term is not well understood (Chong et al., 2020).

Research is made more challenging by the fact that the Sunda pangolin is a species that is not only rare but also elusive and primarily nocturnal. Conservation efforts aimed at pangolins have been impeded by inadequate information on their ecology and population, posing a significant challenge to their conservation (Chong et al., 2020). No population estimates are available for Sunda pangolins in Southeast Asia in general, except Singapore, which is home to approximately 1,046 individuals (Nash et al., 2020). Monitoring the pangolin population is made more difficult by the apparent lack of standard survey techniques (Kwaja et al., 2019). Researchers have attempted to study Sunda pangolins using sign surveys, primarily searching for footprints, claw marks, and night surveys to search for pangolins (Chong et al., 2020). In addition, researchers also have used techniques such as counting burrows, camera trapping, detection dogs, interviews with local people, global positioning system (GPS) tracking, and radio telemetry, with each of these methods producing varying degrees of success (Willcox et al., 2019; Chong et al., 2020). GPS tracking and radio telemetry help researchers monitor individual movements, home ranges, and habitat use, providing valuable data on pangolin behaviour and population dynamics (Cagnacci et al., 2010; Perras and Nebel, 2012). Nevertheless, the distribution of Sunda pangolins in Sabah currently remains poorly understood. To address these challenges of monitoring pangolins and the paucity of data, strong collaboration among community researchers allowed the maximisation of data for the compilation of Sabah's pangolin presence records. This study was made possible through collaborations among community researchers, resulting in the most comprehensive occurrence data for Sunda pangolins in Sabah.

The lack of data regarding the distribution of the Sunda pangolin can be addressed by identifying and predicting the species' suitable habitats using species distribution model (SDM) approaches. This allows the important habitats and environmental variables data to be highlighted for further study and conservation efforts (Elith and Leathwick, 2009). SDMs are predictive tools that establish associations between observed occurrences and environmental predictors using statistical models or theoretically derived response curves (Elith and Leathwick, 2009; Guisan and Thuiller, 2005). SDMs are broadly divided into two groups: correlative and process-based models, which are derived from various statistical approaches such as Generalised Linear Models (GLMs), multivariate methods, Bayesian models, locally weighted regression and environmental envelope models (Elith and Leathwick, 2009). Correlative models use species occurrence data and environmental layers of the study area to create the probability of occurrence maps. In contrast, process-based models use species' functional characteristics and physiological thresholds for model fitting (Kearney and Porter, 2009). Both models come with their own features and drawbacks; therefore, it is essential to choose a model appropriate for the data type (**Table 2.1**).

Table 2.1: Comparison of correlative and process-based species distribution models (SDMs): advantages and disadvantages.

Model	**Advantages**	**Disadvantages**
Correlative models (Sillero, 2011; Elith and Leathwick, 2009; Srivastava et al., 2019; Pagel et al., 2020)	1. Easier to implement with available occurrence data. 2. Effective for large-scale predictions. 3. Requires fewer assumptions about species' biology.	1. May not accurately capture the biological processes driving species distributions. 2. Limited by the quality and extent of occurrence data. 3. Potentially less accurate for predicting future distributions under changing environmental conditions.
Process-based models (Kearney and Porter, 2009; Elith et al., 2010; Shabani et al., 2016, Srivastava et al, 2019)	1. Incorporates detailed biological and ecological information. 2. Better suited for predicting species distribution under new environmental conditions. 3. Can provide insights into the mechanisms driving species distributions.	1. Requires detailed and specific biological data, which may be difficult to obtain. 2. More complex and computationally intensive. 3. May be less accurate if the physiological thresholds and functional traits are not well understood.

To ensure the quality and effectiveness of species distribution model (SDM) predictions, it is important to align the study's objective, methodological design, and the type of species' niche and geographic distribution estimates with the specific research question (Tourinho and Vale, 2021). Selecting the suitable SDM approach involves considering several factors. If detailed biological and ecological data are available, process-based models may provide more accurate predictions. Conversely, if only occurrence data are available, correlative models are more practical (Elith and Leathwick, 2009; Kearney and Porter, 2009). For understanding the mechanisms driving species distributions or predicting future distributions, process-based models are preferred due to their detailed biological inputs. For example, the Niche Mapper model simulates species' energy and water balances based on physiological traits and microclimate data to predict where the species can survive under current or future climate scenarios (Kearney and Porter, 2009).

For mapping current distributions over large areas, correlative models are often sufficient (Shabani et al., 2016; Srivastava et al., 2019). For example, the CLIMEX model uses species' growth and stress responses to climate variables to project potential distribution shifts under different environmental conditions (Sutherst et al., 2007). However, process-based models require more computational power and expertise, which can be a limiting factor (Elith et al., 2010). Additionally, the species' ecological traits and the study area's environmental variability must be considered to determine the most appropriate model type (Sillero, 2011; Pagel et al., 2020).

Maximum Entropy (MaxEnt) is one of the most commonly used correlative SDMs (Merow et al., 2003). MaxEnt was used in the present study because it only requires presence-only data (Elith et al., 2010), making it suitable to address the lack of data on species absence (Engler et al., 2004). MaxEnt requires species occurrence points and uses both continuous and categorical data as predictors, allowing for flexible representation of environmental variables and their interactions. The model is relatively insensitive to collinearity between environmental variables, meaning it can handle highly correlated predictor variables effectively (Phillips et al., 2006; Merow et al., 2013; Phillips et al., 2017). Previous studies have utilised MaxEnt to predict global pangolin distribution (Xian et al., 2022) and the distribution of individual species, such as Chinese and Indian pangolins (Suwal et al., 2020; Waseem et al., 2020; Sharma et al., 2020). The effectiveness of these models is determined through performance metrics, specifically using the area under the curve (AUC). A high AUC value (close to 1) indicates good model performance, as it measures the model's ability to distinguish between presence and absence points (Fielding and Bell, 1997; Swets, 1988; Manel et al., 2001). These previous studies reported high AUC values for their MaxEnt models, demonstrating strong predictive accuracy.

The main objective of this study is to enhance the conservation efforts for Sunda pangolins in Sabah by identifying their habitat suitability, understanding the environmental variables influencing their occurrence, and recommending effective conservation actions. This research aims to provide a scientific basis for informed decision-making and targeted conservation strategies to ensure the long-term survival of Sunda pangolins in their natural habitats. The present study aimed to address the following research questions and hypotheses:

1. Research question: What is the habitat suitability of Sunda pangolins within Sabah's natural forests?
   Hypothesis: Sunda pangolins are more likely to inhabit areas with specific environmental conditions that provide optimal habitat suitability.

2. Research question: Which environmental variables are associated with pangolin occurrence in Sabah?
   Hypothesis: The occurrence of Sunda pangolins is influenced by certain environmental variables that are anticipated to limit their distribution.

3. Research question: What actions can be recommended for the effective conservation of Sunda pangolins in Sabah?
   Hypothesis: Implementing targeted conservation actions based on habitat suitability will improve the protection and management of Sunda pangolin populations.

2.2 Methods

2.2.1 Data collection and processing

This study is part of a wider assessment framework of High Conservation Value (HCV) areas within 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 collected from a network of 11 different researchers and organisations, with data covering various regions within Sabah and spanning from the years 2000 to 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, records for the Sunda pangolin were extracted, resulting in the most comprehensive compilation of occurrence data for this species in Sabah. The format of the geographical coordinates was standardised, and any duplicated records (i.e., multiple records of the same species at the same location on the same date) were removed. The location dataset was then visualised, and a filter was applied to ensure that only one data point was contained within a 1 km circular buffer, to minimise the effect of spatial autocorrelation (following Fourcade et al., 2014). Spatial autocorrelation can exaggerate the significance of environmental variables due to clustered data points. To address this, a 1 km buffer, though slightly larger than the typical Sunda pangolin home range (69-116 ha), is widely used in ecological studies to reduce spatial bias and ensure data independence. This buffer size helps account for the spatial scale at which pangolins interact with their environment, ensuring each data point represents a distinct observation. The approach balances computational efficiency and detailed analysis, enhancing the robustness of habitat suitability models by minimizing spatial autocorrelation (Betts et al., 2006; Song et al., 2023). The final set of records used for this study comprised 201 points collected from 2007 to 2017, with most of the data (62%) recorded from 2012 to 2016 (**Table 2.2**).

Presence data were principally collected within forest habitats (98%), including Sabah's Totally Protected Areas (TPAs) and Production Forest Reserves (PFRs) (**Fig. 2.1a**). Although this dataset limits the distribution assessment to forested environments, it is extremely useful for the State's HCV assessment, which aims to identify important forest no-go areas for new oil palm development (Brown et al., 2013). From 2016 to 2018, non-invasive camera trap surveys were conducted in the Lower Kinabatangan Wildlife Sanctuary (LKWS) in Sabah as part of this study. Despite these efforts, no Sunda pangolins were captured by the camera traps at LKWS. This attempt was in addition to the secondary data collected from various researchers, which were also included in the study.

As part of a collaborative effort within a wider assessment framework of High Conservation Value (HCV) areas in the Sabah state, which has been published (Panjang et al. 2024), the decision to not show precise locations of presence points stems from a consensus among all collaborators, who are data providers due to the extreme vulnerability of the Sunda pangolin to poaching in Sabah (FMT, 2019; The Star, 2022). Reports indicate that poachers have documented ease of access to Sabah's Totally Protected Areas (TPAs) and Permanent Forest Reserves (PFRs), prompting calls for a cautious approach in presenting data to safeguard pangolins while still contributing valuable scientific insights (TRAFFIC, 2011; Bernama, 2020).

To align with these recommendations and to prioritise the protection of the species, the location data were generalised and presented in two versions of maps (**Fig. 2.1a and Fig. 2.1b**). This step not only prioritises the protection of the critically endangered Sunda pangolin but also aligns with conservation literature and best practices to mitigate the risk of poaching (Lindenmayer and Scheele, 2017; Chapman, 2020). Additionally, this decision emphasises the importance of balancing scientific detail with conservation ethics. Given that my thesis may be shared publicly in the future, this precautionary measure is essential to ensure the continued protection of the species. The publication (Panjang et al., 2024) also adopted a similar approach.

Table 2.2: Presence records of Sunda pangolins used within for the distribution model in Sabah from 2007 to 2017, along with the respective surveyed areas associated methods of detection.

Surveyed areas	**Years**	**Sampling methods**	**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 WS	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
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
Sungai Pinangah FR	2015	Camera trapping	1
Sungai Talibu FR	2015	Camera trapping	3
Tabin WR	2009-2011	Camera trapping	6
Tangkulap FR	2009-2015	Camera trapping, ground	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 points			201

FR = Forest Reserve, NP = National Park, CA = Conservation Area, Mt. = Mountain, WR=Wildlife Reserve

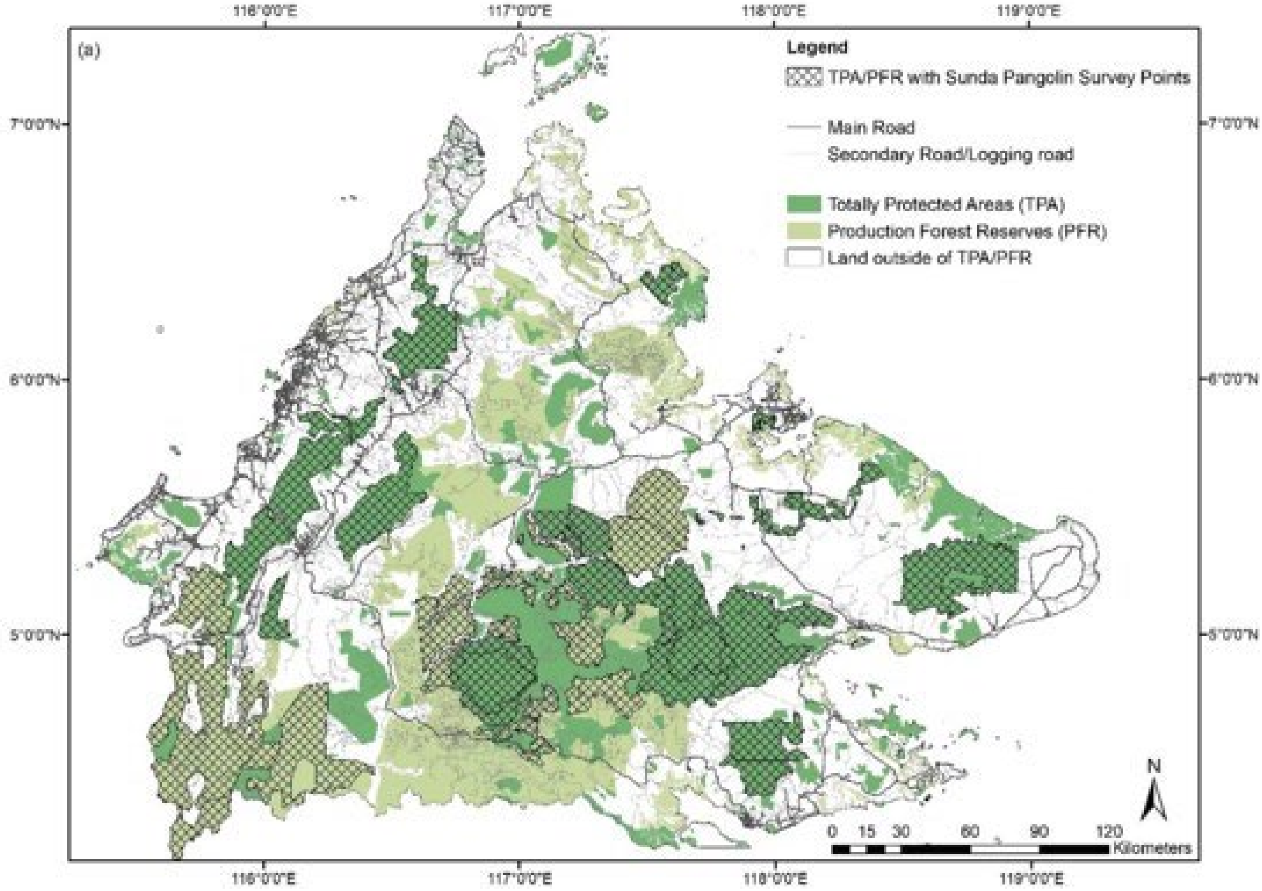

Fig. 2.1a: Map showing Sabah's Totally Protected Areas (TPAs) in dark green and Production Forest Reserves (PFRs) in light green, with areas of black crosshatch showing TPAs/PFRs that have Sunda pangolin presence points.

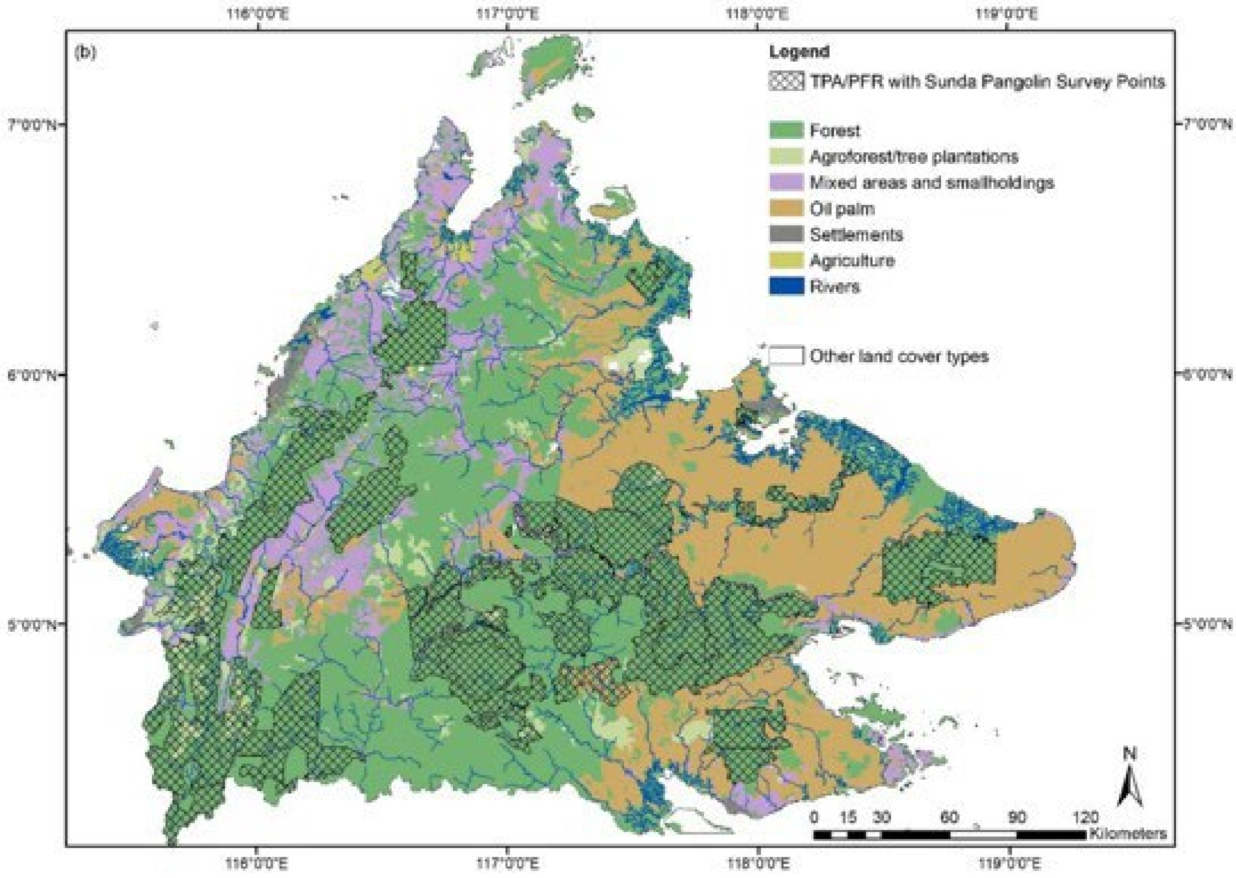

Fig. 2.1b: Map showing land use and land cover for 2014/2015, with black crosshatch showing TPAs/PFRs with Sunda pangolin presence points.

Bias grid

To minimise sampling bias, a “bias grid” was created to represent survey effort. A bias grid is a tool used to represent and adjust for differences in survey effort across a study area, ensuring more accurate and unbiased results in the subsequent stages of analysis. 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, the study determined that appropriate survey methods included those that could, theoretically detect the species based on their known behaviour and habitat use. These methods included camera traps (representing the majority of these data), ground surveys and opportunistic sightings. Camera traps are effective for detecting nocturnal and elusive species like the Sunda pangolin, ground surveys involve systematic searches of habitats known to be used by pangolins, and opportunistic sightings provide incidental records that contribute to understanding their distribution.

All species data from these survey methods were combined into a shapefile and converted to a raster grid (at 91 m resolution). Grid cells that contain at least one species presence were assigned a value of 1, representing areas that were directly surveyed and where species detections occurred. Cells within the survey extent but without any recorded species presence were assigned a value of 0.1. This value indicates that the cell was surveyed but yielded no detections, ensuring the cell still contributes minimally to bias correction and avoids misinterpretation as completely missing data. Finally, cells located outside the surveyed extent (i.e. areas with no survey coverage at all) were assigned a value of 0.0 to represent unsurveyed areas. This distinction between 1, 0.1 and 0.0 is critical for accurately reflecting survey effort and avoiding biases in subsequent analyses (method adapted from Lim et al., 2019).

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). The choice of a three-by-three cell neighbourhood at 91 m resolution was based on the need to balance spatial detail with computational efficiency. This scale was chosen because it adequately captures the spatial variability of survey effort without overly smoothing the data, which is essential for accurately representing survey effort across the study area (Fourcade et al., 2014; Boria et al., 2014). This bias grid helps account for differences in survey effort across the study area and is used to adjust subsequent analyses to improve accuracy (Phillips et al., 2009; Syfert 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.

Spatial predictor variables

Sixteen predictor variables were developed to model habitat suitability. 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 topographical data (**Table 2.3**). The land use and land cover variables were generated through on-screen digitising of high-resolution SPOT 5 satellite imagery (1.5 m, years

2014-2015) in ArcGIS 10.6.1. Forest quality layers (heterogeneity and majority) were derived from data provided by von Hase and Parham (2018). Soil association data (51 classes) were obtained from the Sabah Department of Agriculture’s digitised soil maps (Acres, 1975). Hydrology layers (distance to major rivers) and road data (main and secondary/logging roads) were digitised from SPOT 5 imagery and supplemented with vector data from the Sabah Lands and Surveys Department. Settlement data were initially obtained from the Sabah Lands and Surveys Department online platform (http://www.jtuwma.net/) and verified against SPOT 5 imagery. Climatic variables were sourced from the WorldClim v1.4 database (Hijmans et al., 2005) and only variables with Pearson correlation coefficients below 0.7 were retained to avoid multicollinearity. Topographical variables (elevation and slope) were generated from a 10 m contour vector dataset provided by the Sabah Department of Survey and Mapping.

The spatial data framework was prepared at a 91 m grid resolution for the entire extent of Sabah to balance the need for detailed spatial information with the computational efficiency required for large-scale analyses. This resolution is fine enough to capture relevant environmental variations, and habitat features important for modelling species distributions while still being manageable for processing and analysis in MaxEnt.

Table 2.3: The 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 (m)	Continuous
	Distance to agroforestry (m)	Continuous
	Distance to mixed areas and	Continuous
	Distance to oil palm plantations (m)	Continuous
	Forest heterogeneity (500 m radius)	Categorical
	Forest majority (500 m radius)	Categorical
Soil	Soil association (51 classes)	Categorical
Anthropogenic	Distance to main roads (m)	Continuous
	Road density	Continuous
	Settlement kernel density	Continuous
Hydrology	Distance to main rivers (m)	Continuous
Climate	Annual temperature range (Bio 7)	Continuous
	Precipitation seasonality (Bio 15)	Continuous
	Precipitation during driest quarter (Bio	Continuous
Topographical	Elevation (m)	Continuous
	Slope °	Continuous

Table 2.4: The comprehensive list of bioclimatic data layers, along with their respective explanations.

Bioclimatic	Definition
Bio 1	Annual Mean Temperature
Bio 2	Mean Diurnal Range (Mean of monthly (max temp - min
Bio 3	Isothermality (Bio 2/Bio 7) (x100)
Bio 4	Temperature Seasonality (standard deviation x 100)
Bio 5	Max Temperature of Warmest Month
Bio 6	Min Temperature of Coldest Month
Bio 7	Temperature Annual Range (Bio 5 - Bio 6)
Bio 8	Mean Temperature of Wettest Quarter
Bio 9	Mean Temperature of Driest Quarter
Bio 10	Mean Temperature of Warmest Quarter
Bio 11	Mean Temperature of Coldest Quarter
Bio 12	Annual Precipitation
Bio 13	Precipitation of Wettest Month
Bio 14	Precipitation of Driest Month
Bio 15	Precipitation Seasonality (Coefficient of Variation)
Bio 16	Precipitation of Wettest Quarter
Bio 17	Precipitation of Driest Quarter
Bio 18	Precipitation of Warmest Quarter
Bio 19	Precipitation of Coldest Quarter

The prepared spatial data were then converted into .ascii files for use in MaxEnt (https://biodiversityinformatics.amnh.org/open_source/maxent/).

These predictor variables were chosen based on an understanding of pangolin ecology, including habitat use and behaviour: distance to forest, agroforestry, mixed areas and smallholdings, and oil palm were included because pangolins rely on forested habitats for foraging and shelter, and the distance to different land cover types can influence their presence due to habitat fragmentation and resource availability. Forest heterogeneity and majority variables represent the diversity and dominance of forest types within a specified radius, capturing habitat quality and complexity, which are important for pangolin survival. Soil association was selected because soil characteristics can affect the distribution of ants and termites, the primary diet of pangolins, making it important for modelling habitat suitability. Distance to main roads, road density, and settlement kernel density were included to account for the impact of human activities on pangolin habitats, as roads and settlements can lead to habitat loss, fragmentation, and increased poaching risk.

Distance to main rivers was considered because proximity to water sources is essential for pangolins, influencing the availability of prey and suitable habitat conditions. Annual temperature range, precipitation seasonality, and precipitation during the driest quarter were chosen as climatic variables because temperature and precipitation patterns affect habitat conditions, vegetation, and prey availability for pangolins. Finally, elevation and slope degrees were included as topographical variables because they influence habitat accessibility and the microclimate conditions within pangolin habitats, affecting their distribution and movement patterns. By incorporating these variables, the model aims to capture the complex interactions between pangolins and their environment.

For the land use and land cover variables, the spatial data were generated from on-screen digitising in ArcGIS 10.6.1 using high resolution (of 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 2007-2017) and because most data were recorded between 2012-2016. Further, data collection being primarily done within TPAs and PFRs, the risk of forest conversion was minimal, and at least 98% of the pangolin data was still located within the

2014/2015 mapped forest extent. Land use and land cover categories mapped included forests (of various types and qualities), oil palm plantations (both commercial estates and smallholdings), agroforest areas (i.e., monocrops of industrial tree plantations such as acacia or eucalyptus species), 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. 2.1b**).

The major rivers of Sabah were also digitised (i.e., those identifiable in the SPOT 5 satellite imagery). In addition, Sabah's public road network was digitised, including roads to settlements and roads to forested areas. The roads were divided into two categories: (1) main public roads (asphalt) and (2) various secondary roads, including non-asphalt public gravel/earth roads and certain roads within protected areas and forest reserves (e.g., logging roads). Although both main and secondary roads were digitised (**Fig. 2.1a**), the spatial variables included only the distance to main roads. This decision was made primarily due to the higher reliability and availability of data for main roads, which are significant contributors to habitat fragmentation and accessibility. However, the study acknowledges that secondary roads, especially those leading into forests, can facilitate poaching by providing easy access. While secondary roads are indeed important, the lack of consistent and comprehensive data on their conditions and usage limited their inclusion in the final model. Future work should aim to integrate detailed secondary road data to better understand their impact on pangolin poaching and habitat use.

Settlement data on villages, towns, and oil palm plantation settlements were initially derived from the Sabah Lands and Surveys Department online platform (http://www.jtuwma.net/). This settlement data was 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, a "distance to" layer was created for each using the Euclidian distance tool in ArGIS 10.6.1. This process generated a continuous raster layer representing the distance, in meters, from each point to the closest feature. For features such as roads and rivers, the "distance to" value represents the nearest distance from any given point in the study area to the closest occurrence of these features. Additionally, for the entire road dataset (main and secondary/logging roads) and the settlements dataset, a road density layer was generated 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), and initially categorised into four simplified categories: (1) open areas within forest, (2) degraded forest, (3) low to moderate quality forest, and (4) moderate to high quality forest. These categories were further restricted to the extent of the generic forest layer. Areas outside the forest were classified as 'areas outside of forest.' To capture forest condition heterogeneity within the study area, focal statistics in ArcGIS 10.6.1 were applied. Specifically, the focal statistic ‘variety’ function was used to create (1) a forest heterogeneity layer showing the number of forest classes detected within a 500 m radius of each grid cell, and (2) a majority forest condition layer indicating the dominant forest condition type within a 500 m radius. The majority forest condition layer was refined into five categories to provide greater detail: 1 = low, 2 = moderate, 3 = moderate-high, 4 = high, and 5 = very high.

Additionally, a digitised soil map generated by the State Department of Agriculture (Acres, 1975), containing 51 soil associations for Sabah, was used, as soil is a strong influential factor in determining forest types. The nature of the soil has a significant impact on the types of forests that can grow there, but it also affects other ecological factors, such as the distribution of ants and termites, which are important for pangolin diets. While there may be some correlation between soil type and forest majority, these variables were included separately to capture the different ecological processes they represent. Soil association provides information on soil conditions that influence not only forest types but also the availability of food resources for pangolins. Forest majority, on the other hand, captures the dominant forest type within a specified radius, reflecting habitat quality and structural complexity, which are critical for pangolin shelter and foraging behaviour.

To complement these variables, the WorldClim version 1.4 dataset (http://www.worldclimate.org) was used to retrieve 19 bioclimatic data layers (between 1950 and 2000) at a resolution of 30 arc seconds (Hijmans et al., 2005). Although 19 climatic variables were initially retrieved to provide a comprehensive overview of the climatic conditions, only three key climatic variables were ultimately used in the final model: annual temperature range, precipitation seasonality, and precipitation during the driest quarter. This decision was made to avoid issues with multicollinearity among the 19 layers, which could result in overfitting of the model (Pearson et al., 2007; Raes et al., 2009). The independence of the 19 bioclimatic variables was assessed using correlation analysis to identify and address multicollinearity. Pearson's correlation coefficients were calculated between pairs of variables, and those with a coefficient ($|r|$) greater than 0.7 were considered highly correlated. A correlation threshold of $|r| > 0.7$ was used, following common practice in ecological modelling, as it balances the removal of strongly collinear predictors with the retention of sufficient environmental variability for ecological interpretation (Guisan and Thuiller, 2005; Dormann et al., 2013). Highly correlated variables were excluded to ensure that only independent variables were used in the final models, preventing multicollinearity, and improving model performance and interpretability. The selected variables were chosen for their anticipated impact on the primary food resources of pangolins (Lim, 2007). The three selected 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 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 important in understanding the pangolin's habitat preferences, linking their survival and reproductive success to the climatic conditions of their environment.

They were reclassified from a resolution of 30 arc seconds (approximately 1 km) to a resolution of 91 m on a grid. Additionally, to generate elevation and slope topographical variables, a contour vector file (at 10 m intervals) was used to generate a Digital Elevation Model using ArcGIS 10.6.1.

2.2.2 Data analysis

<u>Habitat suitability analysis</u>

MaxEnt software version 3.4.1 was used to model the habitat suitability of the Sunda pangolin (Phillips and Dudik, 2008; Elith et al., 2006). MaxEnt software is a robust tool for niche modelling, especially when species absence records are unavailable (Elith et al., 2011). The specifications used in MaxEnt included logistic output, 500 iterations, 10,000 background points, a regularisation multiplier of 1.0, and the “auto-features”. These settings were chosen to balance model accuracy and complexity. Logistic output provides easy-to-interpret probability estimates. The 500 iterations ensure stable results. Using 10,000 background points helps compare presence points accurately. The regularisation multiplier of 1.0 prevents overfitting, and “auto-features” allows MaxEnt to choose the best features for the data.

The Jackknife test was also used to measure the relative contribution of each of the 16 spatial variables to the overall model's performance. The area under the receiver-operator curve (AUC) was used to evaluate the model. The bioclimatic variables were not included in the Jackknife test because the focus was on understanding the impact of land use, soil, and anthropogenic factors on habitat suitability. The AUC score indicates the model's ability to discriminate between presence and absence points. The AUC score ranges from 0 to 1, with a score less than 0.5 indicating poor model performance, a score between 0.5 and 0.7 indicating poor model performance but better than chance, a score between 0.7 and 0.9 indicating moderately good model performance, and a score greater than 0.9 indicating excellent model performance (Manel et al., 2001).

Post-processing, review, and revision

The output of MaxEnt is a probability score, represented as a grid across geographical space. This was then transformed into a categorical map using the average values of the Minimum Training Presence (MTP) and Maximum Training Sensitivity and Specificity (MTSS), which define areas deemed moderately or highly suitable. The MTP threshold predicts a more liberal extent of suitable areas with no omission of training data, whereas the MTSS threshold estimates a more conservative extent (Liu et al., 2005, 2013). To create the final model, the MTP and MTSS thresholds were used to define moderately and highly suitable areas. The output was then clipped to a forest extent to determine the distribution within naturally forested areas. This approach retains the primary research focus on pangolin distribution within natural forest environments, as most of the pangolin presence data (98%) was collected in these environments. Therefore, there is limited data to meaningfully model distribution in other land use types.

Next, the categorical habitat suitability layers were overlaid in ArcGIS 10.6.1 with the boundaries of Sabah's TPA network, Production Forest Reserves and cadastral datasets. This spatial overlay allowed us to calculate the surface area (km²) and percentage of suitable habitat that overlapped with each land-use category, providing a quantitative assessment of protection coverage.

An expert review process was carried out in a workshop (on the 13th of December 2018 in Kota Kinabalu, Sabah) and via email for more widespread participation from the contributing researchers. These experts were data providers who, although not necessarily specialists in pangolins, were very familiar with their own data and had extensive experience in their study areas. This helped to further refine the map of the species distribution. The purpose of this review was to ensure the accuracy and completeness of the species distribution map by incorporating local knowledge and field observations that might not have been captured by the modelling process alone. This helped to further refine the map of the species distribution.

During this process phase, experts reviewed the preliminary distribution map and provided additional feedback in written format. They suggested areas where the species was not known to be found and more generally, identified additional areas where the species had been observed, although these observations were not in a form that could be incorporated into a re-run of the model. This collaborative approach allowed for the integration of diverse datasets and expert insights, improving the reliability of the final distribution map. The map was then revised qualitatively based on the input from the experts to reflect these observations and corrections. The results of the expert review process were important in validating the modelled distribution and identifying potential inconsistency. This step ensured that the final distribution map was not only based on modelled predictions but also grounded in empirical observations from the field.

Data on Sabah's Totally Protected Area (TPA) network for 2017 included the Wildlife Sanctuary, Class I Protection Forest Reserve, Class VI Virgin Jungle Reserve, Class VII Wildlife Reserve, Parks, and Wildlife Conservation Area were utilised to estimate the surface area of Sunda pangolin habitat that overlaps with legally protected land categories. The purpose of this was to understand better the degree to which the modelled potentially suitable habitat of the Sunda pangolin is protected. In addition, data on Production Forest Reserves, such as Class II Commercial, Class III Domestic, Class IV Amenity, and Class V Mangrove Forest Reserves, which allow for various land uses, were also utilised. Additionally, cadastral data were obtained from the Lands and Surveys Department (acquired from www.jtuwma.net). These data were used to identify lands alienated under various granted land titles, including provisional or country lease titles, field register or native titles, and townlands. State lands included lands outside of Protection and Production Forests and alienated lands. In Sabah, state lands typically encompass areas designated for various uses such as agriculture, settlement, infrastructure development, and other public purposes. These areas are managed by the state government and may also include undeveloped lands and lands that are subject to future development planning (Sabah Land Ordinance 1930 (Cap 68)). Malaysia's National Land Code (1965) defined alienated land as land purchased from traditional landowners by the government for either using the land for its purposes or selling it to private developers for private development requiring a mortgage or other guarantees.

Accessibility

To better understand the potential level of poaching, hunting, and the capture of animals for the live wildlife trade within pangolin habitats and the associated threats, an accessibility layer was generated using a time-distance-surface approach, adapted from a cost-distance modelling method (Weiss et al., 2018) and informed by empirical studies on hunting pressure and road impacts in Southeast Asia (Clements et al., 2014). This method allows for the modelling of human access to these areas and the identification of potential risks to wildlife. This approach accounts for travel time, distance, and slope to calculate accessibility from settlements. It integrates multiple modes of travel, including roads of different types, river travel and walking, and categorises them based on specific criteria such as speed and slope.

A GIS layer representing the accessibility of habitat to humans was generated using a time-distance-surface technique to understand better the potential level of poaching, hunting, and capture of animals for the live wildlife trade. In the first step of this process, data on roads were collected. This included data on public roads that were either asphalt or secondary gravel/earth roads and data on non-public roads located within protected areas and production forest reserves. Roads were categorised as either being relatively flat (with a slope between 0° and 7°), having moderate slopes (with a slope between 8° and 17°), or having steep areas (with a slope greater than 18°). To account for the time that it takes to cross a section of road based on road type and slope, the following values were assigned: main/asphalt roads in flat areas can reach speeds of 90km/hr, moderate slope areas can reach speeds of 70km/hr, and steep areas can reach speeds of 50km/hr. Flat areas were assigned 60km/hr, moderate slope areas 40km/hr, and steep areas 20km/hr for secondary gravel/earth roads. As people can also access areas by the river, the shapefiles for the key rivers were created, and a boat travel speed of 15 km/h was assigned. Key rivers were first digitized from SPOT 5 imagery and then cross-checked with the Sabah Lands and Surveys Department (www.jtuwma.net), which provided attributes on size and navigability necessary to identify navigable rivers, which are crucial for modelling accessibility to poaching and wildlife trade activities.

In areas without roads or rivers, walking speeds were assigned as follows: 3 km/h for flat areas (with a slope between 0° and 7°), 2 km/h for moderately steep areas (with a slope between 8° and 17°), and 1 km/h for steep areas (with a slope greater than 18°). These times were estimates, combined with settlement data (a point shapefile) to model a raster time-distance surface for Sabah at 91 m resolution. This surface estimates how accessible each raster cell is from each settlement, considering both time and the ruggedness of the landscapes. The model gave continuous values as its output. To facilitate viewing and analysis, the areas were divided into three natural breaks (or Jenks) and then extracted for areas containing Sunda pangolin habitat within natural forested areas (following the method of Jenks, 1967). This categorised data was then used to assess the risk of poaching and human intrusion in different parts of the habitat, providing insights into areas that require more focused conservation efforts and interventions.

These accessibility layers were not included in the SDM because they represent derived measures of human access and poaching risk, whereas the SDM was focused on predicting pangolin habitat suitability based on environmental, climatic and direct land-use factors. However, the accessibility analysis offers a critical perspective on threats to pangolins by highlighting areas at higher risk of poaching and human intrusion. This combined approach provides a better understanding of both habitat suitability and the impact of human activities. Integrating these analyses will be considered in future work to improve the understanding of pangolin conservation needs.

2.3 Results

2.3.1 Predictive performance of MaxEnt model

After removing duplicates and filtering, the MaxEnt model utilised a total of 201 presence location points (**Table 2.2**). Model performance was highly discriminative, with an average test AUC score for the 10 replicate runs being 0.903 (representing excellent model performance), with a standard deviation of 0.026. Based on this result, this model has a high ability to correctly differentiate between areas where the species is present and areas where it is absent.

2.3.2 Identifying key environmental variables influencing the habitat suitability of the Sunda pangolin

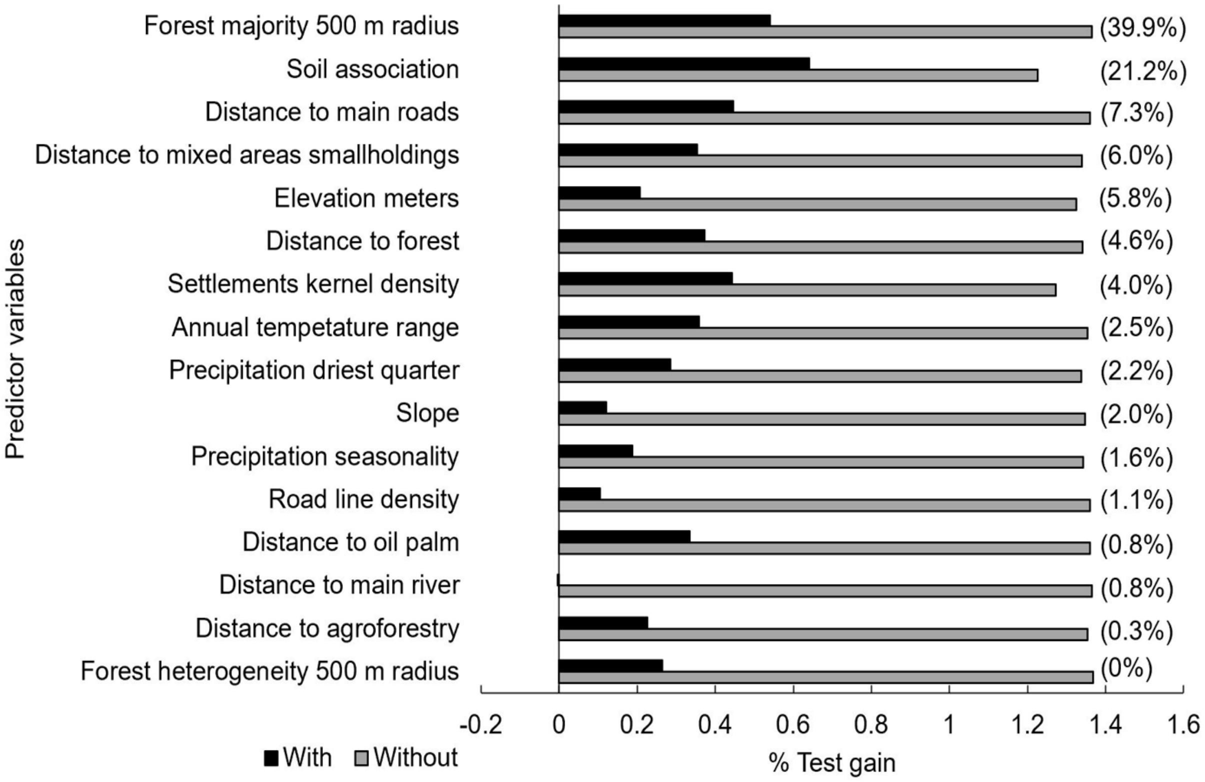

Fig. 2.2: A Jackknife test of the importance of predictor variables in the habitat suitability model of the Sunda pangolin. An estimate of the relative contribution of each variable to the overall model is shown in parentheses (%), with variables ranked in descending order of importance. Grey bars represent the performance of the overall model (or % test gain) without each variable; and black bars indicate the contribution of each variable in isolation.

A Jackknife test (**Fig 2.2**) illustrates the relative contribution of each predictor variable to the overall model, with percentages indicating their importance in parentheses. The variables are ranked in descending order of importance. The grey bars (without) represent the performance of the model (% test gain) when each specific variable is excluded. In this model, the grey bars appear relatively similar, indicating that correlated variables can compensate when one is removed. If excluding a variable significantly reduces the model's performance, it indicates that the variable is important for the model. Furthermore, if excluding a variable has little to no impact, the variable may be less important. The black bars (with) indicate the contribution of each variable in isolation. This means they show how much each variable alone contributes to the model's performance. A higher value suggests that the variable on its own has a strong predictive power for the habitat suitability of the Sunda pangolin. For example, forest majority within a 500 m radius has the highest importance with a contribution of 39.9%. The black bar shows a high gain when this variable is used alone, and the grey bar indicates a considerable drop in model performance without this variable. Soil association is the second most important variable with a 21.2% contribution. The grey bar shows little change when soil association is removed, likely due to redundancy with other predictors, while the black bar highlights its strong individual contribution.

The top six environmental variables that contributed to the MaxEnt model are shown in **Fig. 2.3**. 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 the forest (4.6%).

Specifically, the Sunda pangolin's natural habitat was associated with areas that had moderate to high-quality forests, with forest majority class 3 having the greatest influence (**Fig. 2.3a**). 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. 2.3b**). 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. 2.3c**), and mixed areas with small holdings (**Fig. 2.3d**). Habitat suitability decreased in areas over 200 asl (**Fig. 2.3e**), and with distance from forest (**Fig. 2.3f**). Trimming the data reduced spatial bias but did not change which predictors were most important, instead clarifying their relative effects, particularly for distance to roads and forest.

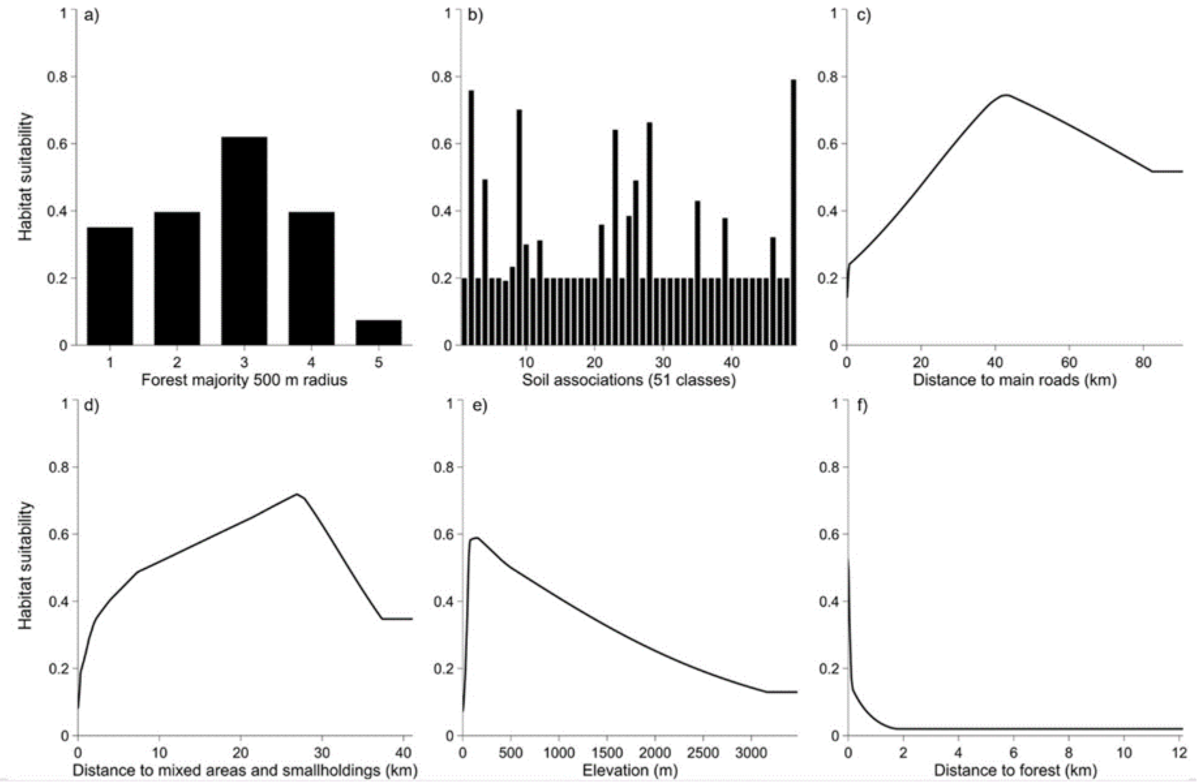

Fig. 2.3: Univariate response curves of the top 6 most influential predictor variables, in descending order, showing: **(a)** forest majority 500 m radius (contributing 39.9% of the variance explained by the model) with moderate-high quality forest (class 3) being the most influential; **(b)** soil (21.2%) 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 from 10 to 3,000 m above sea level; and, **(f)** distance to forest (4.6%) with habitat suitability decreasing dramatically from the forest edge to 2 km outside of forested areas.

2.2.3 Projecting MaxEnt habitat suitability model across Sabah

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 km² were highly suitable areas (**Table 2.5; Fig. 2.4**). Of this total suitable habitat, 43% (approximately 16,998 km²) are within TPAs, and 38% (approximately 15,021 km²) are in PFRs (**Fig. 2.4**). This leaves 19% (approximately 7,511 km²) of suitable habitat outside these protected areas. Within the non-protected areas, there are approximately 5,541 km² of moderately suitable habitat and approximately 1,969 km² of highly suitable habitat. These areas are predominantly within mosaic rural landscapes and agroforest lands, with smaller portions in alienated state lands. The results mean, while a significant portion of the suitable habitat is protected, there remains a considerable area persisting in mixed-use landscapes that may be vulnerable to conversion and poaching pressure.

Of the Sunda pangolin's potential distribution within natural forest areas, 43% was within Totally Protected Areas, 38% in Production Forest Reserves, 14% was earmarked for industrial tree plantations/mosaic areas, 14% was in areas with unknown land use within the Production Forest Reserves and 10% was within areas of Naturally Managed Forests. Alienated lands, in total, harboured 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% were within unknown land title types. The remaining 12% of the Sunda pangolin distribution is estimated to be on State land (**Table 2.5; Fig. 2.5a**).

Table 2.5: 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 Status		
Totally Protected Areas (TPAs) - 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
Industrial tree plantations/mosaic areas	(2,103)	(14)
Unknown land use	(2,103)	(14)
Naturally Managed Forests	(1,502)	(10)
Outside Protected Area - State Land	4,744	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	2,767	7
Total	**39,530**	**100**

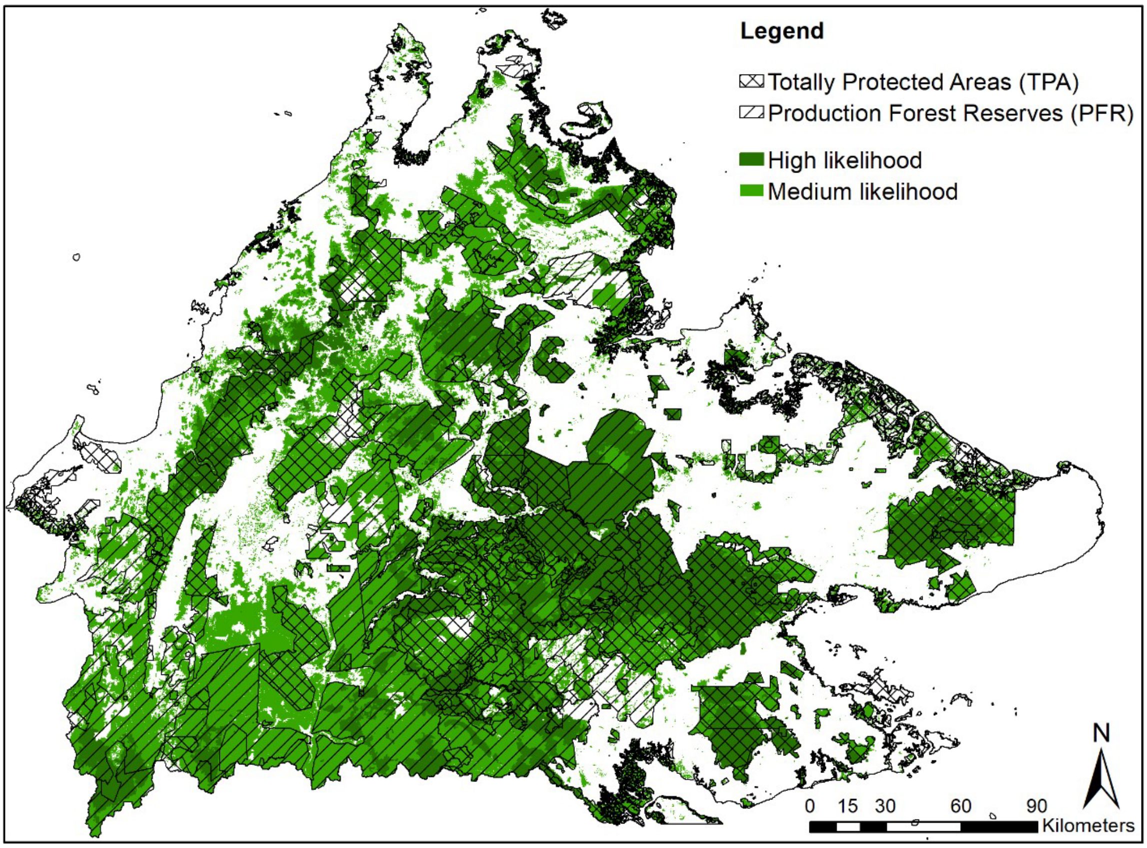

Fig. 2.4: Map showing areas of high and medium likelihood of potential distribution and suitable habitat for the Sunda pangolin within natural forests (as of 2014/2015), overlaid with Totally Protected Areas (crosshatch) and Production Forest Reserves (diagonal line).

2.3.3 Projecting accessibility model across Sunda pangolin habitat

Of the estimated 39,530 km² of habitats suitable for Sunda pangolins, it was found that 53% was categorised as very accessible, 38% was within moderately accessible areas, and only 9% was in less accessible areas (**Fig. 2.5b**). When overlaid with the 201 confirmed presence records (**Table 2.2**), the majority of records fell within the very and moderately accessible categories, reflecting both the reality that pangolins occur in areas with high human access and the bias of survey effort towards more accessible sites.

Table 2.6: Accessibility of Sunda pangolin habitat

	Area (km²)	**%**
Accessibility		
Very accessible	20,951	53
Moderately accessible	15,021	38
Less accessible	3,558	9
Total	**39,530**	**100**

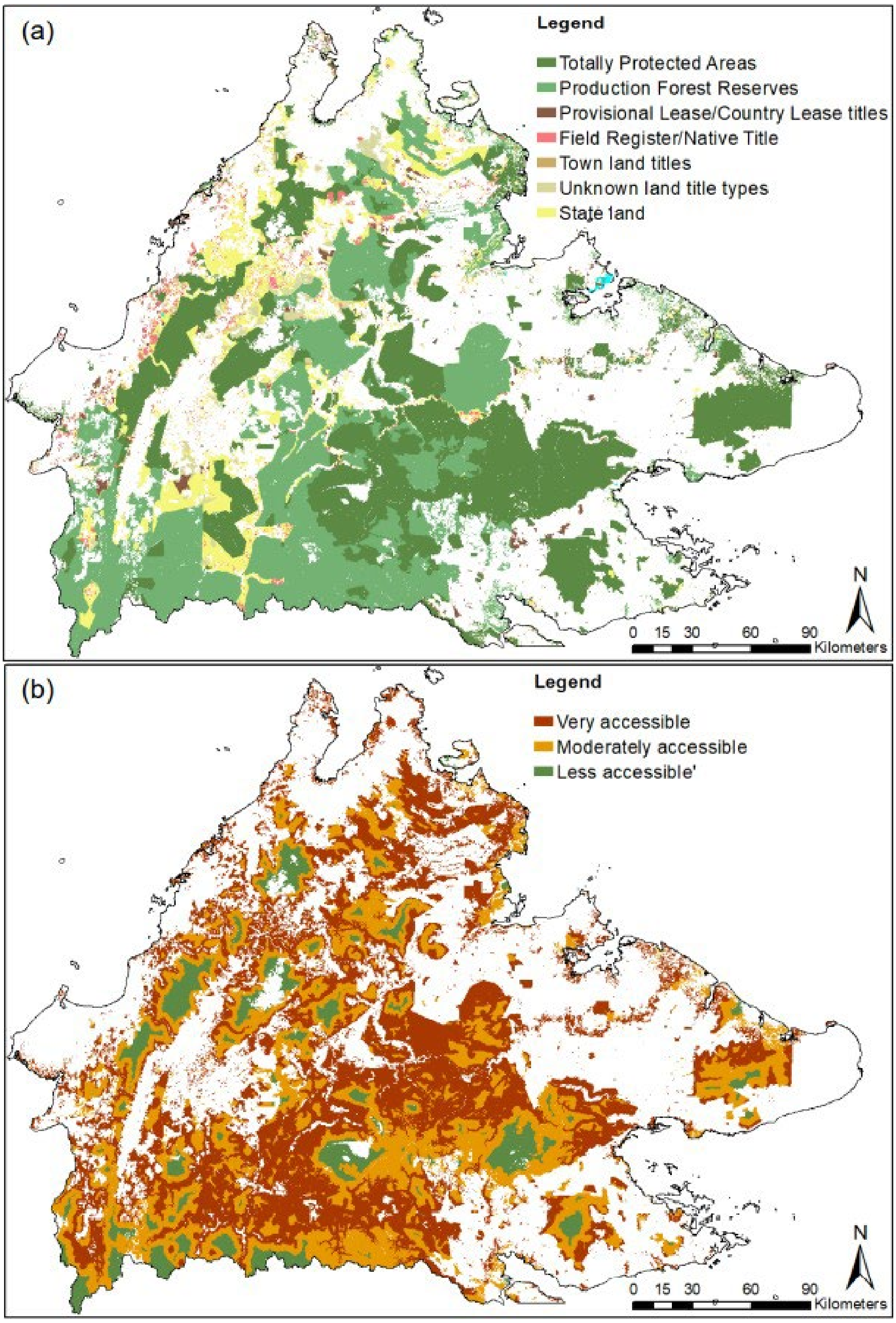

Fig. 2.5: Maps of the distribution and accessibility of Sunda pangolin habitat. **(a)** Highlights the extent of suitable habitats within various land title categories, emphasizing the significant overlap with Totally Protected Areas and Production Forest Reserves. **(b)** Shows the relative accessibility of these habitats, with a concerning proportion falling in highly accessible areas, indicating potential risk for poaching and human intrusion.

2.3 Discussion

2.4.1 Habitat suitability

This study aimed to bridge the knowledge gap on the distribution of the Sunda pangolin in Sabah. The Sunda pangolin is a rare and mainly nocturnal species that primarily lives solitary (Chong et al., 2020). Little is known about their distribution in Sabah (Panjang and Goossens, 2022). The species is constantly threatened by illegal hunting and poaching, posing a significant risk to their survival in the region. This study addressed the current lack of understanding regarding the distribution of Sunda pangolins in Sabah. Using maximum entropy models to predict habitat suitability, the study predicted that the Sunda pangolin is distributed extensively throughout Sabah. Sabah encompasses a total land area of 73,600 km^2, with forested areas covering approximately 65% of the total land cover (Sabah Forestry Department, 2018).

The analysis indicates that approximately half of Sabah's land area constitutes potentially suitable habitat for Sunda pangolins, with approximately 43% (16,998 km^2) of this suitable habitat falling within Sabah's Totally Protected Areas (TPA) (Table 2.4). Sabah's commitment to expand its TPAs from 26% (19,000 km^2) to 30% (22,000 km^2) 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 increase TPA coverage to secure approximately 50% (19,765 km^2) of Sunda pangolin's suitable 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 requires that areas housing RTE species are conserved, prohibiting new oil palm expansion in such areas and mandating habitat management (Senior et al., 2015; Sabah Forestry Department, 2021). Findings from the present study, for example, can guide RSPO High Conservation Value (HCV) assessments by identifying priority pangolin habitats that require protection.

These commitments collectively signify promising conservation strides in Sabah. The findings of this study are highly relevant to these conservation efforts, as they provide detailed insights into the current and potential distribution of Sunda pangolins within Sabah. By identifying key habitats and areas at risk, this study offers critical information that can inform the expansion of TPAs and the implementation of sustainable palm oil practices. Furthermore, the study highlights areas that require focused conservation interventions, supporting Sabah's broader goals of biodiversity protection and sustainable land management.

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. The Production Forest Reserves (PFR) accounted for around 38% (15,021 km^2) of the Sunda pangolin's forested habitat (**Table 2.5**). At the same time, the forests within TPA and PFR are overseen and managed by the Sabah Forestry Department, Sabah Wildlife Department, and Sabah Parks. Approximately 12% and 7% of the remaining potential habitats were located on state and alienated lands, respectively (**Table 2.5**).

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 6,000 km^2 (up from 1,600 km^2 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. Our results can also guide land-use planning by identifying areas of low suitability or unsuitable habitat, where the expansion of industrial tree plantations (ITP) or infrastructure projects would likely have less impact on Sunda pangolins.

The findings of this study emphasise the vulnerability of Sunda pangolin habitats to these threats. By identifying the distribution of suitable habitats and areas of high accessibility, this research highlights regions that are particularly at risk from deforestation, infrastructure development, and plantation expansion. The detailed habitat suitability maps can guide conservation priorities, emphasising the need to protect critical habitats within PFRs and other vulnerable areas. Furthermore, the study's insights into habitat accessibility can help in planning and implementing effective conservation interventions to mitigate the impacts of human activities on Sunda pangolin populations.

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). The results emphasise the significance of forest condition in determining suitable habitats for this species. The 'majority of forest condition' metric emerged as the dominant predictor of these areas (**Fig. 2.3**), indicating a strong association between moderate to high forest-quality forest conditions and pangolin presence (**Fig. 2.4a**). This could mean that forests with higher structural complexity, larger and older trees, and minimal human disturbance are likely important for supporting Sunda pangolins.

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 sites, they exhibit a preference for tall and large trees with hollows, especially those entwined by climbing plants (see this thesis, chapter 4). These are predominantly large, aged dipterocarp trees, serving as sleeping, breeding, and reproductive sites. 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).

The study from Singapore and research in Kinabatangan both emphasise the importance of tall, mature trees with cavities as critical habitats for Sunda pangolins. My SDM findings, which identify areas of high habitat suitability, can reinforce these conclusions by highlighting regions where such trees are prevalent. The SDM can show the overlap between suitable pangolin habitats and areas with old-growth forests containing large dipterocarp trees. This connection emphasises the need to protect these key habitats from logging and fragmentation to conserve the Sunda pangolin effectively.

The result that 43% of Sunda pangolin habitat falls within TPAs aligns with the strict conservation measures in these areas, where all forest harvesting activities, including wildlife hunting and crop plantation activities, are strictly prohibited by the government. On the other hand, in PFR, where forest harvesting activities such as logging and oil palm plantations are permitted, the forest condition and habitat suitability for Sunda pangolins may be affected. Although 38% of the potentially suitable habitat falls within PFRs compared to 43% in TPAs, the activities allowed in PFRs can degrade the quality of the habitat over time (Ratnasingam et al., 2020; Daily Express, 2021). While degraded forests may still favour ant and termite abundance and thus provide foraging opportunities for pangolins, microhabitat features such as large hollow trees used for sleeping and reproduction (Lim and Ng, 2009; Chapter 4) are likely reduced. Furthermore, the greater human access to PFRs increases the risk of poaching. This highlights the need for sustainable management practices in PFRs to maintain their suitability as pangolin habitats. Additionally, the model indicates that habitat suitability rapidly decreases with increasing distance from forested areas, emphasising the importance of maintaining a continuous forest cover in the Sunda pangolin habitat.

The study found a strong association between Sunda pangolin habitat suitability and five soil classes, particularly in Bang, Dagat, Lokan, Sipitang, and Wullersdorf. Sedimentary soils, such as Bang, Dagat, and Lokan (associated with mudstone/sandstone), are commonly found in both lowland and highland areas, providing essential nutrients that support dense dipterocarp forests, which are critical for pangolin habitats. These forests likely offer abundant foraging opportunities and shelter due to their structural complexity and biodiversity. Peat and alluvium soils, associated with Sipitang, are typically found in coastal zones, river valleys, and floodplains. These soils are highly fertile and support wetlands, floodplain forests, and swamp forests, likely creating rich foraging grounds and suitable nesting sites for Sunda pangolins. The dynamic and moist environments of alluvial soils promote the growth of vegetation that harbours ants and termites, essential food sources for pangolins (Acres, 1975; Boettinger, 2005; Yassoglou et al., 2017; Lim et al., 2019; CAIMS Sabah, 2023).

Chapter 4 findings showed that the distribution of Sunda pangolin sleeping sites was primarily associated with freshwater swamp forests, particularly those with soils from Dagat, Lokan, and Sipitang. Peat, clay, and alluvial soils are commonly found in these forests. These soil types may play a role in distributing sleeping sites for the Sunda pangolin in the Kinabatangan study area. This affinity suggests that the likelihood of pangolins selecting sleeping sites is significantly higher in these freshwater swamp forests. Detailed findings are presented in Chapter 4.

Intermediate and igneous soils, associated with Wullersdorf, are predominant in mountain ranges and support diverse vegetation. While igneous soils can support rich biodiversity, the higher altitudes at which these soils are found can present constraints for Sunda pangolins. The model identified elevation as an important factor affecting habitat suitability, suggesting that certain altitude thresholds may limit pangolin distribution despite the presence of suitable soils. Therefore, while igneous soils can support diverse vegetation, the cooler temperatures and reduced prey availability at higher elevations might restrict pangolin presence in these areas (Acres, 1975; Lim et al., 2019; CAIMS Sabah, 2023). A potential hypothesis for further study is that despite the rich biodiversity supported by igneous soils in high-altitude areas, the cooler temperatures and reduced prey availability at these elevations limit the distribution and habitat suitability for Sunda pangolins. This study aims to investigate the specific altitude thresholds and environmental factors that constrain Sunda pangolin presence in high-altitude regions with suitable soil types.

Dipterocarpaceae is a family of mainly lowland tropical forest trees. It includes about 695 known species distributed across pantropical regions, from northern South America to Africa, India, Indochina, Indonesia, Malaysia, and the Philippines. Dipterocarp trees are a dominant family of hardwood trees found particularly in Southeast Asia. The greatest diversity of Dipterocarpaceae occurs in Borneo, where as many as 240 different tree species can grow within one hectare. They are known for their tall stature, large girth, and emergent crowns, often rising above the forest canopy. These trees play a crucial role in the structure and ecology of rainforests, providing habitat and food for a wide range of wildlife. Dipterocarps are also important for timber production due to their high-quality wood (Guan and Yen, 1999; Corlett and Primack, 2005; Ghazoul, 2016; Saner et al., 2017). Paoli et al. (2006) reported that lowland dipterocarp species dominate sedimentary and alluvial soils. The lowland dipterocarp trees comprise a significant portion of the emergent basal area

(Manokaran and Swaine, 1994). These forests provide the main structure and support for the complex rainforest ecosystems (Guan and Yen, 1999).

Sunda pangolins prefer tall, mature trees with hollows as sleeping sites and natal dens (Lim and Ng, 2008). Dipterocarp forests may provide suitable microhabitats for hollow-dependent species, such as the Sunda pangolin, as hollows are relatively common in old-growth dipterocarp forests (Heineman et al., 2015).

Although there is no specific study on the density or abundance of tree hollows for dipterocarp trees in Borneo, other studies have shown that old-growth dipterocarp forests tend to have a higher density of tree hollows, which are crucial for wildlife that depend on these features for nesting and shelter. This contrasts with secondary or younger forests, where the density and abundance of tree hollows are significantly lower (Ashton et al., 2011; Heineman et al., 2015). Old-growth trees are more likely to have large, stable hollows, while new-growth forests may have smaller, less developed hollows (Ghazoul, 2016). The tree density was highest in the dry dipterocarp forest (3,624 trees/ha), followed by the dry evergreen forest (2,451 trees/ha) and mixed deciduous forest (1,102 trees/ha) (Khamyong et al., 2018).

The MaxEnt model identified elevation as important factors affecting habitat suitability for Sunda pangolins. The altitude of these habitats might play an important role in Sunda pangolin distribution. The specific altitudinal range favourable for the species in Sabah has been somewhat ambiguous (Chong et al., 2020). However, the analysis suggests a diminishing presence of the species beyond 200 m asl (**Fig. 2.3e**). This observed trend contrasts with records showing that Sunda pangolins have been identified at altitudes up to 1,700 m asl in regions such as Borneo and Laos (Duckworth et al., 1999; Payne and Francis, 2007; Kaicheen and Mohd-Azlan, 2018). This difference may partly reflect survey bias, since most records in Sabah were collected in lowland forests and ecological factors, as lowland habitats typically support greater ant and termite abundance. Nevertheless, while Sunda pangolins can occur at higher altitudes, this study indicates they are more concentrated in the lowlands, where conditions may be more favourable for sustaining populations.

Although Sunda pangolins occur up to ~1,700 m asl (Duckworth et al., 1999; Payne & Francis, 2007; Kaicheen & Mohd-Azlan, 2018), this study shows a decline in predicted suitability beyond ~200 m within the study's dataset. The study interprets this as a relative concentration in lowlands rather than an upper elevational limit, likely influenced by sampling bias toward accessible lowland forests and by collinearity between elevation, climate and forest type. Thus, while dietary constraints may contribute, the study avoids inferring a physiological threshold and emphasises that high-elevation occurrence is under-represented in the input data.

The reported intolerance of Sunda pangolins to cold temperatures was observed in rescued and captive individuals, where individuals showed signs of stress and reduced survival from 20°C to 5°C (Hua et al., 2015; Save Vietnam's Wildlife, unpubl. data). Although captive conditions differ from wild habitats, these observations suggest potential thermal constraints on the species. Mount Kinabalu, located in Sabah, at 4,095 m is the tallest mountain between New Guinea and the Himalayas and is a significant biogeographic feature of Borneo (Sheldon et al., 2001). The temperatures at higher elevations, such as on Mount Kinabalu, decrease by approximately 0.55°C per 100 m of elevation gain (Kitayama, 1992). This means that from a baseline of 27°C at sea level, temperature may drop to approximately 16°C at 2,000 m asl, close to the reported thermal stress threshold. Such temperature drops, combined with reduced prey availability, can negatively impact the species' survival in higher altitudes. However, Sunda pangolins have been observed at elevations up to ~1,700 m asl (Duckworth et al., 1999; Payne & Francis, 2007; Kaicheen and Mohd-Azlan, 2018). These occurrences may reflect localised microclimates (e.g., warmer valley systems, sheltered forest), behavioural thermoregulation (such as burrow use) or occasional movements through higher elevations rather than long-term, resident populations. Although temperature was not identified as a key predictor in this analysis, it may interact with elevation and prey availability, but further study would be required to clarify this relationship.

Although the model indicates that most of the potential habitat for Sunda pangolins was confined to natural forests, around 19% of potential habitats lie outside protected or production forests, primarily in the southwestern, western, and eastern regions of Sabah. Unfortunately, these regions are highly degraded and fragmented due to human infrastructure developments such as settlements, road constructions, and oil palm plantations (Abram and Ancrenaz, 2017). Habitat loss and fragmentation are leading causes of illegal hunting and poaching, threatening the survival of various vulnerable species, including Sunda pangolins (Chong et al., 2020). Thus, this study evaluated the risk of poaching, hunting, and live capture for the wildlife trade.

2.4.2 Accessibility and poaching

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). 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).

Recent records, such as approximately 278 pangolin rescues in Sabah between 2019 and early 2023 (Panjang et al., 2023), indicate frequent use of urban, suburban and oil palm plantation areas, suggesting possible increased reliance on human-modified habitats, though long-term data to confirm such a trend are lacking. Ongoing infrastructural expansions in Sabah, including new settlements, roads and plantations, will likely further worsen the vulnerability of this species to poaching and requires robust conservation strategies (Wong and Linkie, 2013; Brodie et al., 2015).

According to the model, nearly 91% of the Sunda pangolin's potential habitat in Sabah is at risk of illegal hunting and poaching. The expansion of oil palm plantations, which occupy over 1.52 million hectares in Sabah (Statista Research Department, 2022), poses a significant threat to the endangered species. The development of roads and logging trails, associated with plantation expansion, facilitates access for hunters and poachers (Wong and Linkie, 2013; Brodie et al., 2015). These roads and trails not only traverse the plantations but also extend into adjacent natural forest areas, making it easier for poachers to reach previously inaccessible regions. This increased access to remaining natural habitats exacerbates the threat to Sunda pangolins, as it allows hunters to penetrate deeper into forests that were once more difficult to reach.

Furthermore, the existence of jungle routes or unofficial forest access routes have been reported in Sabah, which may also provide opportunities for poachers to access the forest areas (Berita Harian, 2020). While more than 50 poachers were arrested in a single year, the scale of the problem is likely greater, as many cases may go undetected and unreported (Borneo Post, 2021). However, it should be noted that this study did not include mapping or quantifying these access routes. This is an area for future research and data collection, which could provide further insights into the patterns and impacts of illegal poaching activities. Reports from Malaysia indicate that undocumented persons (illegal immigrants) have been arrested and some prosecuted for involvement in wildlife crimes, such as possession of turtle eggs and tiger parts (TRAFFIC, 2019; Sabah Parks, 2021), although there is no specific evidence linking such cases to pangolin poaching in Sabah.

This study suggests that suitable pangolin habitats within protected areas (TPAs) and production forest reserves (PFRs) in Sabah may be vulnerable to illegal hunting and poaching, given their accessibility via roads and logging trails (Wong and Linkie, 2013; Clements et al., 2014). While this study did not directly assess poaching activity, the findings highlight the urgent need for strict enforcement, regular monitoring and community involvement to mitigate potential threats to pangolins and other endangered species.

Indigenous people and local communities (IPLCs) living close to protected areas and production forests play a critical role in biodiversity conservation. Their traditional knowledge and practices can significantly contribute to the conservation of endangered species like the Sunda pangolin. Involving IPLCs in conservation efforts has proven effective in various regions (Reyes-Garcia et al., 2018; Garnett et al., 2018). Therefore, the study strongly recommends adopting a community-based conservation approach that actively involves these communities in pangolin conservation efforts.

A prime example of successful community-based conservation is Vietnam's effort in utilising hunters' knowledge to conserve pangolins (Newton et al., 2008). This approach can be adapted to Sabah by focusing on the valuable knowledge and skills of local hunters and trackers. Semi-structured interviews and field surveys informed by local expertise could not only improve data collection but also identify priority habitats and poaching hotspots. These outputs can directly support enforcement agencies, guide land-use planning (e.g., HCV set-asides in RSPO-certified landscapes) and strengthen awareness programmes with local communities. In this way, research methods become tools for applied conservation.

Engaging IPLCs in conservation has multiple benefits. Enhanced monitoring and enforcement can be achieved as IPLCs can provide real-time information on poaching activities, leading to more effective monitoring and quicker responses to illegal activities. Moreover, conservation programmes that include IPLCs can offer alternative livelihoods that reduce the economic incentives for poaching. Sustainable practices such as eco-tourism, which highlights pangolin conservation, can provide economic benefits to these communities while promoting conservation. Additionally, IPLCs possess extensive knowledge about local ecosystems and species behaviour (Cooney and Challender, 2020; Wilson-Holt and Roe, 2021). Integrating this knowledge with scientific research can enhance the effectiveness of conservation strategies, ensuring they are culturally appropriate and ecologically sound.

The study indicates that habitat suitability for Sunda pangolins decreases in areas close to mixed-use smallholdings and major roads, with reduced suitability observed within approximately 27 km of these features (**Fig. 2.3d**). Suitability increases with greater distance from roads and mixed-use areas, suggesting that human disturbance and habitat fragmentation negatively influence pangolin presence. Ecological observation further supports this pattern, as Sunda pangolins typically rely on forest habitats and construct burrows in grassland and shrubland patches within forests, where human disturbance is lower.

While road verges, which are semi-natural habitats with vegetation strips adjacent to roads or pavements (Phillips et al., 2020), can provide rich habitats and support wildlife, including pangolins (Plantlife et al., 2019), the overall impact of roads remains negative due to increased human access and disturbance. Although Sunda pangolins have been reported to adapt to modified habitats such as oil palm plantations, degraded forests and urban areas (Lim and Ng, 2008; Chong et al., 2020), these regions also expose them to greater threats, including habitat loss from development, risk from vehicle collisions and increased vulnerability to poaching.

However, well-managed cultivated areas, urban gardens and parks on state and alienated lands may provide crucial refuges for pangolins outside of protected areas, as shown in Singapore. Singapore is known for its advanced legal system, societal order and high development, offering efficiency, stability and prosperity. In contrast, Sabah faces challenges like economic development and infrastructure but is rich in natural resources and cultural diversity. While Sabah does not yet have the same governance conditions as Singapore, similar approaches can still be adapted by strengthening community engagement, improving management of village plantations and smallholdings and expanding RSPO High Conservation Value (HCV) set asides. Conserving these modified habitats, especially those close to protected areas, could be a critical strategy for preserving Sunda pangolins.

The rising number of Sunda pangolins rescued by the public emphasises the importance of education and public awareness, which, while not the immediate focus of this study, should be included as an added conservation recommendation. Between 2019 and 2023, authorities rescued over 278 individual Sunda pangolins, with most cases involving pangolins found outside protected areas such as residential and business areas, oil palm plantations, and roadsides (Panjang et al., 2024). This situation likely results from habitat loss and fragmentation, forcing pangolins to move out of their natural habitats.

SDMs can help identify and predict suitable habitats for Sunda pangolins, highlighting areas at risk due to habitat fragmentation and human encroachment. Although further studies are needed to better understand the factors contributing to these rescue locations, the data obtained from SDMs can inform conservation strategies by pinpointing critical habitats that need protection and restoration. While pangolins may adapt to living outside protected areas, they become more vulnerable to illegal wildlife trade, feral dog attacks, and road accidents (Chong et al., 2020; Panjang and Goossens, 2022).

Education and public awareness efforts, informed by SDM data, play an important role in preserving suitable habitats for Sunda pangolins beyond protected areas by promoting the preservation and maintenance of neighbourhood green spaces, including forest remnants, road verges, gardens, and parks. Integrating SDM insights with public outreach can enhance conservation efforts, ensuring that both protected and non-protected areas contribute to the survival of Sunda pangolins.

2.4 Limitations of the study

The modelling approach used in this study was based on existing and available occurrence data, which were combined to create the largest meta-dataset for the Sunda pangolin to date. The use of high-resolution imagery facilitated the development of various spatial layers for the models, enabling the production of the first statewide habitat distribution model for the Sunda pangolin in Sabah. However, further research is needed to address knowledge gaps and limitations within both the current dataset and the modelling approach.

One limitation of the current dataset is that it was restricted to natural forest areas. This may not fully capture the potential distribution of the pangolin, as the species is known to show adaptability to human-modified landscapes. Incorporating data from surveys conducted across different land cover types would improve our understanding of pangolin distribution and provide a more comprehensive view of their environmental preferences and tolerances.

Another limitation lies in the timeframe of presence data, which spans over a 10-year period and has some regional biases in the survey locations. Given that surveys are resource-intensive, few presence surveys have specifically targeted pangolins in Sabah. Future surveys should aim to cover areas that have not yet been explored to reduce biases in location data and expand the current meta-dataset. Additionally, as more presence data becomes available, future analyses could model distributions over longer time frames to understand to understand the impacts of forest loss on pangolin distribution.

Lastly, it is recommended that ongoing monitoring of landscape changes employ 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 technologies have the potential to significantly enhance our understanding of how habitat changes impact the Sunda pangolins and can guide the development of adaptative conservation strategies that respond effectively to the rapidly changing environmental landscape.

2.4 Key conservation recommendations

Based on the data and results of this study focused on habitat suitability and accessibility, the following recommendations are made: (1) strengthening enforcement and policies can be guided by SDM findings to target critical habitats and high-risk areas for poaching more effectively; (2) expanding TPAs should be informed by SDM, which highlights regions with high habitat suitability that are currently unprotected; and (3) managing human-modified environments can be improved by using SDM to identify overlaps with suitable pangolin habitats.

Strengthening enforcement and policies: Poaching threatens the survival of viable pangolin populations in Sabah. The SDM and accessibility analysis showed that many highly suitable pangolin habitats overlap with the areas of high human accessibility, particularly near roads and settlements, highlighting priority zones for enforcement. Targeted anti-poaching strategies, especially regular patrols in protected areas, bordering habitats, and intelligence-led operations are important 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, such as the PROTECT Unit and the Rapid Response Team, is essential (NST, 2022; The Star, 2023). These anti-poaching units, as the frontline defence against wildlife crimes, require sustained support and resources for maximal effectiveness.

This includes advanced training, better equipment, and reliable funding to ensure continuous and effective operations. Regular patrols need to be well-coordinated and frequent to deter poachers. This is especially important in protected areas and bordering habitats, where pangolins are most vulnerable. 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).

Intelligence-led operations are also vital. These operations rely on accurate and timely information to anticipate and intercept poaching activities before they occur. Collaborating with local communities can provide valuable intelligence. Indigenous Peoples and Local Communities (IPLCs), with their intimate knowledge of the terrain and local activities, can offer critical insights into poaching networks and methods. Their involvement can significantly enhance the effectiveness of anti-poaching strategies (Cooney and Challender, 2020; Wilson-Holt and Roe, 2021). Involving IPLCs in conservation efforts has proven effective in various regions (Reyes-Garcia et al., 2018; Garnett et al., 2018). Therefore, the study strongly recommends adopting a community-based conservation approach that actively involves these communities in pangolin conservation efforts.

Expanding Totally Protected Areas (TPAs): Expanding TPAs is important for curbing poaching, preserving biodiversity, mitigating habitat loss, and facilitating the recovery of wildlife populations (Geldmann et al., 2013; Steinmetz et al., 2014; Terraube and Llamazares, 2020; Nuttall et al., 2021). The SDM indicated that 43% of suitable habitat lies within TPAs, leaving 57% outside, mainly PFRs and state land. Expanding TPAs into these unprotected but suitable habitats would secure critical areas for pangolins. TPAs serve as a cornerstone for conserving the Sunda pangolin, ensuring that its natural habitat is maintained or enhanced. While the species can be found in non-forest habitats, most pangolin presence points collected during the study period were located within TPAs and areas under natural forest management. This highlights the importance of these protected areas in providing critical habitat for the species.

TPAs are vital for maintaining ecological balance and protecting wildlife. They offer a sanctuary where ecosystems can function without significant human interference, allowing flora and fauna to thrive. For the Sunda pangolin, TPAs provide essential habitats that support their foraging, breeding, and shelter needs. Expanding these areas helps mitigate the adverse effects of habitat fragmentation and loss, which are significant threats to pangolin populations (Chong et al., 2020). Sabah has pledged to increase its network of TPAs, which would significantly contribute to pangolin conservation. This commitment aligns with global conservation goals and emphasises the need for protected areas to be sufficiently large and connected to support viable wildlife populations. By expanding TPAs, Sabah aims to create a more extensive network of protected habitats that can sustain larger and more genetically diverse populations of pangolins and other wildlife.

In addition to expanding TPAs, establishing buffer zones around these areas can provide additional refuge for pangolins. Buffer zones act as transitional areas between protected habitats and human-dominated landscapes. These zones can help reduce the edge effects of habitat fragmentation and offer additional habitats where pangolins can thrive. Effective enforcement in these buffer areas is important to reduce potential threats such as poaching and habitat encroachment (Martino, 2001; Ahmad et al., 2013). Ensuring that these buffer zones are well-managed and patrolled can enhance the overall effectiveness of TPAs in conserving pangolin populations.

Human-modified environmental management: To ensure the survival of the Sunda pangolin, it is critical to minimize habitat destruction and mitigate anthropogenic disturbances within their habitats. The SDM revealed that some suitable pangolin habitats overlap with human-modified landscapes such as smallholdings and agroforestry mosaics, showing that these areas also require careful management. While the species demonstrates unexpected resilience and survival in non-forest habitats, transitioning towards sustainable and responsible management of the extensive oil palm landscapes in Sabah becomes paramount for securing viable pangolin populations. Assigning a High Conservation Value (HCV) Forest designation to all forest fragments within plantations would require plantation managers to maintain and manage the ecological value of these forest patches. These fragments could serve as potential refugia for Sunda pangolins, if poaching is effectively eradicated.

Effective management of Sunda pangolin habitats must involve a range of conservation strategies beyond protected areas, especially since nearly all suitable habitats for Sunda pangolins are within Sabah's protected forests, such as TPAs and PFRs. Habitat restoration and the establishment of wildlife corridors are essential for connecting fragmented habitats, particularly outside protected areas (Hofman et al., 2018; MacKinnon et al., 2020). These strategies can help mitigate the effects of habitat fragmentation, ensuring that pangolins have access to a neighbouring landscape that supports their ecological needs.

The conservation of modified habitats, especially those close to protected areas, is crucial for the long-term conservation of Sunda pangolins. Well-managed cultivated areas, urban gardens, and parks on state and alienated lands may provide refuges for pangolins outside of protected areas, as evidenced by successful conservation efforts in Singapore (Lim and Ng, 2008). Policies and regulations that support sustainable land-use practices, including habitat restoration and the establishment of wildlife corridors, are essential to ensure the conservation of Sunda pangolins in modified habitats (Keeley et al., 2018).

The accessibility analysis identified high-risk areas that could be targeted for education and awareness campaigns, while the SDM can guide selection of suitable release sites for rescued pangolins. In addition to the recommendations, two further strategies have been identified that, while falling outside the immediate scope of this study, emerged as important for the conservation of the Sunda pangolin: education and public awareness, and enhancement of rescue facilities. SDM findings can identify areas where pangolins are most vulnerable, guiding targeted educational campaigns to increase public support and reduce poaching. Before translocation, genetic studies should be conducted to avoid moving pangolins between genetically distinct populations (e.g., from the West to East coast of Sabah). This helps preserve genetic integrity and prevents negative impacts on local populations. Once genetic compatibility is confirmed, SDM can identify suitable habitats for releasing rescued pangolins, ensuring that translocation efforts are directed towards areas with high habitat suitability to improve survival rates and stabilise populations.

Education and public awareness: As pangolins are being highly exploited, strategic awareness efforts are essential to ensure sustained support for their conservation (Thomson and Fletcher, 2020). Addressing the root of the poaching crisis requires confronting the driving demand for pangolin products. 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, consume, and sell pangolins—encompassing both rural and urban communities—are crucial. By emphasizing the ecological importance of pangolins and the consequences of their illegal trade, awareness campaigns can induce significant behavioural changes, thereby reducing demand and curbing the increase in pangolin poaching (Burgess et al., 2020). These campaigns should include educational programs in schools, community workshops, and widespread media campaigns. Engaging local influencers and community leaders can also help spread the message more effectively.

Enhancement of rescue facilities: Considering the rising numbers 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). Rescue centres should be equipped with proper veterinary care, quarantine areas, and specialised enclosures that mimic the natural habitat of pangolins. 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). Collaboration with local communities and authorities is essential to ensure that these areas remain safe for released pangolins. Through these facility improvements and targeted release strategies, the recovery of Sabah's Sunda pangolin population can be better supported. Enhanced rescue operations, combined with comprehensive public awareness efforts, will play a crucial role in the conservation and recovery of this endangered species.

Chapter 3: Home range and movement of the Sunda pangolin in the highly fragmented Lower Kinabatangan landscape

3.1 Introduction

One of the most important factors that have led to the current extinction crisis is the destruction of natural habitats (Sodhi et al., 2009; Kumari et al., 2021). It is not a single process but is intricately connected to the fragmentation of habitats (Kumari et al., 2021). Habitat loss and fragmentation have occurred due to various natural and anthropogenic activities that alter land use patterns (Loewe and Hill, 2010). Fragmentation of habitat impacts the entire forest ecosystem, permanently damaging the functioning of remaining fragments and causing species extinction (Haddad et al., 2015; Crooks et al., 2017). For example, most of Borneo's primary forest has been destroyed due to extensive land clearing caused by human activities such as logging and oil palm plantations (Gaveau et al., 2014). Habitat modifications have the potential to have a significant impact on a wide range of ecological processes, including population dynamics (Arthur et al., 2005), genetic diversity (Mekomen et al., 2018b), the predator-prey relationship (Schneider, 2001), and dispersal (Banks and Lindenmayer, 2014; Awade et al., 2017), as well as causing major conservation issues such as poaching (Wong and Linkie, 2013; Brodie et al., 2015) and human-wildlife conflicts (Othman et al., 2017; Hearn et al., 2018). For example, larger wildlife species, such as carnivores, are especially susceptible to habitat fragmentation because they rely on expansive habitats for survival (Woodroffe and Ginsberg, 1998). In addition, the loss and fragmentation of natural habitats facilitate illegal hunting and poaching of endangered species, such as the Sunda pangolins (Chong et al., 2020).

Movement and space use is influenced by how habitat patches are distributed and organised within fragmented landscapes, which has consequences for individual fitness and survival (Cattarino et al., 2016). For example, earlier studies conducted in fragmented landscapes in Lower Kinabatangan, Sabah, Malaysian Borneo revealed significant findings demonstrating the effect of habitat fragmentation on the movement and use of space by species. For example, in the Lower Kinabatangan proboscis monkeys *Nasalis larvatus* were reported to move faster near oil palm plantations than they did inside “high-intensity” habitat patches, which are areas with significant human alteration and high levels of human activity, such as agricultural or logged regions.

This likely reflects risk-avoidance and commuting behaviour (Stark, 2018). Some species may be less likely to cross open areas as habitat patches become smaller and more isolated, thereby restricting animal movements, as seen in the Sunda clouded leopard *Neofelis diardi*, which moves shorter distances in fragmented habitats than in continuous habitats (Hearn et al., 2018). The home range of scavenging species, such as the Asian water monitor lizard *Varanus salvator,* has shrunk in oil palm plantations compared to forested areas, likely reflecting differences in resource availability and distribution (Guerrero-Sanchez, 2019). Additionally, conflicts between Bornean elephants, *Elephas maximus borneensis* and humans have arisen due to habitat loss and fragmentation, which has become one of the most significant challenges facing the conservation of Asian elephants (Othman, 2017). On the other hand, species with a higher tolerance for modified landscapes, such as the common palm civet *Paradoxurus hermaphroditus*, are less restricted by habitat boundaries and can move further distances as habitat fragmentation increases (Evans, 2019).

To understand the habitat requirements of a species, it is necessary to have information about the size of the area occupied by the species, the types of habitats it uses, and its movement patterns (Paxton et al., 2003). The Sunda pangolin is a species of medium-sized mammal that inhabits a variety of habitats. Despite this, the species is highly specialised in the microhabitats it uses. For instance, it has been found that Sunda pangolins frequently sleep in tree holes in the forest, and female pangolins typically use tree holes as nesting sites (Lim and Ng, 2008). Occasionally, Sunda pangolins have been observed utilising riverine habitats, sleeping beneath tall elephant grasses or also known as Napier grasses (*Pennisetum* spp*.*) that grow along the river, outside their typical sleeping areas. Pangolins may move away from their preferred sleeping areas to acquire resources (e.g., food and water) or to find mates. Therefore, it is important to record potential uses of different habitats to understand habitat requirements.

Animal movement is essential to their survival, as it allows them to search for food, find mates, avoid predators, and locate suitable habitats. The study of home range and movement has been significantly advanced due to the development of animal tracking. Tracking animals involves observing and recording their movements in their natural habitats. Indigenous cultures utilise animal tracking for hunting and survival (Bartholomew et al., 2021), whereas modern scientists employ it to study animal behaviour, ecology, and conservation (Millspaugh and Marzluff, 2001; Smith et al., 2018). Traditionally, indigenous people or local hunters track animals by following their footprints, tracks, scats, and other animal signs. Technology such as radio telemetry and GPS collars, typically worn by animals for a limited amount of time, allows scientists to keep track of animals. Data collected through tracking can provide information on animal movement patterns, home ranges, behaviour, and interactions with other species; all information can be helpful for conservation and management (Millspaugh and Marzluff, 2001; Cooke et al., 2004; Rutz, 2009; Klimley, 2013; Kays et al., 2015). In addition, animal tracking can aid in monitoring elusive and endangered species (Martin et al., 2009), such as the Sunda clouded leopard (Hearn et al., 2018), Malayan sun bear *Helarctos malayanus* (Guharajan, 2016), and Sunda pangolin (Lim and Ng, 2008).

Home range estimation is one of the primary applications of tracking data and is essential for understanding animal ecology and behaviour (Kie et al., 2010). Home range, defined as the area that a particular animal or group frequently uses for activities such as foraging, mating, and caring for the young (Burt, 1943), is a critical concept in understanding habitat and landscape use. In contrast, the territory refers to the part of the home range that is actively defended by an individual or group (Burt, 1943; Powell, 2000). The size and shape of a home range can vary greatly among species and are influenced by various factors, such as feeding ecology, body size, group size, and habitat quality (Gregory, 2017). By estimating home ranges using tracking data, ecologists can gain valuable information about the spatial requirements and movements of species; for instance, it can aid in identifying critical habitats, migration corridors, and areas that are essential for breeding or foraging (Powell, 2000; Othman, 2017; Stark, 2018; Hearn et al., 2018; Evans, 2019).

There is no single standard method for estimating the home range of an animal or group of animals; however, there are several methods for doing so (Powell, 2000). Home range estimators that are utilised the most frequently include the minimum convex polygon (MCP) (Mohr, 1947), kernel density estimators (KDE) (Worton, 1989), and, more recently, the local convex hull (LoCoH) (Getz et al., 2007). How an animal or group utilises an area, or how the utilisation distribution is weighted, greatly determines methodological differences. The MCP estimate (Mohr, 1947) is a simple and straightforward method that involves creating a convex polygon (that is, a polygon with no internal angles greater than 180°) encompassing all locations where animals were detected. Another option is to use a subset of the points (e.g., 95% and 50% of the points) to determine the “core” of the home range. This method assumes that animals utilise their entire home range equally and does not give greater weight to areas utilised more frequently. For example, a single point visited once a year could significantly increase the home range, and the high-use areas cannot be distinguished (Gregory, 2017). Despite this, researchers have found that it poses fewer problems than other methods, making it the method of preference. For example, Boyle et al. (2009) found that MCP methods were more accurate than KDE methods when the sample size was small. The KDE methods involve a more complicated, nonparametric analysis of home range data, where the frequency of an animal’s presence at various locations is used to estimate a utilisation distribution. This distribution estimates the likelihood of finding an animal at any given point within its home range, effectively highlighting areas of higher and lower use (Worton, 1989; Gregory, 2017). Powell (2000) reported that KDE methods are more accurate because they produce results independent of variables such as grid placement. However, Boyle (in press) reported that several issues might arise with KDE, such as the issue of home range overestimation. KDE, like MCP, exaggerates its home range by including unoccupied areas.

LoCoH (Get et al., 2007) is a method developed in the early 2000s that uses MCP construction to overlay polygons calculated using different subsets of the overall dataset, in order to identify hotspots of activity and the gaps in activity in between. This method is particularly useful because it can exclude areas that are unusable to animals, such as rivers and cliffs, from the estimated home range. However, one limitation is that by focusing on localised areas of use, LoCoH may underestimate the total home ranges, potentially overlooking less frequently used areas that are still important for the species (Gregory, 2017).

Another method is modelling distribution using generalised additive models (GAMs) (Hastie and Tibshirani, 1986). GAMs model the relationship between an animal's location and environmental or behavioural factors using smoothing functions, which account for non-linear relationships (Hastie and Tibshirani, 1986). Regardless of the method used it is important to have a detailed description of both the method used and the data set, and to have the methods standardised.

In fragmented landscapes, understanding animal movement and behaviour becomes even more critical for effective conservation (Dyck and Baguette, 2005; Yahner et al., 2002). Habitat fragmentation can lead to changes in movement behaviour, as animals may need to navigate through different patches of suitable habitat, encounter novel environmental conditions, and avoid potential barriers (Yahner and Mahan, 2002; Dyck and Baguette, 2005; Hansen et al., 2019). These changes in movement behaviour can have significant implications for the survival and persistence of species in fragmented landscapes (Cattarino et al., 2016). For pangolins, whose movement behaviours are poorly understood, it is essential to understand how fragmentation affects their movements and how they respond to landscape changes. By gaining a better understanding of pangolin movement behaviour in fragmented landscapes, conservation efforts can be better tailored to address the unique challenges faced by this species.

The present study represents the first use of radio telemetry to estimate the home ranges and movements of Sunda pangolins in Sabah, Malaysia, focusing on the highly fragmented and degraded landscape of the Lower Kinabatangan floodplain. While previous studies have applied radio telemetry to Sunda pangolins on a smaller island in Singapore (Lim and Ng, 2008) and in translocated populations in Vietnam (Gray et al., 2022), this research presents new insights into the behaviour and space use of wild Sunda pangolins in their natural habitat under challenging conditions. In addition, the study will examine the translocation of Sunda pangolins into habitats that have been fragmented, with a focus on evaluating the success of this strategy, identifying the challenges involved, and considering its broader implications for pangolin conservation. The study aims to provide critical information for the long-term management and conservation of Sunda pangolins and implications for translocation efforts in fragmented habitats. Specifically, this study aimed to achieve three primary objectives: 1) to estimate the home range sizes of Sunda pangolins, 2) to describe their movements within the highly fragmented landscape, and 3) to understand the differences in home range sizes and movement patterns between wild and translocated Sunda pangolins. The findings of the study will provide important insights into the conservation of pangolins in fragmented landscapes.

3.2 Methods

3.2.1 Ethical statement

In this study, the proper handling of animals was ensured by adhering to the current regulations of the Sabah Wildlife Department's Standard Operation Procedures governing animal capture, anaesthesia, and welfare. Furthermore, the task was delegated to trained wildlife veterinarians with the necessary expertise and training. The Sabah Wildlife Department (SWD) is a government agency in Sabah that is responsible for the conservation and management of wildlife and their habitats. Under the Wildlife Conservation Enactment 1997, the SWD is responsible for enforcing the law by issuing licences and permits for capturing wildlife and taking legal action against those violating the law. All research activities carried out in Sabah require a permit from Sabah Biodiversity Centre (SaBC). The SaBC is a government agency in Sabah that is responsible for regulating access to Sabah’s biodiversity, genetic resources, and traditional knowledge. Approval for this study was obtained from the SaBC with permit JKM/MBS.1000-2/2 JLD.3 (73).

3.2.2 Radio telemetry of Sunda pangolins

Prior to the application of radio telemetry, extensive efforts were made to locate and tag Sunda pangolins within the study site. These efforts included setting up camera traps strategically positioned to detect pangolin activity, conducting night walks to actively search for pangolins, and surveying tree hollows and burrows, which are known to serve as potential sleeping sites.

Between December 2016 and January 2022, a total of 17 adult Sunda pangolins were involved in this study both sampling and tracking. These pangolins were categorised into two groups: wild pangolins and translocated pangolins.

Wild pangolins: Two individuals were captured opportunistically within the study area. These pangolins are found either by the research team or by local communities, including villagers and plantation workers, within the boundaries of the study site. These pangolins are considered wild because they were located within their natural range in the study area, demonstrating typical behaviours and habitats associated with wild individuals. Both were fitted with radio-transmitters for movement monitoring.

Translocated pangolins: Ten individuals were obtained through various rescue efforts and were considered translocated due to their origins outside the study area or their uncertain origins. These pangolins were either retrieved from rescue centers after being confiscated by authorities due to illegal trade or hunting activities, found outside the defined study area by local authorities, villagers, or plantation workers, or of unknown origin, making it unclear whether they originated within or outside the study area. All ten were fitted with radio-tags for tracking.

Tagging and monitoring: A total of 12 individuals were fitted with GPS and VHF tags and subsequently monitored during the study (refer to **Table 3.1a** for a detailed breakdown of these individuals, including their categories, origin, and tagging status). Of the tagged pangolins, two were identified as wild ("resident") pangolins, while the remaining 10 were categorised as translocated. Upon receiving information about the pangolins from local authorities, I, as the project leader, arranged to retrieve the animals from the rescue facilities and transport them to the laboratory at the Danau Girang Field Centre for measurement, sampling and tagging. The pangolins were transported in a large, well-ventilated plastic container with lid holes. The project leader sampled and tagged the pangolins, assisted by a wildlife veterinarian and two research assistants.

In this research, pangolins were not anaesthetised. Their eyes were covered with small towels to reduce stress, the room contained a minimum number of people, and the noise was kept to a minimum. Blood, ectoparasites (ticks), and hair samples were collected and stored in the field centre's laboratory before these samples were transported to the Wildlife, Health, Genetic, and Forensic Laboratory (WHGFL) in Kota Kinabalu for further analysis. The attachment method for the tracking tags varied depending on the type of tag used. Three pangolins were fitted with E-obs GPS tags, which were attached to their scales using plastic cable ties inserted through holes drilled in the scales. One pangolin was fitted with a Bio-Track VHF tag, which was directly attached to the scale using screws. Another pangolin was fitted with both a Telenax GPS tag and a Telenax VHF tag, while five other pangolins were fitted with only the Telenax VHF tag. The Telenax GPS and VHF tags were designed with strong nylon spandex fabric as part of the attachment mechanism. The fabric was secured to the pangolin's scale using screws (see **Fig. 3.1**).

Before attaching any tag, a suitable scale was carefully selected, ideally one that was strong and located near the rear leg or tail, as recommended by Ching et al. (2019). The centre of the selected scale was marked with a marker pen, and a hole was drilled using a portable hand drill. The tag was then attached to the scale either with a screw, a cable tie, or a fabric, depending on the tag type. The pangolins were then placed back in the box to allow them time to adjust to the tag. Pangolins were held for no more than 24 hours before release, ensuring minimal stress. Releases were scheduled in the early morning or evening, coinciding with the pangolins' active periods, to facilitate their ability to quickly find food or water.

For wild pangolins, release occurred at the exact location where they were initially found. In the case of translocated pangolins, although release sites are often determined by the authorities, in this study all 10 tagged translocated individuals were released within the study area, which allowed me to monitor them. For pangolins rescued by nearby local communities, I coordinated with the authorities upon receiving the animals to obtain permission to release them within the study area. Translocated pangolins were released near potential sleeping sites, such as trees with hollows, and close to water sources, providing them with immediate access to necessary resources. Before release, the handheld radio, antennae, tag, and frequency were thoroughly tested to ensure proper functionality.

The tracking tags used in this study varied in their specifications, as outlined in **Table 3.1c**. The E-obs Tamandua 2AA GPS tags were the first to be purchased and were tested on three pangolins. Subsequently, Bio-Track TW VHF tags from Lotek were acquired, followed by Telenax TGB-311Sling GPS and TXE-304Sling VHF tags from Telenax. The selection of which pangolins received which tags was not based on specific criteria but rather on the availability of the tags at the time. The tags were purchased in stages, based on the research programme's evolving needs and the availability of funding. The variation in tags allowed for testing different tracking systems to determine their effectiveness under the study's conditions.

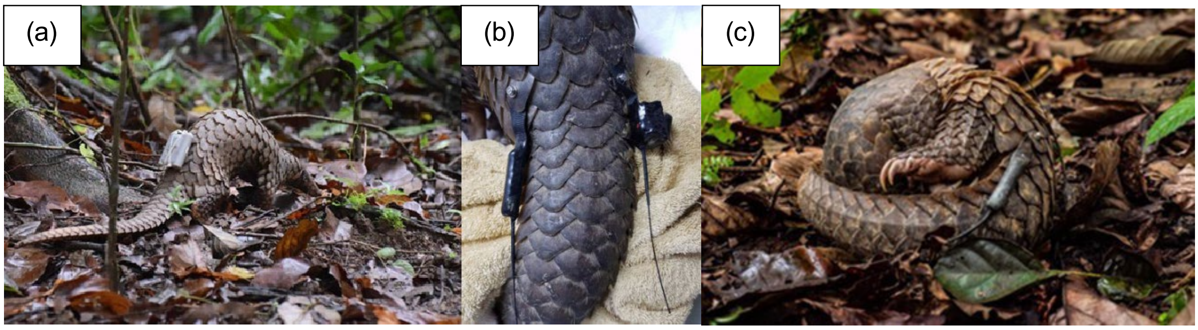

Fig. 3.1: Tracking devices fitted to Sunda pangolins between December 2016 and January 2022: (a) E-obs GPS tag secured to the scales using cable ties, (b) Telenax GPS and VHF tags attached to the scales using nylon spandex fabric and secured with screws, and (c) Telenax VHF tag attached to the scale with nylon spandex fabric and secured with screws. Researchers monitored the pangolins' behaviour and tracked their movements over time.

Table 3.1a: Summary of captured and rescued Sunda pangolins in Sabah between December 2016 and August 2021, including sex, age, body measurement, weight, and status. In addition, one dead pangolin was discovered, and an autopsy was conducted.

ID	Sex	Age	Head length (cm)	Head to base of tail length (cm)	Tail length (cm)	Total length (cm)	Weight (Kg)	Group	Origin	Status
Anggun	Female	Adult	NA	58.00	54.00	112.00	4.30	Translocated	Oil palm, Kinabatangan	Rescued, radio-tagged and released
Pesona	Female	Juvenile	NA	50.00	49.50	99.50	2.50	Translocated	Oil palm, Kinabatangan	Rescued, radio-tagged and released
Suka	Male	Adult	12.50	53.00	53.00	106.00	5.40	Translocated	Oil palm, Kinabatangan	Rescued, radio-tagged and released
Oroi	Female	Adult	11.00	71.00	48.00	117.00	5.00	Translocated	Beluran	Rescued, radio-tagged and released
U2	Female	Juvenile	14.00	48.00	34.00	82.00	1.60	Translocated	Oil palm, Kinabatangan	Rescued and released
Gagah	Male	Adult	13.00	72.00	68.50	140.50	10.00	Translocated	Ranau	Rescued, radio-tagged and released
Berkat	Female	Adult	11.00	59.00	44.00	103.00	4.06	Resident	Study area, Kinabatangan	Captured, radio-tagged and released
Tuah	Male	Adult	6.00	72.00	52.00	124.00	6.50	Translocated	Sandakan	Rescued, radio-tagged and released
Cekal	Female	Adult	13.50	52.00	40.50	92.50	3.40	Translocated	Kota Kinabalu	Rescued, GPS-tagged and released
Kirana	Female	Adult	5.00	60.96	45.72	106.68	5.85	Translocated	Sandakan	Rescued, GPS-tagged and released
Asa	Female	Adult	10.00	58.00	36.50	94.50	7.72	Translocated	Oil palm, Kinabatangan	Rescued, GPS-tagged and released
U3	Male	Adult	17.00	82.00	68.00	150.00	11.20	Resident	Study area, Kinabatangan	Captured and released
U4	Female	Juvenile	9.00	28.00	36.50	64.50	2.90	Translocated	Kinabatangan	Rescued and released
U5	Male	Adult	16.00	52.50	63.00	132.50	13.00	Resident	Study area, Kinabatangan	Captured and released
Galak	Male	Adult	14.30	79.90	62.60	142.50	11.85	Resident	Study area, Kinabatangan	Captured, radio-tagged and released
Wira	Male	Adult	NA	52.00	45.00	97.00	5.00	Translocated	Sandakan	Rescued, radio-tagged and released

Table 3.1b: Mean body measurement (cm) and body mass (kg) with standard deviation for the eight males and nine female juvenile and adult Sunda pangolins. Individuals were captured and rescued in Sabah between December 2016 and August 2021. Differences between sexes were assessed using t-tests.

Measurement	Sex	Mean	SD	t	df	p value
Head length (HL)	Male	12.400	4.050	0.996	1	0.339
	Female	10.500	3.014			
Head to base of tail length (HB)	Male	64.325	13.443	1.702	1	0.109
	Female	53.884	11.866			
Tail length (TL)	Male	56.425	10.799	3.065	1	0.008
	Female	43.191	6.783			
Total length (ToL)	Male	122.875	22.450	2.772	1	0.014
	Female	96.853	16.080			
Mass (M)	Male	8.380	3.509	3.160	1	0.006
	Female	4.148	1.862			

Table 3.1c: Specifications of the transmitters used for tracking Sunda pangolins in the study, including model, supplier, system type, size, weight, and battery life.

Model	Supplier	System	Size (mm)	Weight (g)	Battery Life (months)
Tamandua 2AA	E-obs, Germany	GPS	65x55x35	80.0	6
Bio-Track TW	Lotek, Canada	VHF	10diameterx32	15.5	8
TGB-311Sling	Telenax, Mexico	GPS	26x60x29	45.0	4
TXE-304Sling	Telenax, Mexico	VHF	12diameterx44	17.0	9

Pangolins fitted with VHF tags were tracked daily, with tracking efforts to locate each tagged pangolin conducted once a day. The tracking usually occurred in the morning when the pangolins were sleeping, as this made it easier to locate them since they were not moving. However, the timing of tracking could change depending on weather conditions. For example, if it rained in the morning, tracking would be conducted in the afternoon instead. The primary objective was to obtain at least one location per day to ensure consistent data collection. Tracking frequency was also influenced by whether a location had been successfully obtained on that day. If the tracking was unsuccessful, additional efforts were made later in the day or on subsequent days to ensure that the pangolin was re-found. In cases where it rained for several consecutive days, the tracking effort was increased to locate the pangolins, as continuous weather conditions could hinder consistent data collection. Additionally, if a pangolin went missing and no data were collected, tracking efforts were intensified until the pangolin was found to maintain continuity in the study and ensure a consistent record of the animal's movements.

Point locations were determined primarily through triangulation. For triangulation, at least two or more azimuths are typically used to determine the position of the animal (Pace, 2001). In this study, I used four azimuths. I pointed the directional receiver (antenna) in four different directions from different known locations to determine the direction of the signal coming from the animal's transmitter. Whenever possible, after triangulation, I attempted to confirm the pangolins' locations visually to ensure the accuracy of the data. Additionally, I set up camera traps outside the sleeping sites to monitor the pangolins, providing further confirmation of their presence and behaviour in these areas.

The GPS tags were set to record one location point every hour between 2000 hour and 0600 hour, capturing 11 points each night. This timing was chosen because it aligns with the pangolins' active periods, ensuring that location data was collected when the animals were most likely to be moving. Additionally, the GPS timeout was set to 150 seconds to ensure that the device could acquire a satellite fix within this period. The Ultra High Frequency (UHF) pinger, which assists in tracking, was programmed to activate between 0700 hour and 0900 hour, coinciding with the time when active tracking for pangolins was conducted. Accelerometer data, which provides insights into the animals' movement patterns, was collected between 0800 hour and 2000 hour, with data recorded every 10 minutes. This duty cycle was selected to maximise data collection during critical periods of pangolin activity while also conserving battery life to support the long-term monitoring of the animals. This duty cycle was chosen to gather important data during the pangolins' most active times while also saving battery power for long-term monitoring.

3.2.3 Home range estimation

The home range analysis in this study was conducted using the "adehabitatHR" package in R (Calenge, 2015) and R 4.2.2 software (R Development Core Team 2022). The methods employed included Minimum Convex Polygon (MCP) (Mohr, 1947), Kernel Density Estimation (KDE) (Worton, 1989, 1987), Local Convex Hull (LoCoH) (Get et al., 2007) and Generalized Additive Models (GAMs) implemented using the “mgcv” package in R (Hastie and Tibshirani, 1986).

Minimum Convex Polygon (MCP)

The Minimum Convex Polygon (MCP) method was used to estimate the home range of Sunda pangolins. MCP creates the smallest convex polygon (i.e. a polygon with internal angles of >90 degrees) that includes all recorded locations of an animal. It is widely used because of its simplicity and its established use in previous studies of Sunda pangolins, such as those by Lim and Ng (2008). In this study, MCP was calculated at three levels: MCP 100%, MCP 95%, and MCP 50%. MCP 100% estimates the total potential area that an animal is known to have occupied, including all recorded points, regardless of their distribution. All data points were included in the analysis, and no outliers were excluded. MCP 95% and MCP 50% were also estimated to provide additional insight into the core areas of use by excluding the outermost 5% and 50% of points, respectively, relative to the centroid (i.e., the median latitude and longitude) of the animal’s distribution. All data points were included in the analysis, and no outliers were excluded. Furthermore, MCPs were used to assess the degree of overlap between individuals to determine home range overlap, providing important insights into the ecological relationships and interactions between individuals (Bivand and Rundel, 2021).

Kernel Density Estimation (KDE)

Kernel Density Estimation (KDE) was employed to identify core areas and hotspots within the home range of Sunda pangolins. The analysis used three levels of estimation: KDE 95% to estimate the overall home range, KDE 50% for core areas, and KDE 25% for hotspot areas where the pangolins spent most of their time. KDE works by estimating the probability density function of the animal’s location data, allowing researchers to map areas of high activity (Worton, 1987, 1989). In this study, the bandwidth (smoothing parameter) was selected using the "href" method, which is a commonly applied approach in home range studies as it balances bias and variance effectively (Worton, 1989). The grid size for the KDE analysis was set to the default automatic calculation by the kernelUD function in R, which adjusts the grid resolution based on the extent of the data. The kernel type used for the density estimation was the default bivariate Gaussian kernel, which is standard for home range analysis and provides a smooth, continuous estimate of the probability density of the animal being present at any location.

Local Convex Hull (LoCoH)

The Local Convex Hull (LoCoH) method was used to estimate the home range while accounting for potential physical barriers to movement. For Sunda pangolins in this landscape, barriers of concern include large river (Kinabatangan River), tributaries and areas of steep terrain, which can restrict movement. LoCoH extends the MCP method by constructing convex hulls based on a specified number of nearest neighbours, denoted by 'k'. In this study, the fixed-k LoCoH method (k-LoCoH) was employed, with k = 5 used to identify core areas and k = 10 for estimating the broader home range (Getz et al., 2007; Reinecke et al., 2014). The analysis used Euclidean distance by default to determine the nearest neighbours. No additional smoothing factor was applied, as LoCoH does not require smoothing when constructing local convex hulls.

Generalized Additive Models (GAMs)

Generalized Additive Models (GAMs) were used to estimate the home range by comparing the distribution of the pangolin's presence locations with pseudo-absence locations. These models, which allow for non-linear relationships between the predictor variables (spatial coordinates x and y) and the binomial response variable (presence vs. pseudo-absences), were fitted using the "mgcv" package in R (Hastie and Tibshirani, 1986). The smoothing parameter was automatically selected using generalised cross-validation. Pseudo-absence locations were uniformly distributed across a grid encompassing the pangolin’s known locations (presences). The GAM model was used to create a heat map of predicted presence probabilities across this grid, with a logit link function applied in the binomial family. A probability threshold was then applied to this map to delineate the estimated home range (Royle and Dorazio, 2008).

3.2.4 Analysis of movement patterns

In this study, the Expectation Maximization binary Clustering (EMbC) method was used to analyse the movement behaviours displayed by the Sunda pangolins, with the goal of identifying and categorizing different types of movement behaviours, such as foraging, resting, or traveling, based on their movement data. The analysis focused on the key parameters of heading and distance covered, to classify behaviours based on turning angle, and velocity. Out of the 12 pangolins monitored, nine were included in this analysis. These nine pangolins were selected because their tracking datasets met the minimum requirements for EMbC analysis, specifically having enough location fixes (≥12 fixes) collected over multiple consecutive days without large temporal gaps to yield meaningful results. This provides a meaningful basis for identifying and interpreting movement patterns. Of these nine pangolins, two were wild and seven were translocated.

EMbC was chosen because it is particularly effective at classifying complex movement data into clear behavioural categories, especially when working with small sample sizes. It provides a flexible and straightforward approach, using the Bayesian Information Criterion (BIC) to create optimal clusters that reveal patterns of activity, rest, and slow movement (Garriga et al., 2015, 2016). Unlike other methods, such as Hidden Markov Models (HMMs), which require assumptions about underlying processes, extensive data preparation, and large data sets (Leos-Barajas et al., 2017; Conners et al., 2021), EMbC is easier to use and interpret. However, while HMMs model the sequence of movements over time and can reveal how behaviours transition, EMbC categorises behaviours based on observed patterns at individual moments without considering their order or sequences of transitions. In summary, HMMs suit studies that need to model and understand the sequence of behaviours over time, whereas EMbC suits studies focused on classifying distinct movement behaviours based on observed data, especially with smaller sample sizes and when transitions between behaviours are not the main focus. Given that this study focused on classifying distinct movement behaviours from observed data, EMbC was the ideal choice. Its objective and data-driven approach minimises bias and error, making it well-suited for accurately identifying movement patterns in studies with limited data.

EMbC is a modelling approach that identifies clusters in binary data based on the likelihood that distinct underlying distributions generated the data (Garriga et al., 2015, 2016). The location data collected from nine pangolins were prepared and passed through the EMbC method. These clusters were expected to reveal patterns in the pangolins' movements, such as periods of intense activity versus periods of rest or slow movement. Several functions provided by the EMbC approach were employed to interpret the resulting clusters and examine specific aspects of the pangolins' movement behaviour. For example, the stbc function (speed-turn binary clustering) was used to cluster the data based on velocity and turning angle, which are key parameters in understanding animal movement patterns. The clustering algorithm was fine-tuned using the BIC to identify the most likely behavioural states. Following clustering, the sctr function was used to visualise the clusters, and the lblp function provided a temporal series of labelled behaviours. Additional analysis included examining histograms of distance covered (dst), heading (hdg), and the behaviour classifications (@A), which were derived from the clustering process. For each GPS deployment, the relevant variables extracted from the data frame included the latitude (lat), longitude (long), and DateTime variables. These variables are essential as they provide the spatial coordinates and temporal data needed for the clustering process. The id variable was also included to analyse the tracks of the individual pangolins. These selected variables were then passed to the stbc function, which is the core of the EMbC method, to perform binary clustering based on speed and turning angle.

The resulting clusters were interpreted using several key functions from the EMbC approach, each designed to provide specific insights into the movement patterns of the pangolins. The stts function was used to generate summary statistics for each cluster, helping to understand the overall distribution and characteristics of the movement behaviours. The sctr function produced scatter plots that visually represented the relationship between the key movement parameters (velocity and turning angle), allowing for the identification of distinct behavioural states. Different behavioural states were classified by the EMbC approach (LL, LH, HL, HH, NC), which are explained below, and in the discussion. These color-coded visualisations help to differentiate and interpret the movement patterns of the pangolins more effectively.

The lblp function labelled each cluster, enabling a clear temporal visualisation of how behaviours evolved over time, and chkp was used to check the accuracy and consistency of the clustering. A KML file was generated using the pkml function to enable detailed spatial inspection of the pangolins' movement paths in Google Earth, providing a geospatial context to the identified behaviours. These functions identify and visualise different aspects of the pangolins' behaviour. Understanding these patterns is important to understand the species' ecology, such as how they use their habitat and how their behaviours change in response to environmental factors. No specific parameters were needed to be manually set for these functions, as they are designed to automatically adapt to the input data.

The movement behaviour of the pangolins was examined using key attributes provided by the EMbC method, including distance covered, heading, velocity, and turning angle. Specific combinations of these attributes were used to distinguish behaviours; such as low velocity with high turning angles was indicative of localised foraging (LH); low velocity with low turning angles suggested resting (LL) and high velocity with low turning angles suggested directed traveling (HL). The histogram function (“hist”) was employed to plot the distribution of these attributes for each pangolin, which helped in visualising how frequently certain behaviours occurred, and in what context.

The observed locations and home range kernels for each pangolin and the home range kernel for each behaviour class were plotted using the "plot" and "points" functions, and the resulting data and figures were visualised and interpreted following the method of Garriga et al. (2015, 2016). This method involves using the EMbC framework to classify movement data into distinct behavioural categories based on parameters such as velocity and turning angle. By clustering these data points, the method allows for the creation of spatial kernels that represent the different behavioural states, enabling a detailed analysis of how each pangolin utilises its home range.

3.3 Results

3.3.1 Performance of tracking tags

After three days of tracking, Asa's GPS tag was found affixed to a tree, entangled in thick vines, on the fourth day. The tree was approximately 10 m tall and the tag was located about 6 m up in the tree, with one of the pangolin’s scales still attached. Cekal was successfully tracked for three days before the GPS tag was dislodged and found wedged between tree roots. On the 21st day, Cekal's carcass was discovered and identified through the microchip ID. An on-site wildlife veterinarian conducted an autopsy, which revealed that Cekal died of starvation, with little food found in its stomach. Cekal had been confiscated from illegal trade and was kept in captivity by the smuggler and authorities for more than 14 days, unlike other pangolins in the study, which were rescued and kept for only 1-3 days. This will be discussed in detail in the discussion section, below. Kirana was tracked for three days, after which the GPS tag was removed. Kirana’s initial tag was removed when the pangolin remained in its initial location. The decision was made to excavate the burrow, and after excavating it, it was discovered that the pangolin's tag was stuck on a tree root, impeding its mobility. Therefore, it was decided to replace the GPS tag with a VHF tag (BioTrack). After three days of tracking, the VHF tag was also dislodged and was found beneath dense shrubs.

VHF tags (Telenax) were attached to seven translocated pangolins: Wira, Tuah, Gagah, Oroi, Suka, Pesona, and Anggun; the tracking periods varied between 12 and 163 days. Wira was additionally fitted with a GPS tag (Telenax). Nonetheless, all but one of the pangolins disappeared, and their tags could not be located despite a thorough search of forest, river, and road routes. The only exception was Oroi, whose tag was found in an open area close to its sleeping site. The day before the tag was found, researchers observed another pangolin, presumed to be male based on its large size, inside Oroi's previous sleeping site. This was an unknown wild pangolin with no tag, as confirmed by camera trap images. This observation led to the hypothesis that the two pangolins may have interacted, possibly engaging in a fight or mating, which could have resulted in the tag becoming detached. However, there were no physical signs on the tag itself, such as damage or other indicators, that would confirm this hypothesis. Therefore, without direct evidence, this remains speculative. The tag was attached following the same method used for all radio-tagged pangolins.

The attachment to Oroi was comparable to the wild pangolins, which maintained long tracking periods, and the same tag was subsequently reused on another pangolin. This suggests that the detachment was more likely due to natural incidents (e.g., snagging on roots or animal interactions) rather than equipment failure.

Camera traps were set up outside Oroi's sleeping site to monitor potential interactions and to assess the effectiveness of the VHF tag in maintaining contact with the animal. However, no further images of pangolins were captured because the camera batteries ran out, which limited the ability to correlate the tag's performance with the pangolin's behaviour. Additionally, at the time, researchers did not have a fully working tag available to replace the dislodged one, which further hindered the ability to continue monitoring Oroi. This highlights the importance of ensuring that all equipment, including tags and cameras, is fully operational to effectively track and study the animals.

Two wild (“resident”) pangolins, Berkat and Galak, were fitted with VHF tags (Telenax, Mexico) and tracked for 134 and 202 days, respectively, during the study period. The tag of Berkat was later discovered on the ground beneath dense shrubs, whereas tracking of Galak continued until the end of the study period.

During tracking days, the GPS tag from e-Obs, Germany, only achieved 20% of the expected data download, indicating poor performance, as the tag could not retrieve as much data as anticipated. The GPS tag from Telenax, Mexico, was presumed to be defective because no data could be downloaded.

For individuals carrying both a GPS and a VHS tag, the average location error of the GPS and VHF tags was approximately 3 m during this study, based on a comparison between the coordinates recorded by the GPS Garmin and the actual location of the pangolins as confirmed visually. This level of accuracy was therefore relatively high, with tags accurately identifying the location of the tagged pangolins to within a few metres.

Regarding the attachment of the tags, the large and boxy shape of the GPS tag appeared problematic, as it caused the tag to become entangled or detached. Likewise, the smaller and more streamlined VHF tags attached to the pangolin's scales with cable ties appeared to fall off. However, VHF tags attached to the scales via flexible fabric appeared to have a more permanent hold. While both tag types were designed to be waterproof and resistant to extreme environmental conditions, including high humidity and temperature, the Telenax tag's failure raises questions about its reliability in tropical climates. In addition, the fact that some pangolins were found crossing rivers, oxbow lakes, and tributaries while wearing the tags indicates that the tags remained functional and effective even when submerged in water.

However, due to the loss of most tags during the study, detailed records of battery life were largely unavailable. Specifically, the e-Obs GPS tags were dislodged early in the study and only tested for a short period, preventing a thorough assessment of their battery performance. Several Telenax VHF tags were recovered, with one tag on Galak continuing to function for the longest recorded battery life of approximately six months. See **Table 3.2** for a summary of the Sunda pangolins captured and tagged.

Table 3.2: Summary of Sunda pangolins captured and tagged between December 2016 and January 2022, including transmitter type, date of capture/rescue, release date, successful tracking days, and reasons for tracking failure.

ID	Group	Transmitter used	Date of capture/rescue	Release date	Tracking day	Reason
Asa*	Translocated	Tamandua, 2AA, e-Obs, Germany	08-12-2016	09-12-2016	4	GPS tag dislodged.
Cekal*	Translocated	Tamandua, 2AA, e-Obs, Germany	23-02-2017	09-03-2017	4	GPS tag dislodged. Animal died.
Kirana*	Translocated	1. Tamandua, 2AA, e-Obs, Germany, and 2. TW3; BioTrack Ltd, Canada	10-08-2017	13-08-2017	9	GPS tag removed and replaced with VHF tag. Later, VHF tag dislodged.
Wira	Translocated	1. TGB-311; Telenax, Mexico, and 2. TXE304; Telenax, Mexico	03-08-2018	03-08-2018	68	Animal went missing. GPS and VHF tag were unable to be found.
Tuah	Translocated	TXE304; Telenax, Mexico	21-10-2018	21-10-2018	53	Animal went missing. VHF tag was unable to be found.
Berkat	Wild	TXE304; Telenax, Mexico	25-03-2019	25-03-2019	134	VHF tag dislodged.
Gagah	Translocated	TXE304; Telenax, Mexico	18-09-2019	18-09-2019	20	Animal went missing. VHF tag was unable to be found.
Oroi	Translocated	TXE304; Telenax, Mexico	15-02-2020	15-02-2020	12	VHF tag dislodged.
Suka	Translocated	TXE304; Telenax, Mexico	09-04-2020	09-04-2020	86	Animal went missing. VHF tag was unable to be found.
Pesona	Translocated	TXE304; Telenax, Mexico	11-08-2020	11-08-2020	163	Animal went missing. VHF tag was unable to be found.
Anggun	Translocated	TXE304; Telenax, Mexico	09-09-2020	09-09-2020	12	Animal went missing. VHF tag was unable to be found.
Galak	Wild	TXE304; Telenax, Mexico	14-03-2021	14-03-2021	202	Tracking ongoing.

*Individuals with insufficient tracking durations (less than 12 days) were not included in the subsequent movement and home range analyses.

3.3.3 Home range

A detailed breakdown of the MCP, KDE, and LoCoH estimates for each individual pangolin can be found in **Table 3.3**, while Appendix 1 includes graphs of the home range estimates for each pangolin using MCP, KDE, and LoCoH.

Home range of resident pangolins

The home range estimates for two wild (“resident”) pangolins, Berkat and Galak, were calculated using multiple methods, including MCP, KDE, and LoCoH (**Table 3.3**).

For Galak, a male resident pangolin, was monitored at 146 locations over a total of 202 days. The MCP estimates for Galak were 1.168 km² (MCP 100%), 0.992 km² (MCP 95%), and 0.514 km² (MCP 50%) (**Fig. 3.2b**). Using the KDE method, Galak’s home range was estimated at 1.929 km² for KDE 95%, 0.535 km² for KDE 50%, and 0.224 km² for KDE 25% (Fig. 3.4c). The LoCoH estimates for Galak were 0.812 km² (k=10) and 0.210 km² (k=5) (Fig. **3.2d**).

Likewise, for Berkat, a female resident pangolin which was monitored at 93 locations over a total of 134 days, the home range estimates were as follows: 0.691 km² (MCP 100%), 0.405 km² (MCP 95%), and 0.183 km² (MCP 50%) as shown in Fig. 3.5b. Additionally, the KDE method provided estimates of 1.302 km² for KDE 95%, 0.289 km² for KDE 50%, and 0.112 km² for KDE 25% (**Fig. 3.3c**). The LoCoH method, with different values of k, produced estimates of 0.319 km² (k=10) and 0.152 km² (k=5) for Berkat (**Fig. 3.3d**).

The LoCoH analysis provided additional insight into the spatial distribution of Berkat and Galak's home ranges. The LoCoH for Berkat exhibited a circular shape with a diameter of approximately 1.1 km, indicating relatively even distribution of movements throughout the home range. In contrast, the LoCoH for Galak was elongated with a major axis of approximately 1.8 km and a minor axis of approximately 1.3 km, suggesting that movements were concentrated in a specific direction. Analysis of the coordinates confirmed that this movement pattern aligns with the river and ridgeline features of the Kinabatangan River and Girang Oxbow areas. The MCP estimates tended to be smaller than the KDE and LoCoH estimates for both pangolins. The KDE 95% estimates were larger than the MCP 95% estimates and tended to capture more of the peripheral areas of the home range. The LoCoH estimates were generally smaller than the KDE estimates and tended to capture the core areas of the home range. Additionally, the home range estimates for Galak were larger than those for Berkat, potentially due to differences in sex, body size, habitat use, or other factors. The use of GAMs provided a more nuanced understanding of the spatial distribution of Berkat's and Galak's use across the study area. The resulting visualisation shows a smoothed distribution of their use, providing more detailed information on the distribution and intensity of pangolin use of the study area compared to traditional home range estimators (**Fig.3.4**)

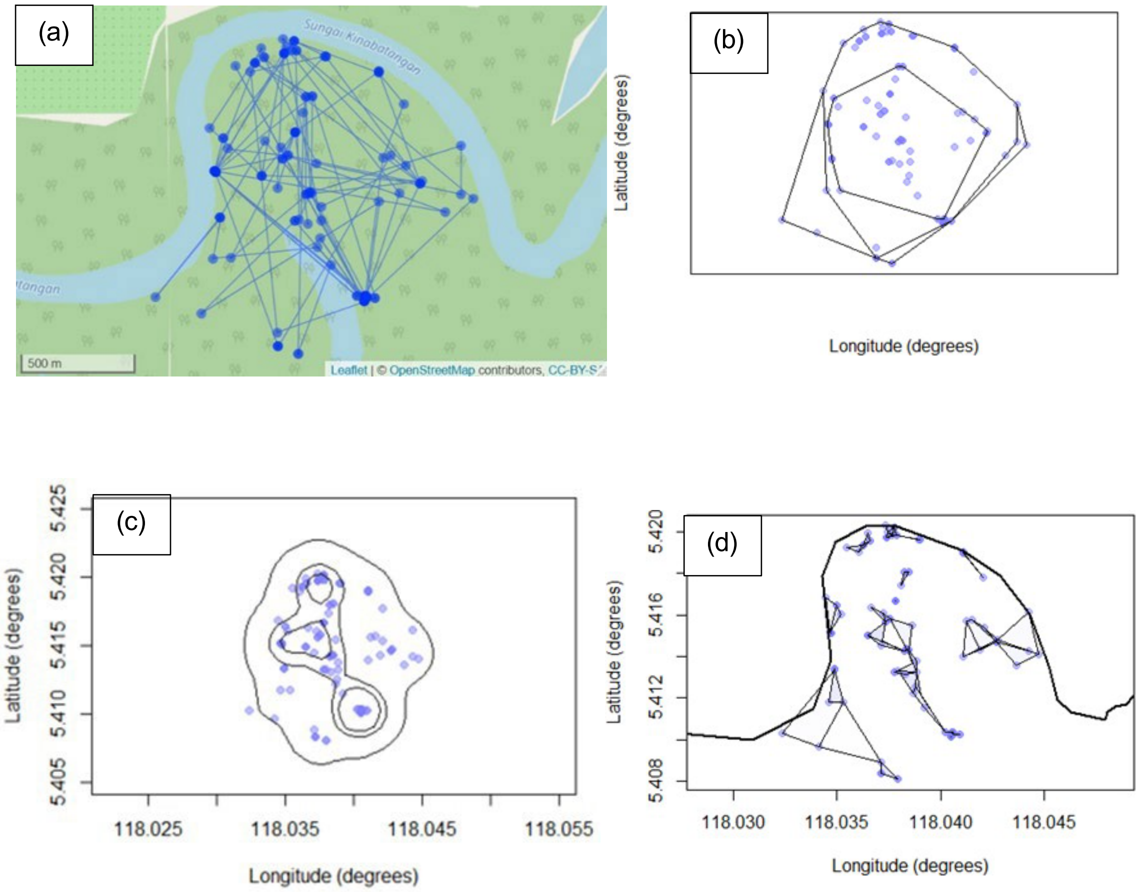

Fig. 3.2: (a) shows the GPS location points of Galak, plotted on a map of the study area, **(b)** displays the MCP 100%, 95%, and 50% estimates for the home range of Galak, plotted on the same map, **(c)** shows the contour plots of the KDE at 95%, 50%, and 25% for Galak's home range, and **(d)** displays the contour plot of Galak's home range using LoCoH method with a kernel density parameter of k=5. In this plot the river boundary is shown as a solid black line.

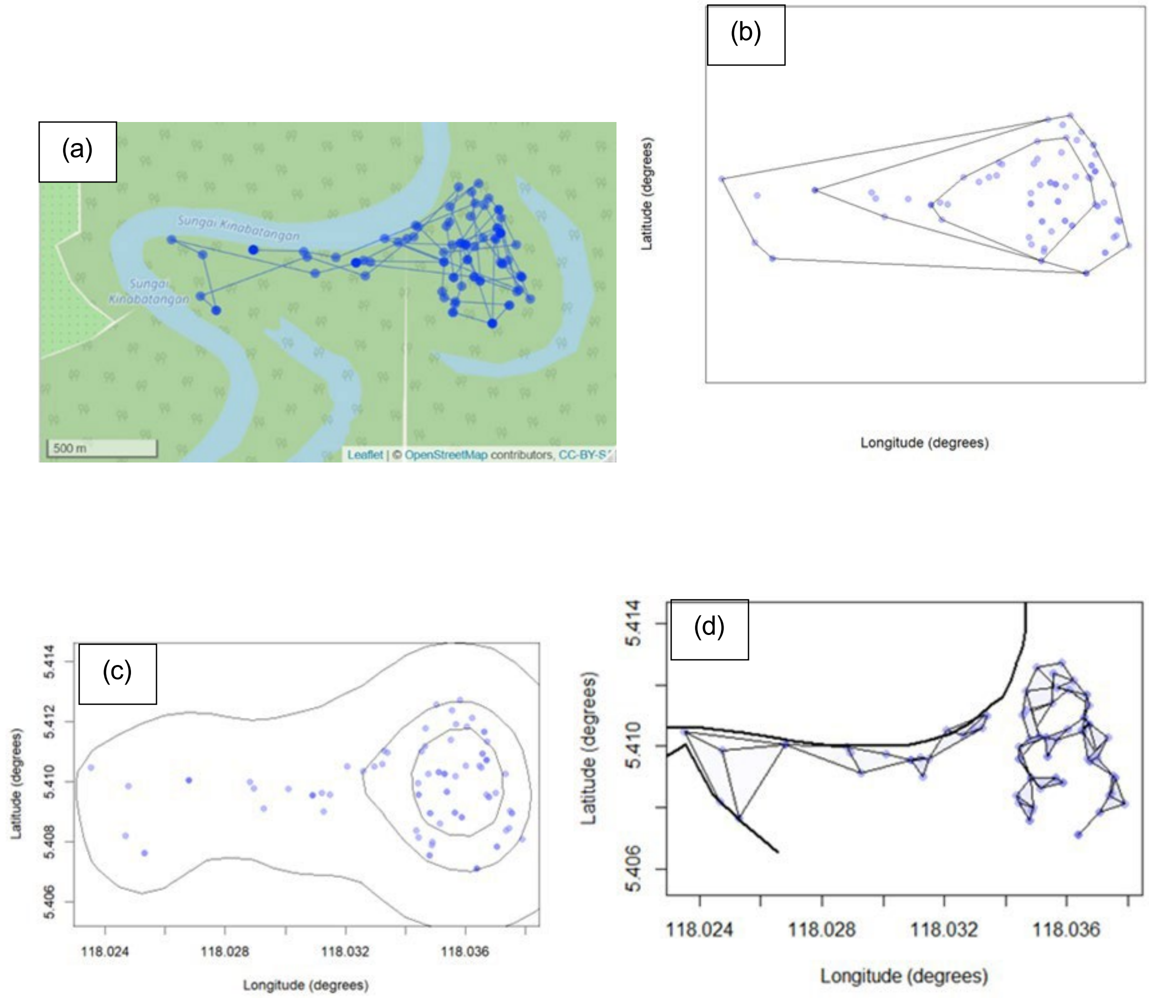

Fig. 3.3: **(a)** shows the GPS location points of Berkat, plotted on a map of the study area, **(b)** displays the MCP 100%, 95%, and 50% estimates for the home range of Berkat, plotted on the same map, **(c)** shows the contour plots of the KDE at 95%, 50%, and 25% for Berkat's home range, and **(d)** displays the contour plot of Berkat's home range using LoCoH method with a kernel density parameter of k=5. In this plot the river boundary is shown as a solid black line.

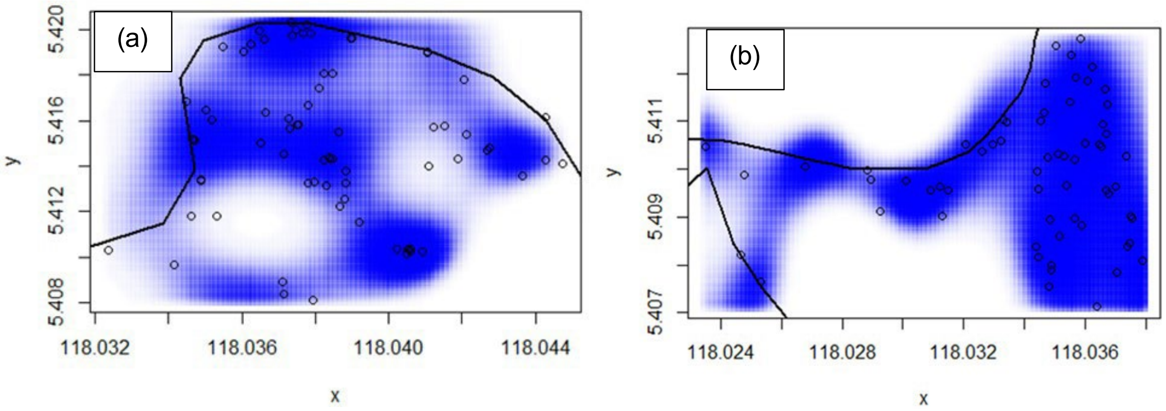

Fig. 3.4: **(a)** shows the smoothed distribution of Galak's use across the study area, and **(b)** displays the smoothed distribution of Berkat's use, as estimated by GAMs. The blue colour represents the probability density of Galak's and Berkat's use of the study area, with lighter blue colours indicating lower probability and darker blue colours indicating higher probability. In these plots the river boundary is shown as a solid black line.

Home range for translocated pangolins

The home range estimates for translocated pangolins tend to be larger than those of resident pangolins. For most individuals, the MCP 100% estimator produces smaller home range estimates compared to the KDE 95% estimator, but larger estimates compared to the LoCoH k=5 estimator (**Table 3.3)**. For example, Gagah has an MCP 100% of 4.435 km^2, while its KDE 95% estimate is 20.189 km^2, and its LoCoH k=5 estimate is 1.762 km^2. Similarly, Pesona has an MCP 100% of 28.905 km^2, but its KDE 95% and LoCoH k=5 estimates are 60.329 km^2 and 2.647 km^2, respectively. Core area and hotspot area estimates tend to be smaller when estimated using KDE and LoCoH compared to MCP. However, certain estimators could not be obtained for some individuals, such as Wira-A and Wira-B for LoCoH k=10 and k=5, which may be due to the limited number of locations and/or short monitoring period for those individuals.

On the other hand, Gagah's home range estimates were comparable in size to those of the resident pangolins. For translocated pangolins, LoCoH was only performed for Suka and Pesona, and GAMs were not performed for any of the translocated pangolins due to the small sample size and potential irregular movements. These estimates should therefore be treated with caution, particularly given the relatively short monitoring period (e.g., 20 days for Gagah). This issue will be discussed in greater detail in the discussion section.

Wira, a male translocated pangolin, was unique in this study as he was released, subsequently recaptured after 10 days, detained for one night and then re-released. This allowed for two distinct sets of home range estimates: Wira-A (10 days after the first release) and Wira-B (18 days after the rerelease). The separation of Wira's estimates into two periods was done to reflect the two discrete tracking intervals rather than a continuous dataset. Wira-A's home range estimates showed a smaller area compared to Wira-B, suggesting that Wira may have acclimatised to the environment better after his re-release, with his behaviour and habitat use becoming more similar to that of resident pangolins. The separation of Wira's estimates into two parts based on his release, recapture, and re-release is unique to this individual and was not performed for the other pangolins.

Home range overlap

The home range (MCP 100%) for the two wild pangolins, Galak and Berkat, were 1.168 km² and 0.691 km², respectively (**Table 3.4**). The overlap area between their home ranges was 0.174 km², accounting for about 15% of Galak's range and 25% of Berkat's range. This represents spatial overlap of sleeping site locations, but no temporal component was assessed. Thus, it indicates potential rather than simultaneous use of the same areas. Translocated pangolins exhibited larger, exploratory ranges compared to the more confined home ranges of resident pangolins. For example, Suka's exploratory range was 5.079 km², with only 20% overlap with resident areas (**Fig. 3.10**), while Gagah, Tuah, and Wira showed even smaller overlaps at 11%, 1.9%, and 3.8%, respectively.

Table 3.3: Summary of home range estimates for individual pangolins, including the population type, number of locations, days monitored, and various home range estimators, including home range (MCP 100%, MCP 95%, KDE 95% and LoCoH K=10), core areas (MCP 50% and KDE 50%) and hotspot areas (KDE 25% and LoCoH k=5). MCP represents Minimum Convex Polygon, KDE represents Kernel Density Estimate, and LoCoH represents Local Convex Hull. (Note: To accurately represent Wira's home range and core area, the analysis was separated into two parts based on Wira's release and recapture data. The home range and core area estimates were calculated separately for Wira's first release (Wira-A) and following recapture and re-release (Wira-B). This separation was necessary to account for any potential changes in Wira's behaviour and habitat use between its initial release and subsequent re-release.)

Individual	**Population**	**No. of locations**	**No. of days monitored**	**MCP 100% (km²)**	**MCP 95% (km²)**	**MCP 50% (km²)**	**KDE 95% (km²)**	**KDE 50% (km²)**	**KDE 25% (km²)**	**LoCoH k=10 (km²)**	**LoCoH k=5 (km²)**
Berkat	Resident	93	134	0.691	0.405	0.183	1.302	0.289	0.112	0.319	0.152
Galak		146	202	1.168	0.992	0.514	1.929	0.535	0.224	0.812	0.210
Anggun	Translocated	12	12	0.167	0.167	0.015	2.475	0.63	0.237	NA	NA
Gagah		15	20	4.435	4.141	0.656	20.189	5.412	1.762	NA	NA
Oroi		12	12	0.043	0.006	0.004	0.214	0.045	0.019	NA	NA
Suka		58	86	5.079	4.934	0.401	14.413	2.941	1.046	1.522	0.689
Pesona		67	163	30.929	28.905	11.776	226.067	60.329	24.529	10.311	2.647
Wira-A		28	68	0.249	0.019	0.000	1.435	0.236	0.092	NA	NA
Wira-B				4.137	3.580	1.670	21.578	5.468	2.170	NA	NA
Tuah		18	53	19.431	12.141	2.293	114.289	26.835	9.846	NA	NA

* NA values in the LoCoH columns indicate that this method was not applied to the corresponding individual due to insufficient data.

For individuals with very short tracking durations and few relocations (e.g., Anggun, Oroi, Gagah), KDE estimates are presented for completeness but should be interpreted with caution. The low sample sizes limit their reliability and they do not accurately reflect stable home range estimates.

Table 3.4: The MCP 100% home range size for each individual pangolin and the overlap area (in km²) between each pair of individuals. Percentage of overlap and MCP 100% home range size are also included for comparison.

	MCP 100% (km²)	Overlap area (km²)	Percentage of overlap	In comparison with	MCP 100% (km²)	Percentage of overlap
Galak	1.168	0.174	0.149	Berkat	0.691	0.252
		1.019	0.872	Suka	5.079	0.201
		0.492	0.421	Gagah	4.435	0.111
		0.368	0.315	Tuah	19.431	0.019
		0.142	0.121	Wira	4.137	0.038

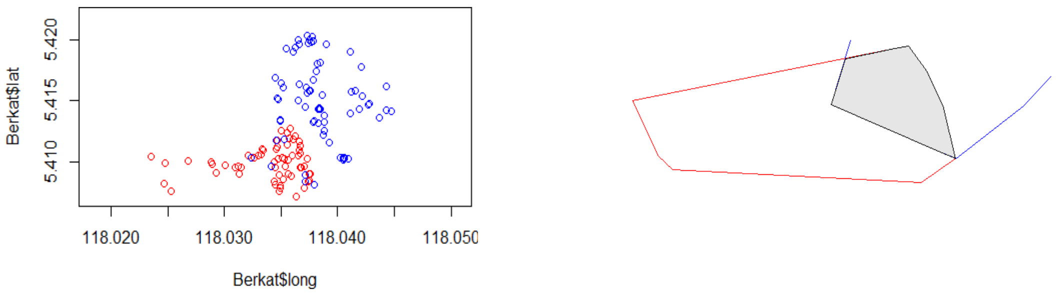

Fig. 3.5: Home range overlap between Berkat and Galak, two resident Sunda pangolins in the study area. The MCP 100% estimates are shown for each individual, with Berkat's home range shaded in red and Galak's in blue. The overlap area is shown in grey, indicating the area where both pangolins were detected.

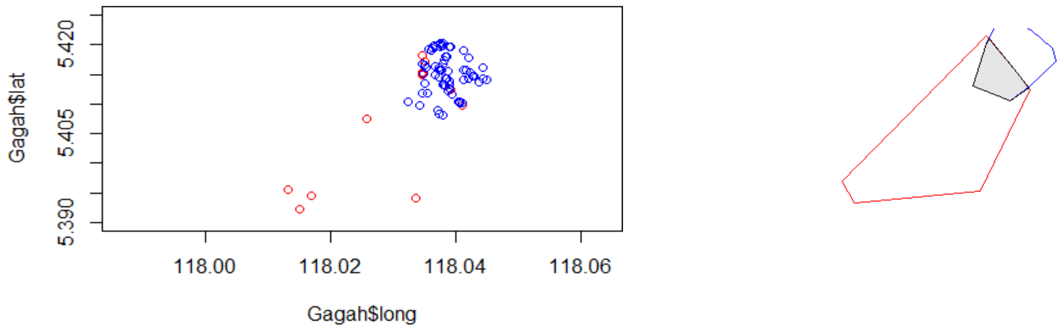

Fig. 3.6: Home range overlap between translocated pangolin, Suka and resident pangolin, Galak in the study area. The MCP 100% estimates are shown for each individual, with Suka's home range shaded in red and Galak's in blue. The overlap area is shown in grey, indicating the area where both pangolins were detected.

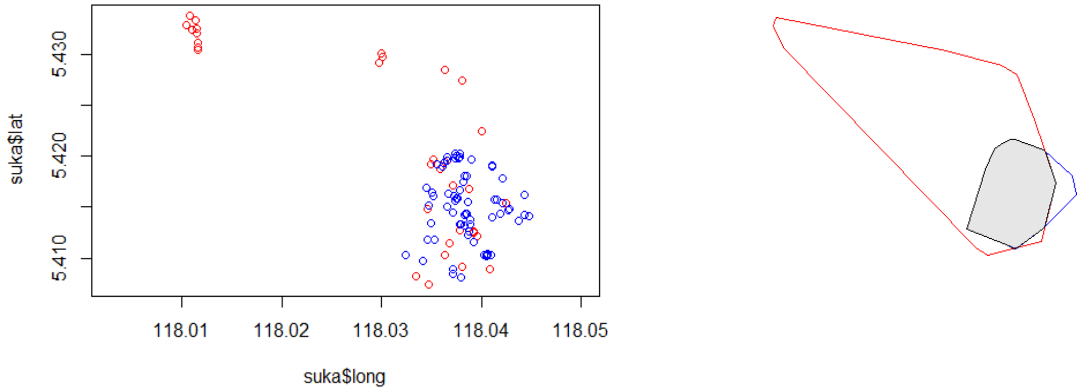

Fig. 3.7: Home range overlap between translocated pangolin, Gagah and resident pangolin, Galak in the study area. The MCP 100% estimates are shown for each individual, with Gagah's home range shaded in red and Galak's in blue. The overlap area is shown in grey, indicating the area where both pangolins were detected.

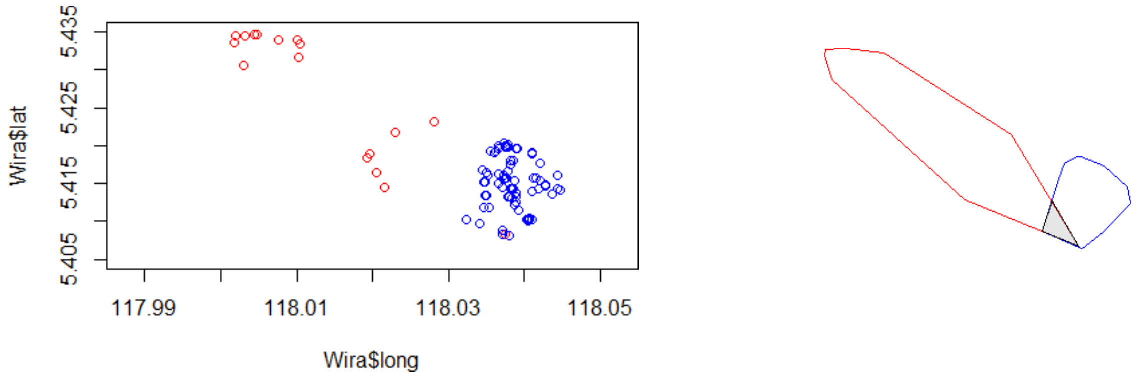

Fig. 3.8: Home range overlap between translocated pangolin, Wira and resident pangolin, Galak in the study area. The MCP 100% estimates are shown for each individual, with Wira's home range shaded in red and Galak's in blue. The overlap area is shown in grey, indicating the area where both pangolins were detected.

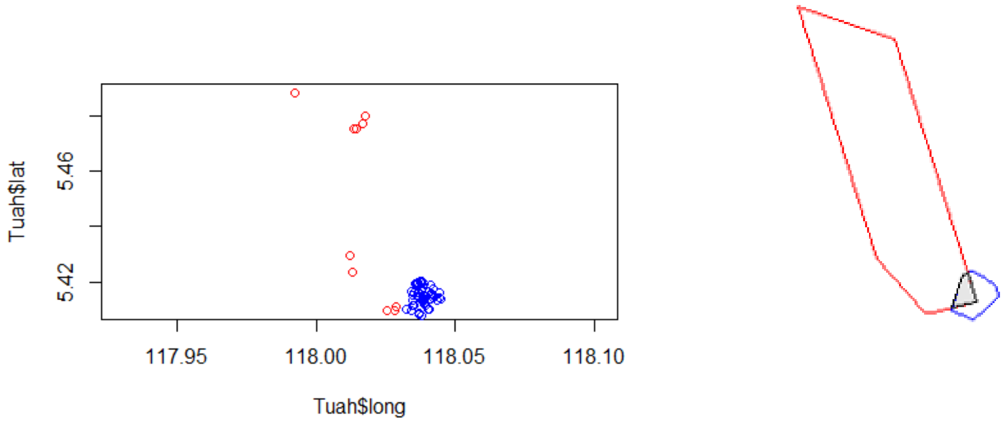

Fig. 3.9: Home range overlap between translocated pangolin, Tuah and resident pangolin, Galak in the study area. The MCP 100% estimates are shown for each individual, with Wira's home range shaded in red and Galak's in blue. The overlap area is shown in grey, indicating the area where both pangolins were detected.

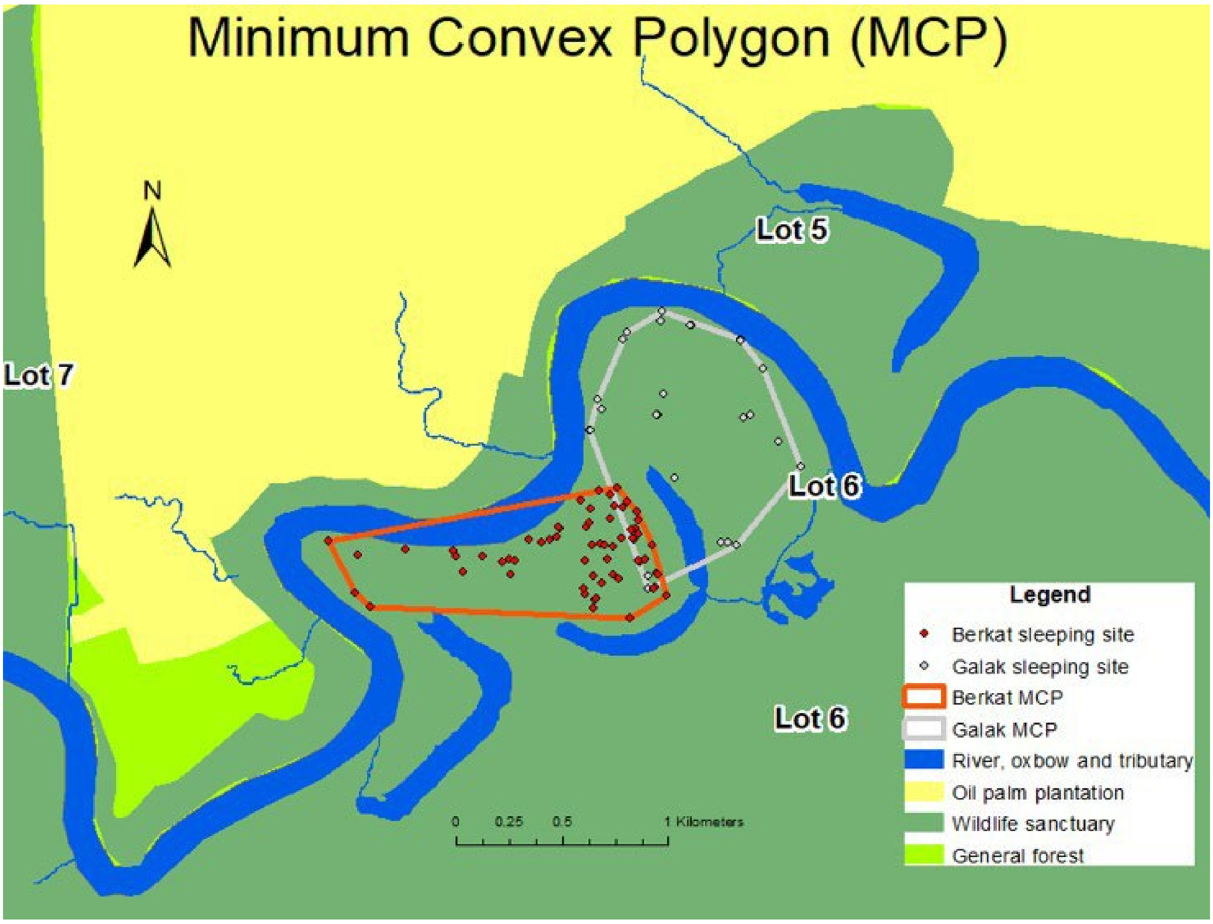

Fig. 3.10: Map depicting the overlap of male and female resident Sunda pangolins' home ranges, highlighting potential areas of intersexual interactions and resource competition.

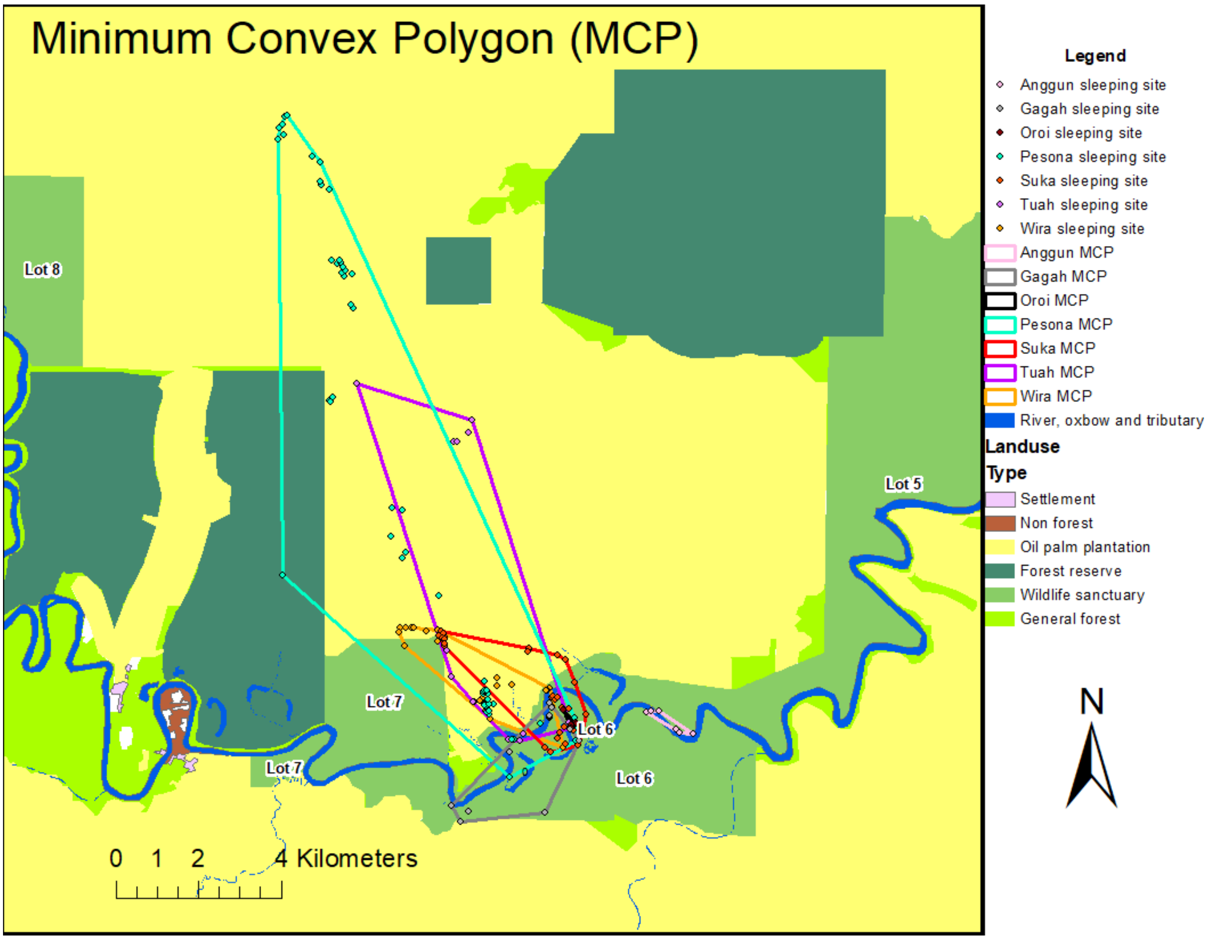

Fig. 3.11: Map showing the overlap of home ranges between resident and translocated Sunda pangolins.

3.3.3 Analysis of movement patterns

This section presents the analysis of the movement patterns in both resident and translocated Sunda pangolins, using the Expectation-Maximization binary Clustering (EMbC) method. The analysis examined turning angle and velocity to classify and differentiate various movement behaviours.

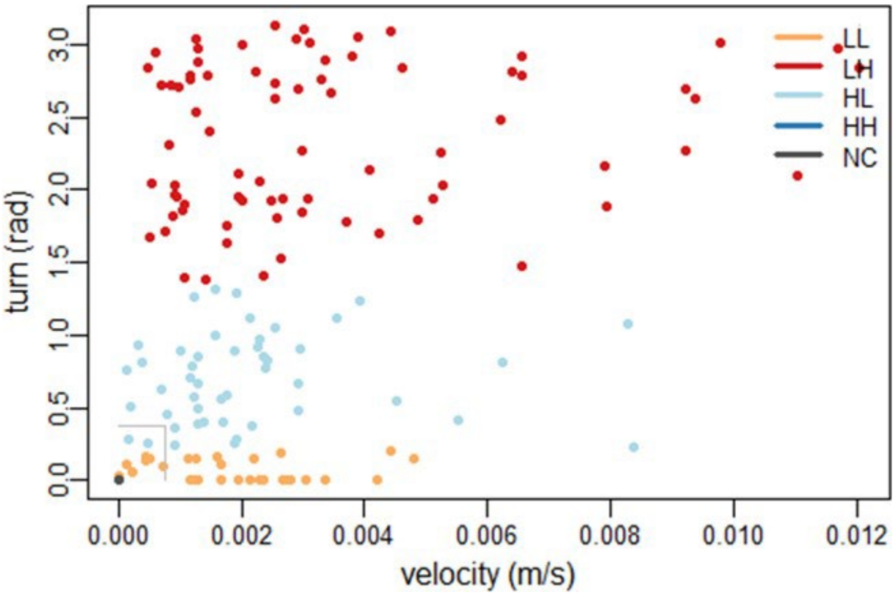

Fig. 3.12: Cluster scatter-plot of behavioural classifications of resident pangolins as determined by EMbC analysis. Different colours of dots represent the following behavioural states: LL (Low velocity, Low turning angle - yellow), LH (Low velocity, High turning angle - red), HL (High velocity, Low turning angle - blue), HH (High velocity, High turning angle - dark blue), and NC (No classification or unclassified - purple).

The EMbC method provided a quantitative analysis of pangolin movement patterns by categorising the data into distinct behavioural modes based on velocity and turning angle. The graph resulting from this analysis (**Fig. 3.12**) shows different colours of dots that represent the behavioural classifications of the pangolins into up to four potential behavioural classifications; low velocity, low turn angle (LL), low velocity, high turn angle (LH), high velocity, low turn angle (HL), high velocity, and high turn angle (HH), as well as NC (not classified). The LH behaviour, characterised by low velocity and high turn values, was the most frequent, suggesting that pangolins often engage in activities like foraging or exploring, where slow speed and frequent direction changes are typical. The HL behaviour, with lower velocity and moderate turn values, was the second most frequent, indicating movements that are slower but still involve some directional changes. The LL behaviour, which had a lower frequency, was associated with low velocity and low turn values, possibly representing resting or minimal movement periods. No HH behaviour (high velocity with high turns) was detected, indicating that resident pangolins do not exhibit fast, sharp-turning movements. The EMbC method allowed for a quantitative assessment of these behaviours, objectively determining the frequency of each movement type beyond visual interpretation.

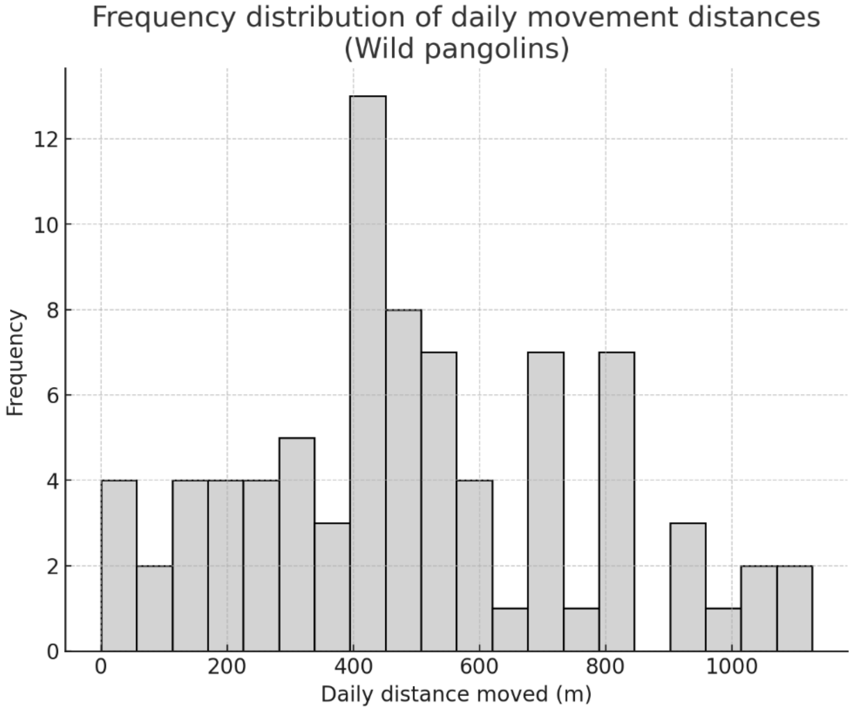

Fig. 3.13: Frequency distribution of movement distances for resident pangolins. This bar chart shows the frequency of movements observed across different distance categories for VHF tagged of two resident pangolins. The data from these two individuals were combined due to the small sample size to provide a more robust analysis.

There was a clear pattern in the frequency distribution across the distance categories (**Fig. 3.13**), with the highest frequency observed within the 0-200 m/day range, showing that the two resident pangolins most often travelled this distance range each day. The frequency values decreased as the distance category increased, with the next highest frequency values falling within the 200-600 m/day distance category, and the lowest frequency values within the 600-1200 m/day distance category. These distance categories were defined based on the observed movement patterns in the study, with each bin selected to capture distinct ranges of daily movement that reflect how far resident pangolins typically travelled within a day. This distribution was based on combined data from two VHF-tagged resident pangolins, one female and one male, due to the small sample size. Because of this, the data were combined to maximise the dataset. The bar chart for translocated pangolins was analysed separately and is presented below, where differences between residents and translocated animals are reported in more detail. This result suggests that resident pangolins most frequently engaged in shorter distance movements, with fewer instances of travelling longer distances.

Resident pangolins' turning angles, measured in radians, are shown in the bar chart (**Fig. 3.14**), which illustrates the distribution of heading values between location fixes on successive days. While the chart suggests some variation in movement directions, there is a noticeable increase in frequency for headings between 5.5 and 6.5 radians. This indicates that pangolins may tend to move more frequently in these directions, possibly due to environmental factors or a natural directional preference. It is important to note that these heading values are relative and do not correspond to specific cardinal directions, as the exact orientation cannot be determined from this data alone.

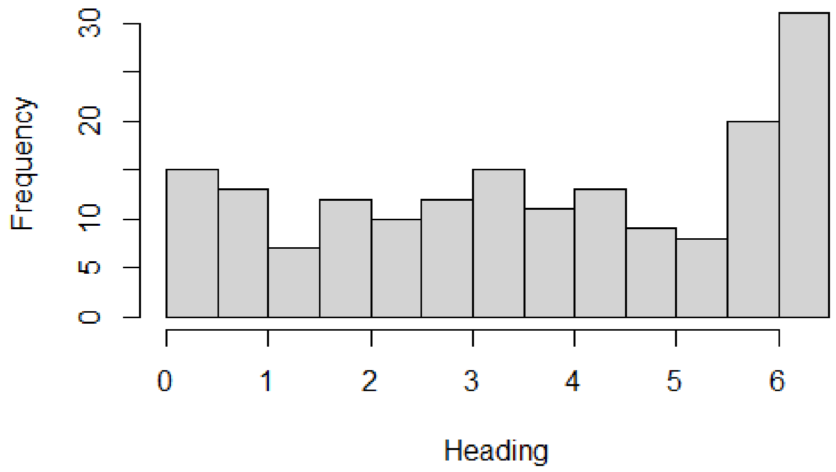

Fig. 3.14: Frequency distribution of movement headings for resident pangolins. This bar chart depicts the frequency distribution of movement headings for resident pangolins.

Movement behaviour of translocated Sunda pangolins

The EMbC analysis of translocated pangolins revealed a distinct pattern in their movement behaviour, as evidenced by the distribution of dots in the velocity-turn graph (**Fig. 3.15**). Most of the dots were classified as HH, with denser concentrations observed in the upper left quadrant of the graph, corresponding to higher turning angles and high velocity, indicating translocated pangolins exhibit rapid movements with frequent changes in direction. LH behaviour was the second most frequently observed, characterized by relatively low velocity but high turn angles. LL behaviour was also present but less frequent, indicating slow and steady movements with little change in direction. Only two purple dots were observed, indicating NC (not-classified) behaviour. HL behaviour, which would be characterised by high velocity and low turning angle, was absent from the graph. This suggests that translocated pangolins do not engage in fast, straight-line movements in the new environment. Instead, their movements are characterised by either rapid, sharp turns (HH behaviour) or slower, cautious turns (LH behaviour).

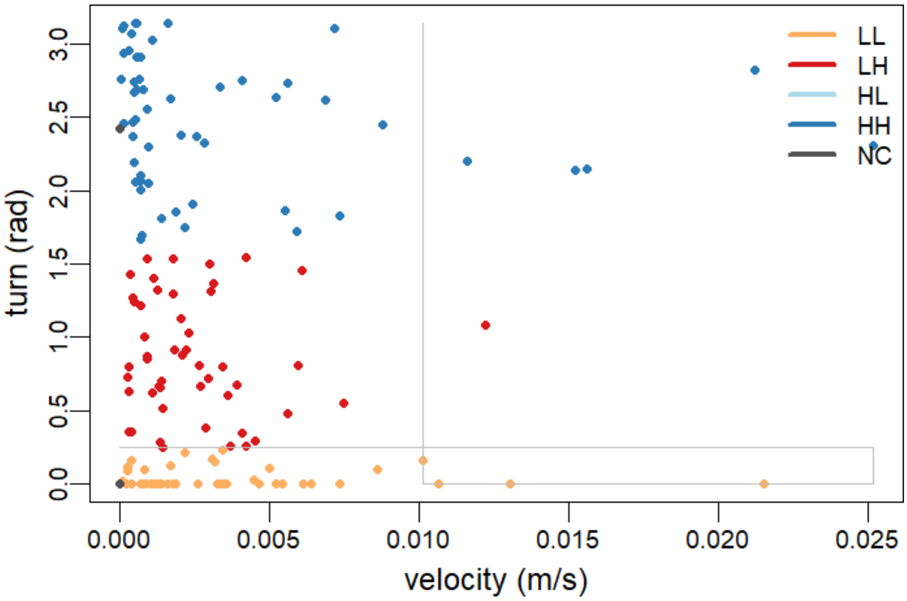

Fig. 3.15: Cluster scatter-plot of behavioural classifications of translocated Sunda pangolins as determined by EMbC analysis. The dots are colour-coded to represent different behavioural states: LL (Low velocity, Low turning angle - yellow), LH (Low velocity, High turning angle - red), HL (High velocity, Low turning angle - blue), HH (High velocity, High turning angle - dark blue), and NC (No classification or unclassified-purple).

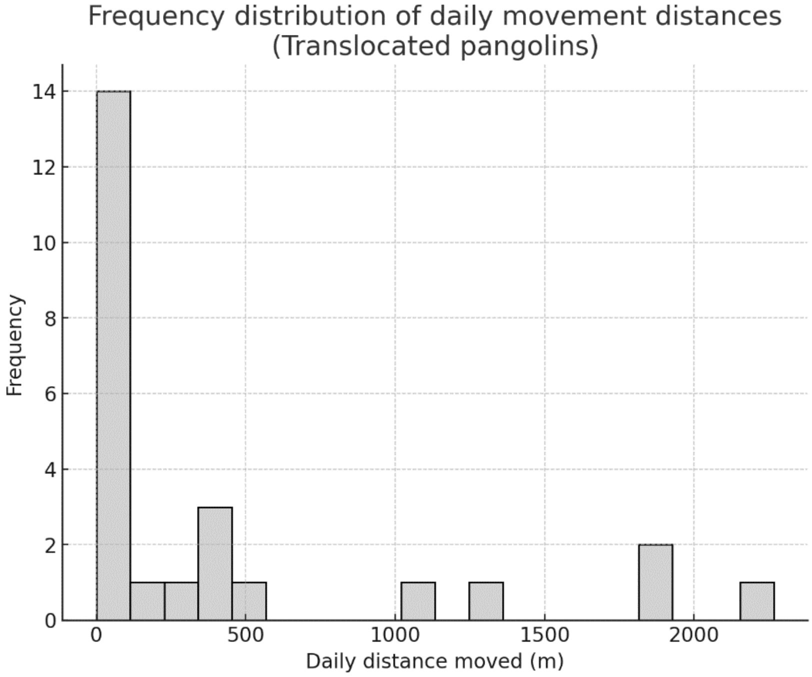

Fig. 3.16a: Frequency distribution of movement distances for translocated pangolins. This bar chart shows the frequency of movements observed across different distance categories for seven VHF tagged translocated pangolins.

The EMbC analysis of movement behaviour revealed that translocated pangolins generally travelled longer distances per day compared to resident pangolins (**Fig. 3.16a**). Specifically, most of the translocated pangolins covered distances between 0 to 2,500 m/day, with a significantly higher frequency observed within this range. These bin distances were defined by analysing the observed movement data and choosing intervals that captured the most common daily travel distances. The choice of 0 to 2,500 m/day as the primary range was based on where the highest concentration of daily movements occurred. Although some individuals reached maximum values of just over 2,000 m/day, the majority of their daily movements remained within shorter ranges. Using the same x-axis scale as **Fig. 3.16b** (0-1,200 m/day), translocated pangolins showed more frequent movements beyond 200 m/day, with occasional movements reaching up to 1,200 m/day.

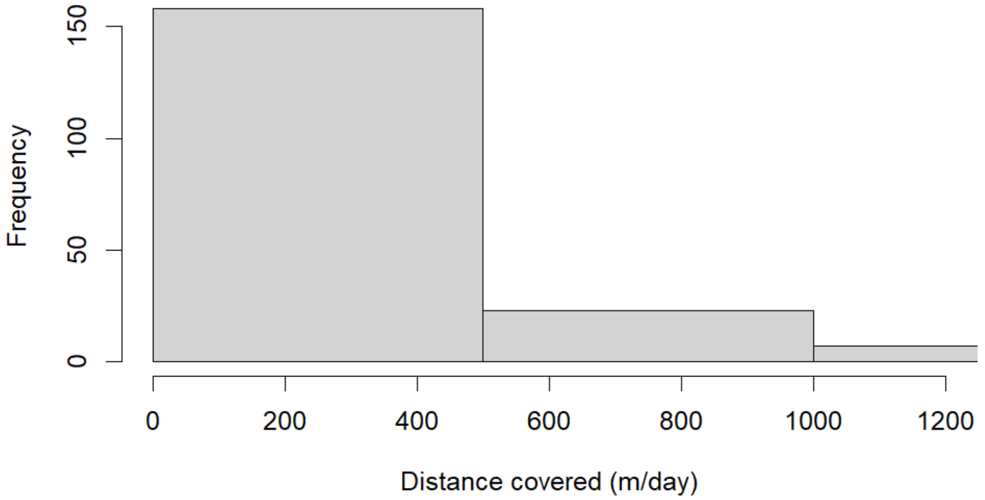

Fig. 3.16b: Frequency distribution of movement distances for translocated pangolins (with x-axis scaled to 0-1,200 m/day). This bar chart shows the frequency of movements observed across different distance categories for VHF tagged of seven translocated pangolins.

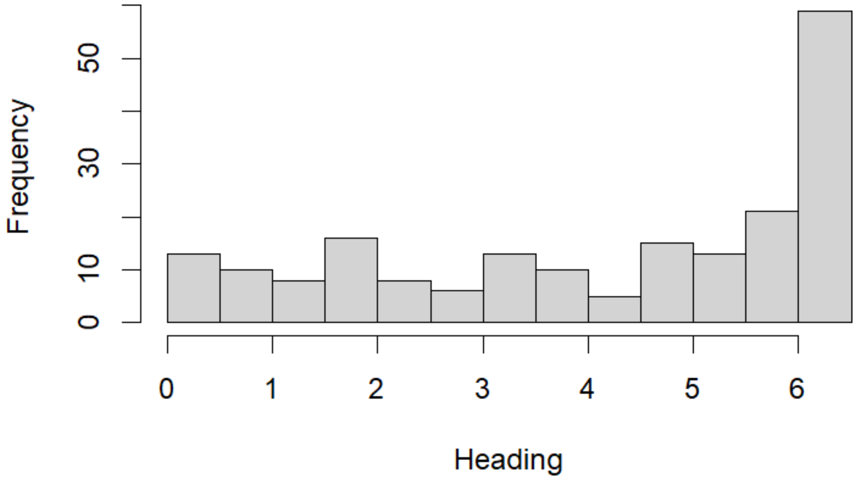

Fig. 3.17: Frequency distribution of translocated pangolins' movement headings. This graph shows the frequency of observed headings across different values.

This EMbC analysis resulted in a graph showing a distribution of heading values with a noticeable increase in frequency towards the right side, particularly for heading values greater than 6. This suggests that translocated pangolins may exhibit a preference for movement in that direction. The pattern observed indicates a potential directional preference, but further analysis would be required to determine if this aligns with specific environmental factors or movement tendencies.

Daily movement by resident and translocated pangolins

The analysis of daily distance travelled showed no significant difference between resident and translocated pangolins **(Fig. 3.18)**. Resident pangolins travelled an average of 292 m/day (±220 m SD), while translocated pangolins travelled slightly further on average at 384 m/day (±236 m SD). However, the Welch two-sample t-test indicated that this difference was not statistically significant (t=-0.52, df=1.64, p=0.67; **Table 3.5**).

Meanwhile, a comparison of daily movement by sex suggested that males travelled further on average than females **(Fig. 3.19)**. Males recorded a mean daily distance of 484 m/day (±202 m SD), compared to 188 m/day (±115 m SD) for females. The Wilcoxon rank-sum test confirmed that this difference was statistically significant (W=2, p=0.038; **Table 3.5**).

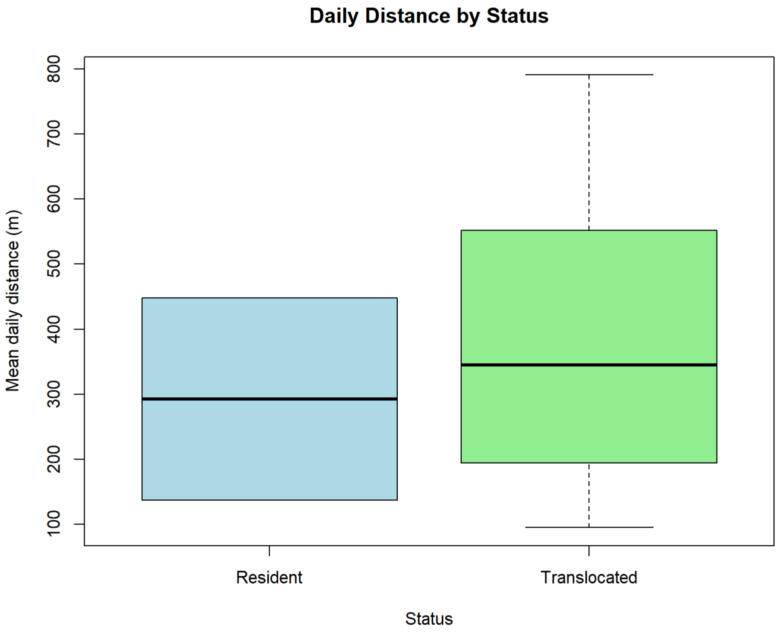

Fig. 3.18: Boxplot showing mean daily distance (m) travelled by resident (n=2) and translocated (n=7). The difference was not statistically significant (Welch t-test, p=0.67).

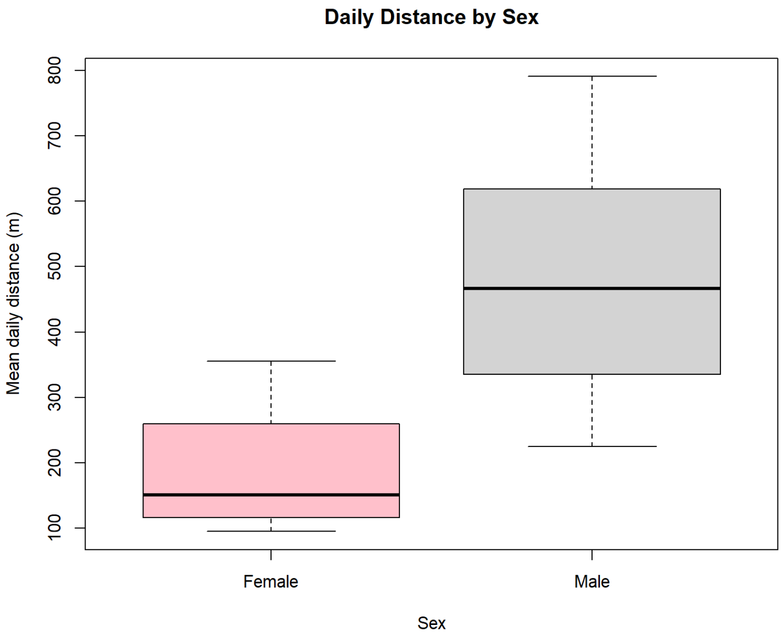

Fig. 3.19: Boxplot showing mean daily distance (m) travelled by female (n=4) and male (n=5) Sunda pangolins. The difference was statistically significant (Wilcoxon test, p=0.038).

Table 3.5: Summary of statistical tests comparing mean daily distance travelled (km) by Sunda pangolins across status (resident vs. translocated) and sex (female vs. male).

Comparison	Group 1	n	Mean (m)	SD (m)	Group 2	n	Mean (m)	SD (m)	Test result
Status	Resident	2	292	220	Translocated	7	384	236	Welch t=-0.52, df=1.64, p=0.67
Sex	Female	4	188	115	Male	5	484	202	Wilcoxon W=2, p=0.038

3.4 Discussion

3.4.1 Detection and tracking of Sunda pangolins

Pangolin detection is a difficult task, as observed in the present study, despite multiple survey methods, including camera trapping, inspection of potentially suitable sleeping sites, and coverage of large areas. This difficulty has also been reported in other studies, including a global study utilising many camera traps (Kwaja et al., 2019). Opportunistically captured pangolins in this study nevertheless provided important opportunities to collect samples and fit radio tags, enabling insights into their behaviour and ecology.

The present study successfully obtained meaningful insights into Sunda pangolins' spatial ecology and movement behaviour through VHF and GPS tagging. Tracking individual pangolins with these devices has proven to be effective in acquiring necessary data and knowledge about the general pangolin population, as demonstrated in previous studies by Lim and Ng (2007, 2008), Ching et al. (2017), and Gray et al. (2022). The trial of GPS tags in this study was not successful, as field observations suggested that the particular GPS models used interrupted or disrupted pangolin behaviour. As a result, GPS tags were discontinued and VHF tags were used instead. These issues relate to the specific models employed here, rather than GPS technology in general.

Despite the limitations of GPS tags, important data on home range and movement were still obtained using VHF tags. The case of Cekal, a pangolin that was released after being held in captivity for an extended period, provides a crucial learning opportunity. Cekal, who had been confiscated from illegal trade and kept in captivity for over 14 days, was found deceased on the 21st day of the study after being released. An autopsy conducted by an on-site wildlife veterinarian revealed that Cekal had died of starvation. This case highlights the complex challenges faced by pangolins that have experienced prolonged captivity. While the tagging process in this study was conducted under strict protocols and with minimal handling time, Cekal's case shows the need to consider the additional previous stress that such animals may have endure. This experience emphasises the critical need for highly trained personnel and specialised protocols when dealing with pangolins that have been subjected to illegal trade and extended captivity. It also strengthens the importance of ongoing improvement in tracking methods and post-release monitoring to ensure the well-being of these animals.

Given the unique anatomical characteristics of pangolins, traditional collaring methods have proven ineffective for this species. However, using smaller and streamlined VHF tag designs, following the attachment method described by Ching et al. (2019), has shown to be more effective in this study. While GPS technology offers greater potential for obtaining more frequent and accurate data, the large and boxy shape of the GPS tags tested here limited their success. Designing lighter and more flexible tags tailored to pangolins could overcome these challenges, enabling higher-resolution movement data without compromising animal welfare. Such developments would be valuable for long-term monitoring and conservation planning, as more precise data on ranging behaviour, dispersal and survival are essential for managing populations in human-modified landscapes.

3.4.2 Home range of Sunda pangolins

Home range estimation is a critical aspect of understanding the spatial ecology of pangolins. The study utilised multiple methods to estimate the home range of Sunda pangolins. A total of 12 individuals were fitted with tracking devices, nine pangolins provided the most consistent and reliable data, which were used to generate the home range estimates. These results describe the space use of these nine individuals and should not be generalised to the wider population given the small sample and variable tracking durations. The different estimators have distinct strengths and limitations, which are considered in interpretation.

The home range estimates for Sunda pangolins in this study were generally small compared to those reported for other medium-sized mammals, with resident individuals (e.g., Berkat and Galak) showing ranges of less than 1.2 km². These findings suggest relatively restricted spatial use, likely reflecting the species' specialised myrmecophagous diet and reliance on specific habitat features such as tree hollows. Conversely, translocated pangolins displayed larger and more variable ranges (e.g., Suka and Tuah), consistent with exploratory movements following release. Different home range estimators (MCP, KDE, LoCoH and GAMs) provided complementary perspectives on space use. MCP offered a simple overview but tended to oversimplify space use; KDE captured irregularities but often inflated range size; LoCoH better highlighted core areas and movement corridors and GAMs illustrated spatial activity patterns but were limited where physical barriers shaped movement.

These differences highlight the importance of using multiple estimators to provide a more nuanced understanding of pangolin spatial ecology.

The study provided insights into the differences in spatial use between resident and translocated pangolins. Resident pangolins exhibited relatively small and stable home range, while translocated pangolins showed much larger and more variable exploratory areas. Although MCP, KDE and LoCoH were applied to estimate space use, it is important to note that these values for translocated individuals are better interpreted as exploratory movement ranges rather than true home ranges in the ecological sense, given the short tracking durations and the likelihood of disorientation after release.

Home range, in ecological terms, is typically defined as the area an animal regularly uses to find food, mates, and shelter over a certain period. For resident pangolins, this concept is relatively straightforward, as these individuals are familiar with their environment, and their movements are likely reflective of their established home range. However, the situation is quite different for translocated pangolins. After release, these animals are placed in an unfamiliar environment, leading to movements that may not reflect an established home range but rather an exploratory phase as they search for suitable habitat, food, and shelter.

Thus, the space use estimates for translocated pangolins in this study should be interpreted as exploratory movement post-release, rather than stable home ranges. While these individuals did not settle within the study area, the patterns still provide useful indications of the scale and nature of their exploratory behaviour immediately after release. This information can help to highlight the challenges of translocation and underscore the importance of careful site selection and post-release monitoring.

The findings from this study suggest that the movements of translocated pangolins are driven by the need to explore and adapt, rather than by established ecological patterns observed in resident animals. Therefore, comparisons between translocated and resident pangolins’ home range estimates should be made with caution, as they likely do not represent the outcomes of similar ecological processes.

One unique and informative case in the study was that of Wira, a male translocated pangolin. Wira was initially released in a forested area but was later recaptured after moving into a nearby oil palm plantations. Researchers were concerned about the risks that Wira might face in these plantations, such as poaching risk and accidental capture from plantation workers. Consequently, the decision was made to recapture and re-release Wira in a more suitable forested area. However, despite this intervention, Wira returned to the oil palm habitat and he was tracked for 18 days before going missing. Wira's case highlights that translocated pangolins may readily utilise oil palm landscapes, which provide abundant ant and termite resources, even though these habitats are also associated with higher risk. This example highlights the need to better understand how pangolins interact with agricultural areas (e.g., oil palm plantations) and to account for such realities in translocation and management planning.

Further studies are needed to determine whether this pattern is consistent across other individuals, particularly in how they might respond to various types of habitats post-translocation. Wira's case shows that estimates for translocated pangolins more likely reflect exploratory use of space rather than stable home ranges. Such estimates must therefore be interpreted with caution when evaluating translocation strategies and release site suitability.

Therefore, the home range estimates for translocated pangolins may not fully represent their preferred home range, as these estimates likely reflect their exploratory movements rather than a stable, established territory. The estimators used might not accurately capture the true spatial behaviour of these individuals in their new environment.

The choice of home range estimation methods, such as MCP and KDE, is critical for representing areas used by animals (Boyle et al., 2009). These estimators are most informative when applied to stable use areas, such as those observed for the resident pangolins. For the translocated individuals, whose movements were highly dynamic, the resulting estimates are better interpreted as exploratory ranges rather than true home ranges. Given the limited dataset, the analysis mainly demonstrates how these methods perform under such contrasting movement contexts, rather than providing definitive measures of space use for all pangolins.

By using both MCP and KDE methods, this study aimed to produce estimates that account for the broader movements of resident pangolins while also identifying core areas. As expected, MCP tends to yield larger estimates compared to KDE, reflecting its tendency to encompass the outermost locations and capture the full extent of observed movements (Boyle et al., 2009; Lavar et al, 2010).

Furthermore, the study's application of these methods to translocated pangolins offers additional insights. For translocated individuals, whose movements may reflect an exploratory phase rather than an established home range, the use of conservative estimates becomes even more critical. By encompassing a larger area, these estimates help to ensure that the animals' movements are not underestimated, which is crucial for understanding their adaptation to new environments and for making informed decisions about future translocation efforts.

This study contributes to the existing literature by showing how conservative home range estimates can highlight differences between resident and translocated pangolins. Resident individuals displayed small, stable ranges, whereas translocated pangolins exhibited much larger, exploratory areas. The practical implication is that release planning must anticipate such extensive movements, which can increase risks and thus identify release sites with sufficient habitat and lower human pressures.

Additionally, the core area should represent the area of highest use, and the hotspot area should represent areas of the highest intensity of use (Gray et al., 2022). For the resident pangolins, the MCP 100% and MCP 50% were used for the home range and core area, respectively, as they are widely used and easily interpreted, whereas the KDE 25% and KDE 50% were used for hotspot areas, as they represent high-intensity use and are also widely used in the literature. For translocated pangolins, both MCP and KDE are valuable methods for estimating home range, but KDE may be preferred over MCP because it allows for the creation of more nuanced and predictive estimates that can better capture the expanded and often irregular movement patterns observed in these animals as they explore and adapt to new environments.

Translocated pangolins are likely to exhibit more extensive and less predictable movement patterns compared to resident pangolins, whose movements are generally more confined and consistent within established home ranges. For example, in this study, translocated individuals like Suka and Pesona showed significantly larger home range estimates when using KDE compared to MCP, despite having a similar number of location points. Suka's KDE 95% estimate (14.413 km²) was much larger than the MCP 100% estimate (5.079 km²), indicating that KDE was more effective in capturing the broader and potentially erratic movements of Suka. Similarly, Pesona's KDE 95% estimate (226.067 km²) vastly exceeded the MCP 100% estimate (30.929 km²), further underscoring how KDE can capture the full extent of movement in such cases. However, because KDE is sensitive to small sample sizes, especially with translocated individuals that were tracked for relatively short periods, these values should be interpreted cautiously as indicative of exploratory movement rather than precise home range estimates.

In contrast, resident pangolins like Berkat and Galak had home range estimates with smaller differences between KDE and MCP, reflecting their more stable and predictable movements within established home ranges. For instance, Berkat's MCP 100% (0.691 km²) and KDE 95% (1.302 km²) estimates are not identical, the relatively smaller difference suggests more confined and consistent space use of resident pangolins.

While these estimates provide important information on the spatial requirements of the pangolins in the study area, it is important to note that they are based on a relatively small sample size and may only be representative of some of the pangolin population in the region. The sample size and data inputs available in this study were sufficient to implement multiple home range estimators, including MCP, KDE, and LoCoH. However, it is important to acknowledge that the accuracy and reliability of these estimates can vary depending on the quantity and quality of the data.

Due to the limited number of locations for some individuals, especially translocated pangolins, LoCoH could not be applied effectively in all cases. This reflects a constraint of the dataset rather than a methodological insight and the results should be interpreted with this limitation in mind.

Despite these challenges, the implementation of different estimators was still valuable in providing a range of perspectives on the spatial ecology of the pangolins. However, further studies with larger sample sizes and more comprehensive data are needed to validate these estimates and provide a more detailed understanding of the home range and spatial requirements of resident Sunda pangolins in Kinabatangan. This will also be useful for more thorough assessment of the strengths and limitations of each estimator when applied to a larger dataset. The factors influencing the size and shape of pangolin home ranges observed in this study are of significant interest. Our findings are consistent with prior research by Lim and Ng (2007, 2008), which reported that larger resident pangolins tend to have larger home ranges. This could be because larger individuals require more resources to meet their metabolic needs and maintain their body condition, leading them to forage over a larger area (Lim and Ng, 2007). It is important to note that the larger resident individual in our study was also a male, which may have contributed to the observed larger home range. In many species, males often have larger home ranges than females, particularly during the breeding season, as they may need to cover more ground to find mates. This could partly explain the larger home range size observed in the male resident pangolin in our study.

However, this pattern does not necessarily apply to translocated pangolins. For example, Pesona, a translocated female, had a much larger exploratory area compared to Suka, a translocated male. To examine whether differences in movement patterns could be related to demographic factors, mean daily distance travelled was compared between resident and translocated pangolins, and between males and females. The results (**Fig. 3.18, Fig. 3.19; Table 3.5**) showed no significant differences between residents and translocated individuals. In contrast, a significant difference was detected between males and females, with males travelling further on average than females. This suggests that while demographic factors such as sex do influence movement, the large variation observed in some translocated individuals, such as Pesona, is more likely driven by the challenges of adapting to unfamiliar environments rather than by sex or body size alone.

In many species, including pangolins and other mammals, home range overlap can occur for various reasons, such as access to shared resources, territoriality, or mating opportunities. The overlap between the home ranges of the resident female pangolin and the resident male in this study was observed to be relatively small. However, because relocations were temporally sparse and largely collected at similar times of day (predominantly single morning fixes) and the individuals were tracked in different months and years, a simultaneous space use could not be assessed. Therefore, this overlap should not be interpreted as evidence of shared resource use or breeding.

Suka, for example, had a much larger home range of 5.079 km², with about 20% overlap with the ranges of the resident pangolins Galak and Berkat (**Fig. 3.10**). As a translocated pangolin, Suka was introduced into an area already occupied by the resident pangolins (Galak and Berkat), which may explain this intersection as part of exploratory movement rather than established home range overlap. In contrast, smaller intersections were observed for other translocated pangolins, such as Gagah, Tuah, and Wira, though the limited sample sizes make their patterns difficult to interpret. These descriptive results underline the importance of considering existing occupancy when planning release sites, while recognising that this study does not allow firm conclusions about territorial competition.

In some species, small home range overlaps between males and females are associated with mating behaviour, where males may temporarily overlap with females' ranges during the breeding season to maximize their chances of mating (Liberg and Sandell, 1988). However, the extent of this overlap and its implications can vary widely across species. For example, in some carnivores, males have overlapping ranges with multiple females, especially during mating seasons, to ensure access to breeding opportunities (Maher and Lott, 2000). In contrast, smaller overlaps might indicate occasional interactions or incidental resource sharing rather than consistent cohabitation.

In pangolins, specific studies on home range overlap are limited, but research on other solitary mammals, such as orangutans (*Pongo pygmaeus*), shows that overlaps can occur but are usually small (Singleton and van Schaik, 2001). In this study, the overlap observed between resident individuals was relatively limited, but given the limited relocations and lack of temporal data, no ecological or behavioural significance can be inferred from this.

Given the relatively small overlap between pangolin home ranges observed in this study, it is possible that the overlap represents incidental encounters or limited resource sharing rather than a significant behavioural pattern. Because relocations were temporally sparse and collected largely at similar times of day and because the resident individuals were tracked in different months and years, temporal overlap could not be assessed. Therefore, the observed overlap should be interpreted cautiously.

The analysis of home ranges of resident and translocated Sunda pangolins indicated some degree of overlap between them. Such overlaps may lead to competition, particularly when individuals compete for the same resources or mating opportunities (Mysterud et al., 2011). In this study, male resident pangolins potentially engaged in fights with male translocated pangolins. These interactions were documented through camera traps set up outside identified sleeping sites. Footage captured wild large pangolins displaying 'wrestling-like' actions toward smaller translocated male pangolins. At one incident, a translocated pangolin vacated the site, after which the larger wild pangolin then occupied the sleeping site for two consecutive days.

These observations should be interpreted cautiously. While overlap with a resident pangolin was observed, the limited data cannot confirm aggressive encounters or conflict. Oil palm plantations and surrounding landscapes may offer resources that pangolins can use, but they also expose them to risks such as poaching and habitat disturbance. Thus, rather than suggesting direct conflict between males, the findings highlight the need for careful consideration of release sites and long-term monitoring to better understand how translocated pangolins adapt.

3.4.3 Movement behaviour of Sunda pangolins

A comprehensive study on the movement behaviour of pangolins has yet to be conducted; therefore, this study aimed to provide baseline insights into this understudied area of research. The EMbC analysis revealed differences in movement behaviours between resident and translocated pangolins. Both groups showed a preference for certain movement direction, with heading values above 5.5 being more frequent, suggesting a non-random pattern. However, because no environmental variables were included in the analysis, the underlying drivers of these directional preferences remain unclear. Additionally, the frequency distribution of distance covered per day for translocated pangolins revealed a high frequency of movements around 0-500 m/day as most commonly observed, with a secondary peak around 2,500 m/day (**Fig. 3.16b**) indicating variability that may reflect exploratory behaviour post-release.

The EMbC analysis also provided information on the velocity and turning angle of resident and translocated pangolins. For resident pangolins, most of the dots on the graph were classified as LL, indicating slow and steady movements with little change in direction. In contrast, translocated pangolins exhibited a higher frequency of HH behaviour, characterized by higher velocity and more erratic turns. This suggests that translocated pangolins may be more active and more exploratory than resident pangolins. Translocated pangolins may have different movement patterns due to their translocation from their natural habitat, which may result in more exploratory and potentially riskier behaviour, also observed in translocated Sunda pangolins in Vietnam (Gray et al., 2022) and Philippine pangolins in Palawan Island (Sabine et al., unpubl. data). In addition, the movement behaviour of resident pangolins is likely influenced by their familiarity with the local landscape, while translocated pangolins may be exploring and adapting to a new and unfamiliar environment (Gray et al., 2022: Sabine et al., unpubl. data). The present study provides valuable insights into the movement behaviours of both resident and translocated Sunda pangolins. The EMbC analysis highlighted distinct differences in movement patterns between these two groups, with resident pangolins displaying slower and more predictable movements, while translocated pangolins displayed higher velocity and more erratic behaviours. These findings suggest that translocated pangolins are likely engaging in more exploratory activities as they adapt to unfamiliar environments, which can increase their exposure to potential risks such as predation or human conflict.

The observed distribution of heading values indicates a preference in movement direction among pangolins, though the underlying drivers of this pattern remain unclear. This directional tendency highlights the need for further research into potential environmental influences on pangolin movement. For translocated individuals, most daily movements were below 2,500 m/day, suggesting that while they are active, their movements are relatively contained within a limited range. These results provide a descriptive baseline for understanding movement behaviour, which can be built upon with future analyses that incorporate environmental covariates.

When choosing release sites for translocated pangolins, it is important to consider the environmental factors that guide their movement. Selecting areas with familiar features, like plenty of trees and nearby food sources, can help them adjust more easily and avoid getting lost or wandering too far from the suitable habitat into which they were released. After release, close monitoring is key, especially during the early stages, to spot any issues quickly and take action if needed, such as moving pangolins that might clash with resident pangolins. Conservation strategies for translocated pangolins should be adaptive, with protocols adjusted based on individual behaviours. Providing extra resources in the release area may be necessary if pangolins struggle to find food or shelter. More research is necessary to understand what influences the movement patterns of both resident and translocated pangolins, including environmental factors, social interactions, and the long-term impacts of translocation. Using this behavioural data in conservation planning is crucial to ensure that protected areas and release sites meet the needs of all pangolins.

3.4.3 Conservation of Sunda pangolins in fragmented habitats

Conserving pangolins in fragmented landscapes is a complex and challenging issue, as habitat loss and fragmentation are some of the main threats facing the species (Chong et al, 2020). The present study found that resident Sunda pangolins had smaller home ranges than translocated individuals. The smaller home ranges of the resident pangolins may be due to their preference for forested areas and their ability to find suitable resources within a smaller area. In contrast, translocated pangolins exhibited more extensive exploratory behaviour, covering larger areas as they searched for suitable habitat and resources in their new environment, or possibly attempting to return to their site of origin. Rather than describing these larger areas as "home ranges," it is more accurate to view them as exploratory zones that reflect the pangolins' efforts to adapt to unfamiliar surroundings. These findings are still important for pangolin conservation in fragmented landscapes, where suitable habitat is scarce, and the risks of human activity and poaching are heightened (Wong & Linkie, 2013; Brodie et al., 2015). For example, as shown in Chapter 4, pangolins select sleeping sites in larger trees with hollows and close to water, features less common in fragmented and degraded areas. Linking movement patterns with such habitat requirements is important to guiding translocation strategies and ensuring that released pangolins can locate and establish viable refuges. Further details on habitat and microhabitat use by Sunda pangolins are explained in Chapter 4.

The observation that resident pangolins in this study only occupied forested areas, as shown in the home range maps, highlights the critical role of maintaining and restoring forest habitats to support the survival and persistence of pangolin populations. These individuals did not move away from forested areas, suggesting a strong preference for this type of habitat, which will be detailed further in Chapter 4. However, in fragmented landscapes, suitable habitat and connectivity are often limited, leading to illegal hunting and poaching, reduced genetic diversity, and increased vulnerability to local extinctions (Hearn et al., 2018; Lim et al., 2019; Verma & Prakash, 2022).

The habitat restoration and creation of habitat corridors that link fragmented patches of forest may be essential to maintaining the long-term viability of pangolin populations in such landscapes (Liu et al., 2018; Lim et al., 2019; Guharajan et al., 2022). The MCP, KDE, and LoCoH home range maps generated in this study provide valuable insights into the spatial extent and movement patterns of both resident and translocated Sunda pangolins. Notably, the home range maps for resident pangolins were restricted to forested habitats, highlighting their preference for these areas. In contrast, translocated pangolins used both forested areas and oil palm plantations, indicating a broader range of habitats encountered as they explored their new environments.

These observations suggest the importance of maintaining connectivity between forest patches to ensure that pangolins can access the full range of habitats they require for foraging, shelter, and breeding. Integrating home range findings with habitat preferences (see Chapter 4) can guide more effective conservation strategies focused on restoring and connecting key habitats.

The analysis of camera trap data from both forested areas and oil palm plantations revealed varying levels of human activity, with higher frequencies of human presence detected in the plantations. This is particularly relevant to the movement ecology of translocated pangolins, as, based on home range maps, they occupied both forested areas and oil palm plantations. Translocated pangolins were mostly observed in both forest and plantation habitats, while resident pangolins were mostly within forested areas. These observations suggest different exposure levels to human presence, but no formal analysis was conducted to link human activity directly to pangolin movement behaviour.

The riskier behaviour exhibited by translocated pangolins in exploring their new environment highlights the need for careful planning and monitoring of translocation programs. The EMbC analysis of translocated pangolins revealed a higher frequency of high-velocity movements and erratic turns, indicating that these individuals are engaging in extensive exploratory behaviour as they navigate unfamiliar terrain. This exploratory phase is further supported by the larger areas covered by translocated pangolins, which, rather than representing stable home ranges, likely reflect the animals' search for suitable habitat and resources in their new environment.

These exploratory areas, which extend beyond the more confined spaces used by resident pangolins, expose translocated individuals to increased risks, particularly in landscapes dominated by human activity (Dickens et al., 2010; Terhune et al., 2010). The protected area where this study was carried out is surrounded by oil palm plantations, villages, and roads, further increasing the likelihood of human-pangolin encounters. In regions like Kinabatangan, where human presence is prevalent, these pangolins may be more vulnerable to poaching and other threats. The combination of high-risk exploratory behaviour and fragmented landscapes require a comprehensive approach to translocation, including careful site selection, thorough post-release monitoring, and robust anti-poaching measures to ensure the safety and successful adaptation of translocated pangolins (Lim et al., 2019; Chong et al., 2020; Guharajan et al., 2022).

While this chapter primarily focuses on the spatial ecology of pangolins, the home range maps, and movement patterns presented also provide valuable insights into individual-level behaviour and habitat preferences. The two resident pangolins primarily occupy forested areas, suggesting a preference for these habitats, which are likely critical for their survival. The confined movement patterns of resident pangolins within these forested habitats further emphasise the importance of preserving these areas to maintain stable and viable populations.

Additionally, the movement patterns of translocated pangolins, as revealed by the EMbC analysis, highlight the more erratic and exploratory behaviour than residents, often spanning both forested areas and oil palm plantations. This exploratory pattern underlines the challenges translocated pangolins face in adapting to unfamiliar environments and highlight the importance of habitat connectivity in conservation planning.

Population-level studies are crucial for understanding the ecology and conservation needs of species (Attard et al., 2016; Ames et al. 2020) but for elusive, rare, and endangered species like pangolins, individual-level studies are particularly important. Pangolins are proven to be difficult to detect and study in the wild due to their secretive and nocturnal nature (Kwaja et al., 2019; Chong et al., 2020), which makes it challenging to obtain accurate population estimates and information on their behaviour and habitat use. If detection methods were improved, it would indeed become easier to conduct population-level studies, providing broader ecological insights.

Nevertheless, even with these challenges, individual-level studies remain valuable. They allow researchers to gather detailed data on home range, habitat preferences, and movement patterns, which are critical for informing conservation strategies, such as identifying priority conservation areas and designing effective translocation and monitoring programs. However, to build on these insights and achieve a more comprehensive understanding of the spatial ecology and conservation needs of pangolins in fragmented landscapes, further research with larger sample sizes and improved detection methods is necessary.

While the exact life span of pangolins is not fully known, they have lived for 12-19 years in captivity (Hua et al., 2015), and it is believed that they can live for over 20 years in the wild (Weigl, 2005). Given this relatively long-life span, it is possible that the rapid loss of forests could be happening faster than pangolins can adapt, forcing them to constantly expand their home ranges as habitats shrink. Pangolins might be expanding their ranges due to habitat loss, but they might also be managing within smaller areas depending on local conditions. The relationship between habitat reduction and how pangolins adjust is complicated and likely depends on many factors. Given the current scarcity of data on this issue, it would be speculative to draw firm conclusions. Further research is needed to understand how pangolins respond to habitat changes over time, particularly in fragmented landscapes, which will be important for developing effective conservation strategies.

Chapter 4: Habitat use and sleeping site preference of Sunda pangolins in the highly fragmented Lower Kinabatangan landscape

4.1 Introduction

Human activities such as logging, mining, and agricultural practices have negatively impacted forest areas and biodiversity (Krishnan et al., 2019). For example, the extensive conversion of natural habitats in Sabah to agricultural or plantation landscapes has caused a significant loss of forest cover and the creation of forest islands in the Lower Kinabatangan region, a biodiversity hotspot (Estes et al., 2012; Abram and Ancrenaz, 2017). In addition, habitat fragmentation resulting from activities like logging, mining, and agricultural expansion can lead to the isolation and fragmentation of natural habitats, reducing the availability of suitable habitats for wildlife and increasing human contact (Othman, 2017; Hearn et al., 2018; Khrisnan et al., 2019). This can increase human-wildlife conflicts, including illegal hunting and poaching (Wong and Linkie, 2013; Brodie et al., 2015). These threats can exacerbate the detrimental effects of habitat fragmentation on wildlife populations, leading to a decline in species abundance and biodiversity (Haddad et al., 2015).

Given the implications of habitat loss and fragmentation for species persistence (Smith and Hellmann, 2002), it is important to understand the habitat use patterns of Sunda pangolins in such landscapes, to inform conservation strategies and management actions aimed at mitigating the effects of anthropogenic pressures on their populations. The Sunda pangolin is a highly adaptable species that can inhabit a wide variety of habitats, including both natural and human-altered landscapes (Chong et al., 2020). This adaptability is partly attributable to their generalist feeding habits, which allow them to exploit a wide range of food resources. Pangolins are predominantly insectivores, feeding on insects such as ants and termites (Chao et al., 2020). In addition, pangolins can utilise a variety of sleeping sites, including burrows, tree cavities, hollow logs, and tree branches, which are found in a variety of landscapes (Wu et al., 2020; Chong et al., 2020; Jansen et al., 2020; Schoppe et al., 2020; Mahmood et al., 2020; Hoffman et al., 2020; Pietersen et al., 2020).

Because little is known about the factors that influence the habitat use of Sunda pangolins in the Lower Kinabatangan region, especially concerning the selection of sleeping sites, more research is needed. Sleeping sites are places where an animal sleeps or rests for a specific period. Sleeping sites play a vital role in many species' life history and survival, providing a safe and secure location for resting, avoiding predators, and conserving energy (Lagos et al., Franklin, 2007; 1995; Di Bitetti et al., 2000; Briscoe et al., 2014). Pangolins rely heavily on their sleeping habitats to survive and maintain their life cycle. There are reports that Sunda pangolins sleep for extended periods, with some individuals sleeping up to 24 hours per day on some days (Kurniawan, unpubl. data). This emphasises the significance of suitable sleeping areas in a pangolin’s home range. When selecting a sleeping site, Sunda pangolins may exhibit preferences for particular types of structures or substrates and requirements for access to food and water sources nearby. Additionally, the availability and quality of sleeping sites may affect the distribution and abundance of Sunda pangolin populations in various habitats. Understanding the factors that influence Sunda pangolins' habitat and sleeping site selection can provide critical insights for developing effective conservation strategies and managing their habitats more effectively.

In this chapter, the study's main objective was 1) to describe the physical and spatial characteristics of sleeping sites used by Sunda pangolins in the Lower Kinabatangan Wildlife Sanctuary and 2) to identify the environmental variables that influence the distribution of Sunda pangolin sleeping sites within the study area. To achieve these objectives, the sleeping site locations were collected from resident and translocated Sunda pangolins fitted with very-high frequency (VHF) tags in the area. In addition, high-resolution raster images of the study area were generated using Light Detection and Ranging (LiDAR) technology. Generalized Linear Models (GLM) and Species Distribution Modelling (SDM) were used in the statistical analysis. Incorporating GLM and SDM allowed the study to analyse how specific environmental and spatial factors impact sleeping site selection by Sunda pangolins. Using these methods, the physical and spatial characteristics of sleeping sites used by Sunda pangolins were described, and environmental variables that determine the distribution of the species populations within the study area were identified. Moreover, the findings have the potential to predict sleeping site distribution. These results will contribute to developing effective conservation strategies to mitigate the impacts of habitat fragmentation and degradation on Sunda pangolins in the Lower Kinabatangan region and beyond.

4.2 Methods

4.2.1 Study site and population overview

This study was conducted in the Lower Kinabatangan Wildlife Sanctuary (LKWS) located in Sabah, Malaysia, where the population size of Sunda pangolins is currently unknown. The study site was described in Chapter 1. Four individuals, one female adult and three male adults, were sampled for measurement, and DNA was collected for a DNA bank to support potential future research, although this aspect was not part of the current analysis. Two of these individuals, comprising one female and one male, were fitted with VHF tags; with one being monitored for 4.5 months and the other still under observation after 10.7 months at the time of this thesis submission; however, for the purpose of this study, data was analysed for the first 202 days. Additionally, seven pangolins rescued from various locations in Sabah were translocated to the study site. These included three females and four males, who were monitored through VHF tagging for periods ranging from 12 to 202 days (refer to Chapter 3, **Table 3.3**).

4.2.2 Data collection

Tracking and sleeping site assessment

Nine Sunda pangolins were fitted with VHF tags and tracked between August 2018 and January 2022, as described in Chapter 3. These pangolins were tracked daily during daylight hours to monitor their movements and to identify their sleeping sites. Each sleeping site was identified, marked on a GPS device, and physically marked at the site using unique coloured tape and nails to ensure accuracy, especially in areas where sleeping and non-sleeping sites were close together. Nearby trees with similar characteristics but not used as sleeping sites were also identified for comparison and both sleeping and non-sleeping sites were subsequently assessed.

Sleeping sites were recorded daily, with each site visited once per day. This method was informed by camera trapping observations, which showed that pangolins typically use a single sleeping site per day and only emerge in the late evening or night. Data collection was not synchronised across all nine pangolins because they were tracked at different times over various months and years. Additionally, tracking schedules were occasionally adjusted due to factors such as bad weather, undetectable pangolins, and movement restrictions related to COVID-19. Despite these challenges, sleeping sites were systematically recorded throughout each pangolin's individual tracking period.

For sleeping sites associated with trees in the forest, three additional non-sleeping trees within an approximately 30-m radius of the identified sleeping tree were assessed. This number was selected to provide a balanced sample size for comparison, ensuring that the data sampling captured variability in the immediate area around the sleeping site tree. The 30-m radius was chosen to ensure that the sample trees were close enough to the sleeping tree to allow for an accurate comparison, as this distance represents a reasonable area that a pangolin might explore when selecting a sleeping site. In cases where fewer than three non-sleeping trees with similar characteristics were available within the 30-m radius, the closest available non-sleeping trees were assessed instead. This adjustment ensured that data were still collected in habitats with sparse vegetation, where excluding sites would have reduced sample representation and biased the analysis toward denser habitats.

This approach was specifically applied to tree-based sleeping sites because trees offer a more consistent set of physical characteristics, such as the presence of hollows, size, and height, that can be directly compared. Conversely, other types of sleeping sites, such as burrows, bushes, grasses, hollow logs, buttress roots, or swampy areas, have physical characteristics that are difficult to compare. The unique and variable nature of these sites made it challenging to apply the same method across all sleeping site types. For sleeping sites associated with oil palm trees, only the sleeping sites themselves were assessed, as the structures of the trees are relatively uniform. Therefore, assessing non-sleeping trees was not considered necessary. However, other relevant information, such as ground cover, distance to water, and elevation, was still collected to provide a comprehensive understanding of the factors influencing sleeping site selection in this habitat.

Sleeping site assessments were conducted, and sleeping site types were categorised as follows:

a) Tree hole: The pangolin slept inside a cavity formed in the trunk of a standing dead or living tree. These sites were assessed based on whether the tree had no hollow, one hollow or multiple hollows (two or more). If no hollow was identified, the sleeping site was marked as a tree branch.

b) Tree branch: The pangolin slept in the tree, but no visible hollow was identified in the tree.

c) Burrow: The pangolin slept in an underground hole, typically an existing natural burrow.

d) Bushes: The pangolin slept underneath a dense growth of small to medium-sized plants.

e) Buttress root: The pangolin slept within the narrow space formed by the large flanges that emerge from the base of a tree trunk.

f) Grasses: The pangolin slept underneath grasses, specifically cogon grass (*Imperata cylindrica*) and Napier grass (*Pennisetum* spp.).

g) Oil palm tree: The pangolin slept either between the narrow spaces of the fronds emerging from the top of the oil palm tree or on top of the crown.

h) Hollow log: The pangolin slept inside a cavity formed in the trunk of a fallen tree or log.

i) Swamp: These sleeping sites confirmed on-site within swampy habitat, characterised by waterlogged soils and hydrophilic plants. While no specific sleeping site was identified within the swamp, these were directly observed and categorised as a distinct microhabitat type.

j) Unknown: These are sleeping sites that could not be accessed or physically marked due to natural barriers, such as flooding or difficult terrain like steep hills. In some cases, signals were detected in areas that appeared swampy from a distance, but without direct confirmation these were placed in the "unknown" category.

Physical and spatial characteristics of each sleeping site and selected non-sleeping sites were recorded. To ensure consistency and accuracy in the assessment, the vine score and ground cover were determined by the same researcher (the author) throughout the study as follows:

a) Sleeping site ID: A unique identifier assigned to each recorded sleeping site.

b) Frequency of use: The number of times a particular sleeping site was used by a Sunda pangolin during the study period.

c) GPS locations: The latitude and longitude coordinates of the sleeping site were recorded using GPS.

d) Habitat category: The type of habitat where the sleeping site was located. Each habitat type was defined based on observable characteristics and the specific environmental context:

   Forest: Includes forest fragments or ‘lots’ in protected areas with dense tree cover and minimal human disturbance.

   Oil palm plantation: Areas dominated by regularly spaced oil palm trees with sparse ground cover, typically managed for agriculture.

   Mixed habitat: Transition zones where different habitats meet, such as:

   - Forest to grassland: Where forest gradually transitions into open grassland.
   - Forest to oil palm plantation: Where forested areas meet oil palm plantations.
   - Forest patches within oil palm plantations: Small forested areas within the broader landscape of oil palm cultivation.

Swamp: Wetland areas with standing water and vegetation adapted to waterlogged conditions.

e) Number of hollows: The number of cavities or holes within the same tree where the pangolin could potentially choose to sleep. In cases where a pangolin slept in one specific hollow, the assessment included other hollows in the same tree that were close by and could also serve as potential sleeping sites. This was recorded to document the overall availability of hollows in the tree, rather than to assess why a pangolin selected one hollow over another.

f) Vine score: A measure of the amount of vine coverage around the sleeping site, rated on a scale from 0 to 5. The scoring was based on the following criteria:

0: No vines present.

1: Minimal vine coverage, with only a few small vines present.

2: Light vine coverage, with some parts of the tree covered but still mostly visible.

3: Moderate vine coverage, where vines cover about half of the tree or structure.

4: Dense vine coverage, with most of the tree or structure obscured by vines.

5: Heavily covered by vines, where the tree or structure is almost entirely obscured by thick, extensive vine growth.

g) Diameter at breast height (DBH) of tree: The diameter of the tree trunk measured at breast height (1.3 m above the ground).

h) Tree height: The height measured from the ground to the top of the tree. Tree height was measured using a clinometer and measuring tape, employing a trigonometric method. The horizontal distance (d) from the observer to the base of the tree was recorded, and the angle of elevation (e) to the top of the tree was measured using the clinometer. The tree height (H) was then calculated using the formula: $H = d \times \tan(e)$.

i) Ground cover: The percentage of ground covered by vegetation within a 3-m radius of the sleeping site, based on the Department of Climate Change, Energy, the Environment and Water (DCCEEW) (2003) guidelines. A 3-m radius was chosen as it represents the immediate microhabitat surrounding the sleeping site, focusing the assessment on the vegetation directly influencing the site.

   20%: sleeping site is sparsely covered with vegetation

   40%: sleeping site is moderately covered with vegetation

   70%: sleeping site is heavily covered with vegetation

   90%: sleeping site is almost completely covered with vegetation

j) Distance to water sources: The distance in meters from the sleeping site to the nearest water source.

k) Elevation: The elevation of the sleeping site above sea level, measured in meters using a hand-held GPS device (Model: GPSMap 64s, Garmin).

Camera trap monitoring

Each sleeping site was monitored using a combination of a Reconyx PC500 or HC500 Hyperfire camera trap and a Browning Strike Full HD trail camera. While both devices are types of camera traps, they were used for different purposes in this study. The Reconyx cameras were primarily used for capturing images, while the Browning cameras, which could record both images and videos, were used to capture more detailed behavioural observations, particularly through video.

When a sleeping site was identified, the Reconyx and Browning cameras were positioned approximately 1 m outside the entrance to the site, such as a tree hole or burrow, to monitor activity. In cases where the sleeping site had multiple entrances (e.g., multiple hollows,), cameras were placed at each entrance to ensure comprehensive monitoring.

Each sleeping site was monitored for the full duration that the pangolin remained there, which ranged from one to six days. Once the pangolin moved to a new site, cameras were repositioned accordingly. For sleeping sites without visible entrances, such as those involving tree branches or bushes, the cameras were positioned to capture the entire structure, increasing the chances of documenting pangolin activity. This approach allowed for a more detailed understanding of pangolin behaviour and the use of their sleeping sites.

Extracting environmental variables from existing LiDAR data and modelling

LiDAR data for this study was sourced from the Sabah Forestry Department, with the original dataset generated by the Carnegie Airborne Observatory of Stanford (Asner et al., 2012). This high-resolution data, which had been previously utilised in studies involving Bornean elephants (Evans et al., 2018) and monitor lizards (Guerrero-Sanchez et al., 2021), provided detailed 3D images of the study area. The LiDAR data enabled the extraction of key environmental variables such as vegetation structure (canopy height) and topography (elevation and slope) (Asner et al., 2012; David and Asner, 2014). While tree species information was considered important, it was not available within the LiDAR data. Efforts to hire local plant specialists to identify tree species on-site were hindered by the Covid-19 pandemic, which coincided with this part of the study.

The extraction and processing of environmental variables from the LiDAR data were conducted using QGIS (Version 3.24.3). Raster images representing canopy height, elevation, and slope were standardised in terms of resolution, projection, and extent. These standardised images were then used to generate slope, elevation, and canopy height variables through QGIS. To ensure consistency and accuracy, the imported raster files were verified for their extent, projection, and resolution. The GPS locations of the monitored pangolins were plotted against the environmental variables to visualise and confirm the spatial data's alignment.

Frequency of Observed Presence (FOP) Analysis: The frequency of observed pangolin presence (FOP) was analysed in relation to each environmental variable. For continuous variables, such as canopy height, slope, and elevation, the relationship between FOP and these variables was visualised using kernel density plots. Categorical variables, such as habitat class, were also analysed by comparing the FOP associated with each habitat type.

Deriving and selecting environmental variables for Maximum Entropy modelling (MaxEnt): Environmental variables were transformed into derived variables using the MaxEnt algorithm, allowing for the creation of various transformations to test their suitability in the model. A Chi-square test was employed to assess the association between pangolin presence at sleeping sites and each environmental variables and binned intervals for continuous variables. The test compared the observed frequency of pangolin presence in each class/interval with the expected frequency under a random distribution. Variables showing significant deviations from expectation were retained for inclusion in the MaxEnt model.

Model building and response analysis: The selected environmental variables were used to build the final MaxEnt model, which predicted the probability of pangolin presence in the study area. Response plots were generated to illustrate how each variable influenced the likelihood of a pangolin selecting a sleeping site.

Predictive mapping and model validation: The final model was used to create a predictive raster map, which identified areas of high suitability for pangolin sleeping sites. This raster map was exported as a .tif file. To validate the model's accuracy, the Area Under the Curve (AUC) was calculated, with values below 2 indicating acceptable model performance (Manel et al., 2001).

Exporting and visualising results: The predictive raster was exported as a GeoTIFF (.tif) file and converted into a .csv file, containing the probability of pangolin presence for each pixel in the study area. This file enabled for additional analysis and visualisation of the spatial distribution of pangolin sleeping sites.

4.2.3 Statistical analysis

This study utilised R 4.2.2 software (R Development Core Team 2022) to conduct statistical analyses, combining data from both resident and translocated Sunda pangolins, as well as non-sleeping sites, to ensure a comprehensive analysis despite the small sample size. Data manipulation and visualisation were performed using the tidyverse and ggplot2 libraries to investigate patterns in the number of uses and types of sleeping sites utilised by the pangolins in the study area. The number of uses of the different sleeping sites and types was represented using bar charts, and comparative statistical analysis was conducted to assess statistical differences between sleeping and non-sleeping sites.

Generalised Linear Models (GLMs)

The analysis included tree height and elevation as primary variables for the Generalized Linear Models (GLMs) because these factors influence the availability and accessibility of sleeping sites for Sunda pangolins, which are semi-arboreal. The LiDAR data provided three variables: tree height, elevation, and slopes. Slope was not included in the analysis because it was considered less directly relevant to sleeping site selection compared to tree-related variables. In most cases, sleeping sites were identified on relatively flat terrain, and there was little variation in slope among the sites assessed, making it unlikely to be a strong predictor. Other characteristics were analysed separately using different models, the presence and number of hollows with Poisson regression, vine score Diameter at Breast Height (DBH), and ground cover with logistic regression (multiple regression analyses). This separation avoided overly complex models and minimised the risk of multicollinearity.

Tree height and elevation were analysed using GLMs because these variables were consistently available for both sleeping and non-sleeping tree sites. Non-tree sleeping sites (e.g. burrows, bushes, grasses) did not have these attributes, and were excluded from this analysis and were instead analysed separately. Other characteristics, such as hollows, vine score, DBH and ground cover, were analysed with appropriate regression models to assess differences between sleeping and non-sleeping sites. The choice of variables and models were guided by their ecological reasoning relevance and the structure of the available data.

The analysis script utilised the raster library (Hijman et al., 2024) to read the data on sleeping site locations and LiDAR raster image of the area. It then converted the coordinates of the sleeping site locations from decimal degrees to UTM format, and extracted the habitat type using the ‘extract’ function to provide context about the environment of sleeping sites. A uniform grid or random distribution of points was created as a sample of available habitat within the pangolin's home range (defined using a Minimum Convex Polygon-MCP 100%). The Gamma distribution was chosen because it is suitable for data such as tree height and elevation, that are always positive (greater than zero) and tend to have more low values and fewer high values. The glm function then tested the difference in tree height or elevation between the observed and available habitat, and the output was visualised using plots and graphs. The results of this analysis identified whether there is a significant relationship between tree height and elevation, and the occurrence of sleeping sites. The ‘glm’ function output provided information on the strength and direction of the relationship.

Multiple regressions analysis and model selection

In this study, a multivariate logistic regression analysis was conducted to investigate the factors influencing the use of sleeping sites by Sunda pangolins. The analysis included several independent variables: Habitat Category, Diameter at Breast Height (DBH), number of hollows, distance to water, elevation, vine score, tree height, and ground cover. These variables were chosen based on their ecological relevance and potential impact on sleeping site selection.

Before including the variables in the models, they were checked for multicollinearity using the Variance Inflation Factor (VIF). VIF values quantify the extent of multicollinearity in a set of predictor variables in a regression model. Variables with high VIF values indicate significant collinearity, which can cause problems in interpreting the model results, thus, there were carefully considered and included or excluded to ensure the reliability of the models. The final models were selected based on their statistical significance and the Akaike Information Criterion (AIC), which helped in identifying the best-fitting models.

Two types of regression models were run: Poisson regression, used to predict the number of times a site was used, and logistic regression, used to determine the likelihood of a tree being used as a sleeping site (binary outcome: used vs. not used). The output from the regression analyses was visualised clearly represent the relationships between the independent variables and the response variables. Error bars indicating +/- 1 standard error were added to each graph to illustrate the confidence intervals for the predicted values, enhancing the interpretability of the results.

Species distribution modelling and environmental variable analysis

Species Distribution Modelling (SDM) was conducted using the MiaMaxEnt R package (Vollering et al., 2019) to assess the environmental variables influencing the distribution of sleeping sites for Sunda pangolins and to predict potential sleeping site distribution of the Sunda pangolin sleeping sites and to predict potential sleeping site locations within the study area using existing LiDAR data. This package, designed for species distribution modelling, applies the Maximum Entropy (MaxEnt) algorithm, a machine learning method that estimates the most uniform distribution (maximum entropy) constrained by the environmental variables provided.

To examine the environmental variables influencing the distribution of these sleeping sites, key variables such as canopy height, elevation, and habitat type were extracted. Habitat type was categorised based on the number of observations of each type of habitat (Guerrero-Sanchez et al., 2021) as follows:

[1] severely degraded areas – highly damaged areas with sparse vegetation due to human activities like logging or farming.

[2] dry lowland forest - forests in lowland areas with relatively dry conditions and a mix of tree species.

[3] limestone forest - forests growing on rocky, limestone-rich soils, often found in hilly or karst landscapes.

[4] peat swamp forest - wet forests on waterlogged, acidic peat soils, important for biodiversity and carbon storage.

[5] seasonal freshwater swamp - wetlands that flood and dry out seasonally, supporting a variety of plant life.

6] freshwater swamp forest - wet forests that stay waterlogged year-round, with trees adapted to standing water.

[7] swamp - general wetlands that may be permanently or seasonally flooded, with mixed vegetation.

[8] cleared areas/young oil palm - recently cleared land or young oil palm plantations with little canopy cover.

[9] oil palm with good canopy - mature oil palm plantations with a dense canopy.

[10] underproductive oil palm - older or poorly maintained oil palm plantations with lower yields and less canopy cover.

These variables were processed in Q-GIS 3.28.1, where they were clipped to the MCP 100% of all tracked pangolins combined to ensure consistency in resolution, projection, and extent. Once standardized, the variables were categorized as either categorical (e.g., habitat type) or continuous (e.g., elevation, canopy height). These datasets, along with the UTM coordinates of the sleeping sites, were then uploaded into the MiaMaxEnt 1.2.0 package for R.

The MaxEnt was used to generate predictions based on these variables, and chi-square tests were conducted on the model's output to identify the most influential factors in sleeping site selection. The initial step of the MaxEnt analysis involved assessing the representativeness of the variables within the study area. The frequency of presence was compared with the kernel data density of each continuous variable, while the observed presence was matched with the number of observations of each feature for the categorical variable.

Next, the data from the environmental variables were transformed into the most appropriate derived variables for use with the MaxEnt algorithm. A total of 39 transformations were evaluated for the five variables, and the best transformation was selected for each variable. The effects of the variables on the use of the area by Sunda pangolins were compared.

To evaluate the predictive accuracy of the model, the Area Under the Curve (AUC) method was employed. AUC values, which range from 0 to 1, serve as an indicator of the model's performance: a value of 0.5 suggests a prediction no better than random chance, while values closer to 1 reflect strong predictive ability. This assessment ensured that the model provided reliable predictions for the potential distribution of sleeping sites across the study area.

4.3 Results

4.3.1 Selection of sleeping sites by Sunda pangolins

This section presents the analysis of physical and spatial characteristics of sleeping sites used by Sunda pangolins in the study area. The study examined a total of 536 sites, including 241 identified sleeping sites and 295 non-sleeping sites, to determine the factors influencing sleeping site selection by two groups, resident and translocated Sunda pangolins.

Sleeping site types

The analysis revealed a diverse range of sleeping site types utilised by Sunda pangolins. As illustrated in **Fig. 4.1**, the most frequently used sleeping sites were tree holes, with 88 occurrences. This was followed by tree branches with 71 occurrences and oil palm trees with 51 occurrences. Other sleeping site types used less frequently, including burrows (20 occurrences), unknown sites (19 occurrences), hollow logs (13 occurrences), grasses (12 occurrences), bushes (11 occurrences), swamps (7 occurrences), and buttress roots (4 occurrences).

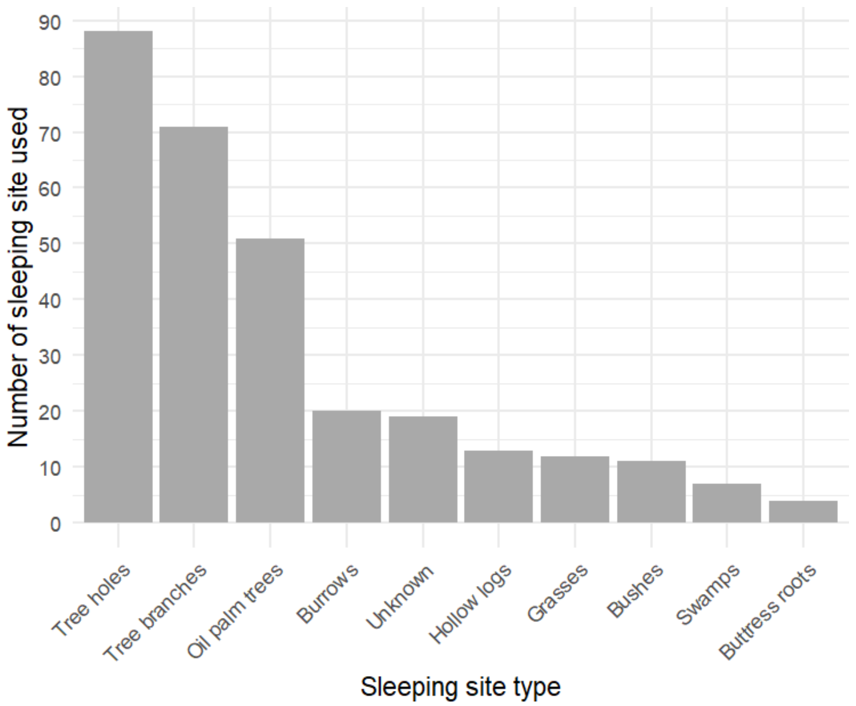

Fig. 4.1: Bar chart showing the number of occurrences for each sleeping site type used by Sunda pangolins (n=241). The x-axis represents the different types of sleeping sites, while the y-axis indicates the number of times each sleeping site type was utilised.

Comparison of sleeping site use between resident and translocated pangolins

A comparative analysis of sleeping site use between resident and translocated pangolins is depicted in **Fig. 4.2.** Resident pangolins primarily utilised tree holes, with 70 occurrences, and tree branches, with 50 occurrences. Other sleeping site types used by resident pangolins included burrows (13 occurrences), unknown sites (9 occurrences), and hollow logs (7 occurrences). Notably, resident pangolins did not use bushes, buttress roots, oil palm trees, or swamps.

Conversely, the translocated pangolins showed a broader range of sleeping site usage. They primarily used oil palm trees (51 occurrences), followed by tree branches (21 occurrences) and tree holes (18 occurrences). Other sleeping site types used by translocated pangolins included burrows (13 occurrences), unknown sites (10 occurrences), hollow logs (7 occurrences), and all various other types (grasses, bushes, swamps, and buttress roots) each with fewer than 10 occurrences.

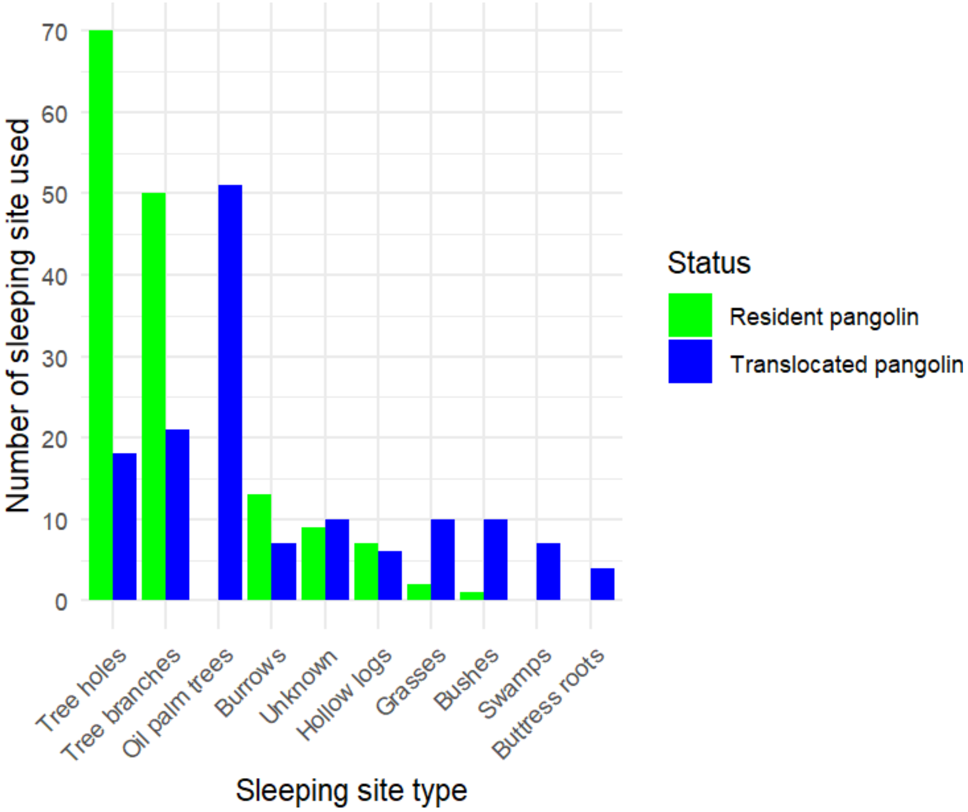

Fig. 4.2: Bar chart comparing the number of occurrences for each sleeping site type used by resident and translocated Sunda pangolins (n=241). The x-axis lists the different types of sleeping sites, while the y-axis shows the number of times each site type was used. Resident pangolins are represented in green and translocated pangolins in blue.

Comparative analysis of sleeping and non-sleeping sites

The statistical analysis of the physical and spatial characteristics of sleeping and non-sleeping sites used by Sunda pangolins revealed several significant differences (**Table 4.1**). As the data were approximately normally distributed, a t-test was carried out which indicated that sleeping sites were on average significantly closer to water sources than non-sleeping sites ($p = 0.0008$). The mean distance to water for sleeping sites was 101.82 m, compared to 127.31 m for non-sleeping sites.

Tree-related characteristics also showed significant associations. A Chi-square test indicated a strong association between site type (sleeping vs. non-sleeping) and whether the site was tree-based ($p < 0.0001$). Further analysis revealed that trees used as sleeping sites had significantly larger diameters at breast height (DBH) with a mean of 0.662 m, compared to 0.565 m for non-sleeping trees (< 0.0001). Similarly, tree height was significantly greater at sleeping sites, with a mean height of 38.38 m compared to 33.83 m at non-sleeping sites ($p = 0.04$).

The analysis of the number of hollows within trees, assessed using a Chi-square test, did not show a significant association between the presence of hollows and the selection of sleeping sites ($p = 0.07$), indicating that while hollows may contribute to the selection of a sleeping site, they are not a decisive factor. Conversely, vine coverage was significantly associated with sleeping site selection ($p < 0.0001$), suggesting that higher vine coverage may enhance the suitability of a site for sleeping.

Table 4.1: Comparative statistical analysis of non-sleeping and sleeping sites used by resident and translocated Sunda pangolins.

Variable	Test type	p-value	Mean non-sleeping site	Mean sleeping site	Interpretation
Distance to water (m)	t-test	0.0008	127.3056	101.8232	Significant difference
Tree	Chi-square	<0.0001	NA	NA	Significant association
Hollow	Chi-square	0.3	NA	NA	No significant association
Vine coverage	Chi-square	<0.0001	NA	NA	Significant association
DBH (m)	t-test	<0.0001	0.5645	0.6623	Significant difference
Tree height (m)	t-test	0.049	33.8270	38.3796	Significant difference
Elevation (m)	t-test	0.03	74.5589	74.3522	Significant difference (very small)
Ground cover (%)	t-test	0.1	50.7200	54.3700	No significant difference
Number of hollows	Chi-square	0.07	NA	NA	No significant association

Elevation showed a statistically significant, but very small, difference between sleeping and non-sleeping sites (p = 0.032). Sleeping sites were located at a mean elevation of 74.35 m, while non-sleeping sites were slightly higher at 74.56 m, indicating that elevation may have a minor influence on site selection.

Ground cover did not show a significant difference between sleeping and non-sleeping sites (p = 0.142), with mean ground cover percentages of 54.37% for sleeping sites and 50.72% for non-sleeping sites. This result suggests that ground cover may not be an important factor in the selection of sleeping sites by Sunda pangolins.

Multiple regression analysis on sleeping site selection

To investigate the factors influencing the selection of sleeping sites by Sunda pangolins, a multivariate analysis was conducted using multivariate logistic regression models. This analysis was performed separately for two distinct groups: resident and translocated pangolins. The objective was to identify the physical and spatial characteristics that significantly affect sleeping site selection for each group. Various predictor variables were considered, including habitat category, diameter at breast height (DBH), number of hollows, distance to water, elevation, vine coverage, tree height, and ground cover. These variables were selected based on their ecological relevance and potential impact on sleeping site selection, as identified in prior univariate analyses. The following sections present detailed results from the multivariate logistic regression analysis, including assessments of multicollinearity using the Variance Inflation Factor (VIF) and the significance of each predictor variable.

Assessment of multicollinearity and significance of predictor variables

Before analysing the results of the logistic regression models for both resident and translocated pangolins, an assessment of multicollinearity was conducted using the VIF. Multicollinearity can lead to unreliable estimates in regression models, making it crucial to ensure that the predictor variables are not highly correlated with each other. For both groups, the VIF values were calculated for each predictor variable included in the models. A VIF value greater than 10 indicates high multicollinearity, which could compromise the model's reliability (James et al., 2021). However, for both resident and translocated pangolins, the VIF values for all variables were found to be well below this threshold, with most values close to 1, indicating minimal multicollinearity.

For resident pangolins, the VIF values for all predictors were below 1.3, suggesting that multicollinearity was not a concern (**Table 4.2**). The logistic regression model included DBH, number of hollows, distance to water, elevation, vine coverage, and tree height. For translocated pangolins, the model focused on the two most significant predictors, habitat category and DBH, as inclusion of other variables introduced higher multicollinearity, which brought the VIF values below 1.2 (**Table 4.2**).

Table 4.2: Variance Inflation Factor (VIF) values for each predictor in the logistic regression models analysing factors influencing sleeping site use by resident and translocated Sunda pangolins.

Term	VIF	VIF 95% CI	CI Increased	SE Tolerance	Tolerance 95% CI	Model
DBH (m)	1.09	[1.06, 1.25]	0.95	0.91	[0.80, 0.94]	Resident pangolins
factor (Number of hollow)	1.02	[1.02, 1.07]	0.98	0.98	[0.94, 0.98]	Resident pangolins
Distance to water (m)	1.03	[1.02, 1.10]	0.98	0.97	[0.91, 0.98]	Resident pangolins
Elevation (m)	1.06	[1.04, 1.13]	0.98	0.95	[0.88, 0.96]	Resident pangolins
Factor (Vine coverage)	1.02	[1.02, 1.06]	0.98	0.98	[0.94, 0.98]	Resident pangolins
Tree height (m)	1.08	[1.05, 1.17]	0.97	0.93	[0.85, 0.95]	Resident pangolins
DBH (m)	1.00	[1.00, 1.15]	0.94	0.99	[0.87, 0.99]	Translocated pangolins
Factor (Habitat category)	1.00	[1.00, 1.15]	0.94	0.99	[0.87, 0.99]	Translocated pangolins

Sleeping site use by the resident pangolins

The logistic regression analysis for resident Sunda pangolins revealed several key factors influencing the selection of sleeping sites. The model included predictor variables, DBH, number of hollow, distance to water, elevation, vine coverage, and tree height. The results, summarised in **Table 4.3**, indicated that several of these variables significantly affected the likelihood of a tree being selected as a sleeping site by resident pangolins.

Table 4.3: Summary of the multivariate logistic regression analysis investigating the factors influencing the use of sleeping sites by resident Sunda pangolins, which exclusively utilised forest habitats. The table provides details on the degrees of freedom (df), deviance, Akaike Information Criterion (AIC), likelihood ratio test (LRT) statistic, corresponding p-values for each predictor variable in the model. The number of asterisks denotes the level of significance, with more asterisks indicating a higher level of significance.

	df	**Deviance**	**AIC**	**LRT**	**Pr(>Chi)**	**Significance**
<none>		299.52	321.52			
DBH	1	305.80	325.80	6.2782	0.0122	*
Factor (Number of hollow)	2	314.96	332.96	15.4404	0.0004	***
Distance to water	1	300.19	320.19	0.6708	0.4128	
Elevation	1	300.91	320.91	1.3872	0.2389	
Factor (Vine coverage)	4	312.47	326.47	12.9530	0.0115	*
Tree height	1	304.17	324.17	4.6536	0.0310	*

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Diameter at Breast Height (DBH) emerged as a significant predictor of sleeping site use ($\chi^2 = 6.278$, df = 1, $p = 0.012$) (**Table 4.3**). The analysis demonstrated a clear trend: as DBH increases, so does the likelihood of a tree being selected as a sleeping site. This finding was visually supported by the scatterplot in **Fig. 4.3**, which illustrated a positive relationship between DBH and the probability of site use.

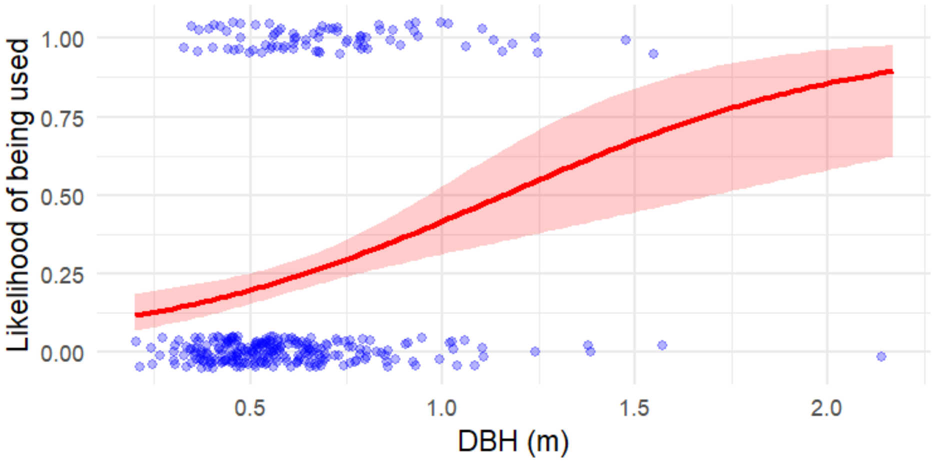

Fig. 4.3: Scatterplot with a fitted regression line illustrates the relationship between tree Diameter at Breast Height (DBH) in m (x-axis) and the likelihood of the tree being used as a sleeping site (y-axis) by resident Sunda pangolins. Each blue dot represents an individual observation, indicating whether a tree was used (1) or not used (0) as a sleeping site. The red line represents the predicted likelihood of site use based on the logistic regression model, while the shaded red area shows the 95% confidence interval for these predictions.

The number of hollows in trees was another significant predictor of sleeping site use by resident pangolins. The logistic regression analysis showed a highly significant association between the presence of hollows and the likelihood of site use (χ^2 = 15.440, df = 2, $p < 0.001$) (**Table 4.3**). The dot plot (**Fig. 4.4**) illustrates this relationship. Trees without hollows had the lowest likelihood of being selected as sleeping sites, with a mean likelihood of 0.12. Conversely, trees with hollows whether single or multiple showed a higher likelihood of being selected, with a mean of 0.31 and 0.34, respectively. Although trees with multiple hollows showed a slightly higher mean likelihood than those with a single hollow, the overlap in confidence intervals indicates no clear statistical difference between the two.

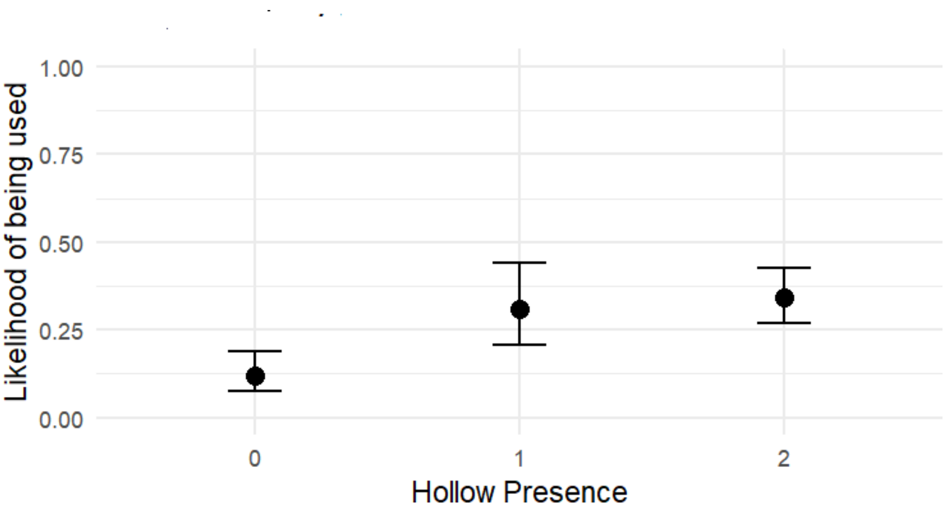

Fig. 4.4: Dot plot with error bars illustrates the relationship between the presence of hollows in trees (x-axis) and the likelihood of those trees being used as sleeping sites (y-axis) by resident Sunda pangolins. The x-axis categories represent trees with no hollows (0), a single hollow (1), and multiple hollows (2). The y-axis shows the predicted likelihood of a tree being used as a sleeping site, ranging from 0.0 to 1.0. Each dot represents the mean likelihood of site use, and the vertical lines represent the 95% confidence intervals for each category.

Vine coverage was also found to be a significant factor associated with sleeping site use by resident Sunda pangolins. The logistic regression analysis revealed a significant association between vine coverage and the likelihood of site use ($\chi^2 = 12.953$, df = 4, $p = 0.012$) (**Table 4.3**). However, the dot plot (**Fig. 4.5**) shows broad overlap in confidence intervals across vine scores, indicating no clear directional trend. Trees with the heaviest vine coverage (score of 5) had a mean likelihood of 0.300 for being selected as sleeping sites. Trees with the minimal vine coverage (score of 1) had a slightly higher mean likelihood of 0.308. Conversely, trees with light (2), moderate (3) and dense (4) vine scores show lower mean likelihoods of 0.179, 0.150, and 0.185, respectively. The vine score of 0 (indicating no vines present) was not recorded in this study.

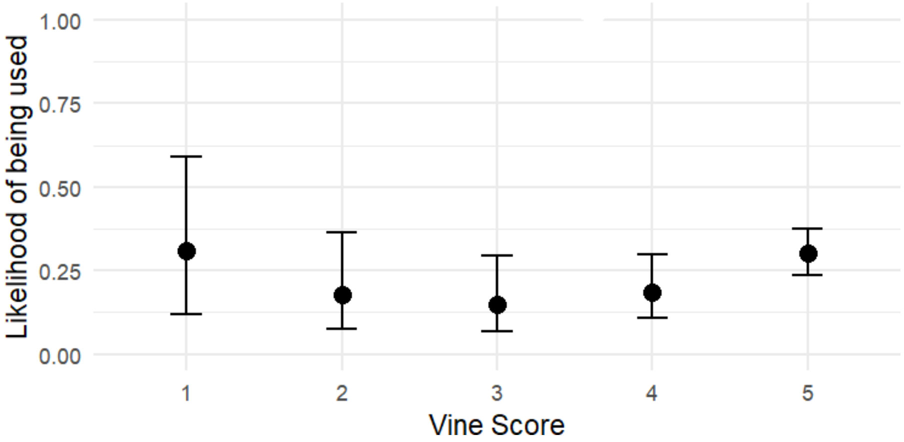

Fig. 4.5: Dot plot with error bars showing the likelihood of a tree being used as a sleeping site by Sunda pangolins based on vine coverage. The x-axis represents the vine score, ranging from 1 (minimal vine coverage) to 5 (heavy vine coverage). The y-axis shows the likelihood of the tree being used as a sleeping site, with values ranging from 0.0 to 1.0. The black dots indicate the mean likelihood of use for each vine score, and the vertical lines represent the 95% confidence intervals. Vine scores are defined as follows: 0 - no vines present, 1 - minimal vine coverage, 2 - light vine coverage, 3 - moderate vine coverage, 4 - dense vine coverage, and 5 - heavy vine coverage.

Tree height was another significant predictor of sleeping site selection by resident Sunda pangolins. The logistic regression analysis identified tree height as a significant factor, with taller trees being more likely to be selected as sleeping sites ($\chi^2 = 4.654$, df = 1, $p = 0.031$) (**Table 4.3**). The scatterplot (**Fig. 4.6**) illustrates this positive relationship, showing that the likelihood of a tree being use as a sleeping site increases as tree height rises. The mean tree height for selected sleeping sites was 35.45 m, indicating a preference for relatively tall trees. This trend highlights the importance of tree height in offering protection and other benefits, making taller trees more suitable as sleeping sites for resident pangolins.

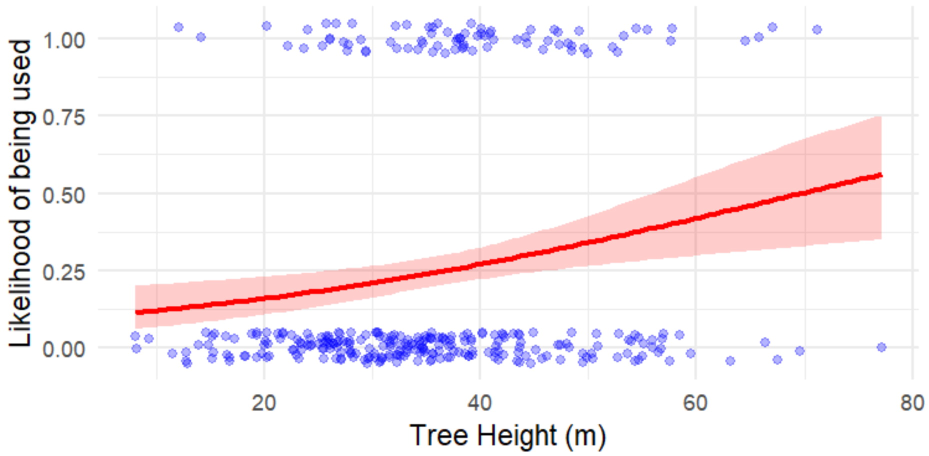

Fig. 4.6: Scatterplot with a fitted regression line illustrates the relationship between tree height and the likelihood of a tree being selected as a sleeping site by resident Sunda pangolins. The x-axis represents tree height in m, while the y-axis indicates the probability of a tree being used, ranging from 0.0 to 1.0. Each blue dot represents an individual observation, showing whether a tree was used (1) or not used (0) as a sleeping site. The red line represents the predicted likelihood of site use based on the logistic regression model, while the shaded red area shows the 95% confidence interval for these predictions.

Conversely, the logistic regression analysis revealed that distance to water was not a significant predictor of sleeping site use by resident pangolins ($\chi^2 = 0.671$, df = 1, p = 0.412) (**Table 4.3**). Similarly, elevation did not significantly influence the likelihood of site use ($\chi^2 = 1.387$, df = 1, p = 0.239) (**Table 4.3**). The mean elevation observed in the study area was 74.51 m, with most sites falling close to this value (**Fig. 4.7**).

Ground cover was excluded from the logistic regression model due to its multicollinearity with other variables, as indicated by the VIF analysis. Additionally, the comparative analysis between sleeping site and non-sleeping sites revealed no significant difference in ground cover (p = 0.142) (**Table 4.3**). The mean ground cover was 54.37% for sleeping sites and 50.72% for non-sleeping sites, suggesting that this variable does not have a strong influence on the selection of sleeping sites by Sunda pangolins. Therefore, its exclusion from the final model helped ensure the reliability and accuracy of the results.

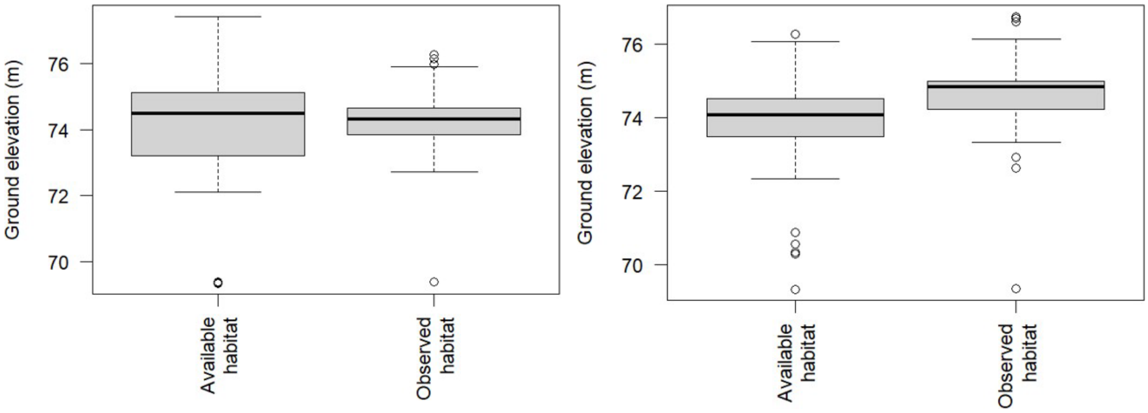

Fig. 4.7: Boxplots comparing the elevation range of available and observed habitats for two resident Sunda pangolins, Galak (left) and Berkat (right) in the study area. The x-axis categorises the habitat into "Available habitat" (elevations across all potential habitats within the study area) and "Observed habitat" (elevations where actual sleeping sites used by the pangolins were found). The y-axis represents ground elevation in meters above sea level. The boxplots illustrate the distribution of elevations, with the horizontal lines within the boxes indicating the median elevation.

Sleeping site use by the translocated pangolins

The logistic regression analysis for translocated Sunda pangolins initially included several predictor variables such as tree height, vine coverage and number of hollows, in addition to habitat category and DBH. However, the irregular and heterogeneous data structure for these individuals led to unstable estimates when too many predictors were combined. This contrasted with the resident pangolins, whose smaller but more stable datasets allowed multiple predictors to be analysed without similar issues. To improve model reliability for the translocated group, the analysis was refined to focus on the two strongest predictors: habitat category and DBH. The refined logistic regression model focusing on DBH and Habitat Category is summarised in **Table 4.4**.

Table 4.4: Summary of the multivariate logistic regression analysis investigating the factors influencing the use of sleeping sites by translocated Sunda pangolins, which utilised forest and oil palm plantation habitats. The table provides details on the degrees of freedom (df), deviance, Akaike Information Criterion (AIC), likelihood ratio test (LRT) statistic, corresponding p-values for each predictor variable in the model. The number of asterisks denotes the level of significance, with more asterisks indicating a higher level of significance.

	Df	Deviance	AIC	LRT	Pr(>Chi)	Significance
<none>		113.59	119.59			
DBH	1	121.28	125.28	7.686	0.0056	**
Tree.Height	1	147.41	151.41	33.816	0.0001	***

Significance codes: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

In the logistic regression analysis for translocated Sunda pangolins, DBH was identified as a significant predictor of sleeping site use ($\chi^2 = 7.686$, df = 1, p = 0.006,) (**Table 4.4**). This indicates that larger trees, as indicated by a greater DBH, are more likely to be selected as sleeping sites by translocated pangolins. The mean DBH of trees used as sleeping sites by these pangolins was 0.555 m. The scatterplot (**Fig. 4.8**) illustrates the positive relationship between DBH, and the likelihood of a tree being used as a sleeping site by translocated pangolins. As shown in the plot, the likelihood of a tree being used as a sleeping site steadily increases as DBH increases, particularly beyond 0.5 m. This trend suggests that translocated pangolins, similar to resident pangolins, prefer larger trees as sleeping sites, likely due to the greater stability, protection, and potential resources these trees offer.

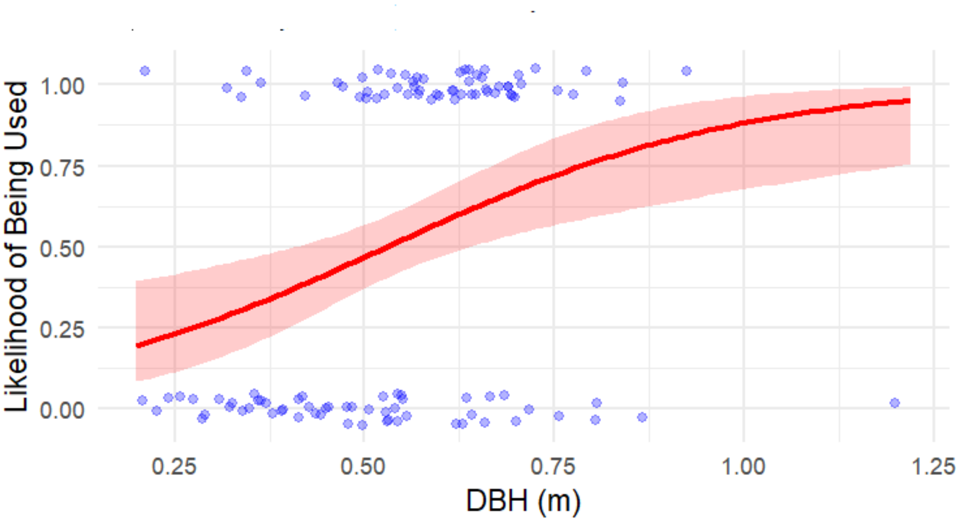

Fig. 4.8: Scatterplot illustrating the relationship between Diameter at Breast Height (DBH) and the likelihood of a tree being used as a sleeping site by translocated Sunda pangolins. The x-axis represents DBH (in meters), while the y-axis indicates the likelihood of the tree being selected as a sleeping site, ranging from 0.0 to 1.0. Each blue dot represents an individual data point, showing the variation in DBH among the trees in the study. The red line denotes the fitted logistic regression model, demonstrating the predicted likelihood of site use as DBH increases. The shaded red area around the line represents the 95% confidence interval, reflecting the uncertainty around the model's predictions.

Based on logistic regression analysis, habitat category is a significant predictor of sleeping site use among translocated pangolins ($\chi^2 = 33.816$, df = 1, $p < 0.001$) (**Table 4.4**). This finding indicates that the type of habitat, whether forest or plantation, plays a crucial role in determining where translocated pangolins choose to sleep. The dot plot (**Fig. 4.9**) supports this statistical finding. Specifically, the mean likelihood of a site being used in forest habitats is 0.576, while in plantation habitats it is considerably higher at 0.926. The black dots represent the mean likelihood of site use in each habitat type, with the plantation habitat showing a notably higher mean likelihood. This suggests that translocated pangolins are more likely to use sleeping sites within plantation habitats rather than forest habitats.

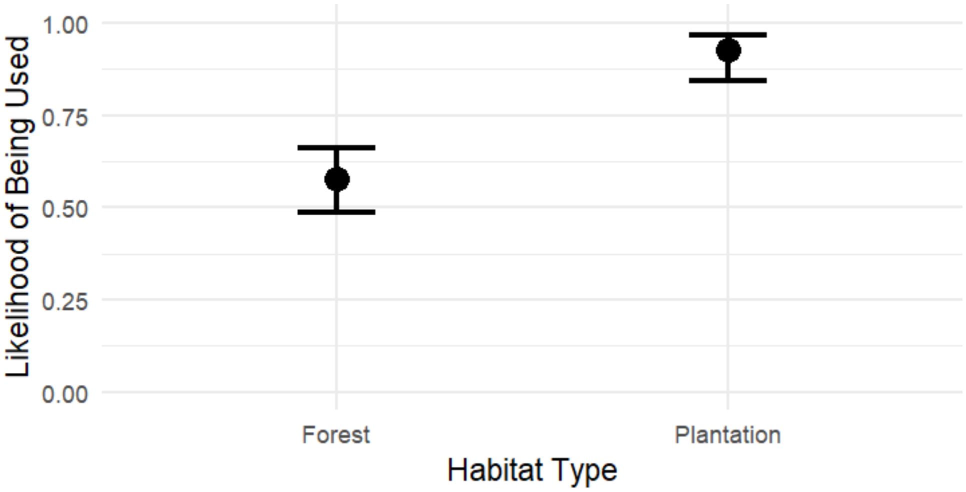

Fig. 4.9: Dot plot with error bars showing the likelihood of translocated Sunda pangolins using sleeping sites in two different habitat types: forest and plantation. The x-axis represents the habitat type, with "Forest" and "Plantation" as the two categories. The y-axis represents the likelihood of a site being used, ranging from 0.0 to 1.0. The black dots represent the mean likelihood of site use for each habitat type, while the vertical lines (error bars) represent the 95% confidence intervals for these estimates.

Species distribution modelling analysis of sleeping site selection

This section presents the influence of various environmental variables on the distribution of sleeping sites used by Sunda pangolins within the study area. A Minimum Convex Polygon (MCP 100%) was constructed to define the home range within the study area using 177 sleeping site locations, out of the 241. These 177 sleeping sites were specifically selected because they fell within the coverage area of the LiDAR data, which is restricted to the Lot 6 study area. Because of this, due to the limited spatial coverage of the LiDAR raster image, only data from seven Sunda pangolins (two residents and five translocated pangolins) were included in the analyses. As a result, the findings reflect the home ranges of these specific individuals and do not encompass the entire pangolin population in the study area. The results consider the effects of environmental variables, such as habitat type, elevation, slope, and canopy height, on the distribution of sleeping sites.

Fig. 4.10: Map of the canopy height raster file and the locations of Sunda pangolins sleeping sites for verification. The raster file represents vegetation height in the study area, with values ranging from 0 to 250 m, where higher values indicate taller vegetation. The colour gradient reflects these height variations. Blue dots mark the locations of sleeping sites used by Sunda pangolins.

The initial step MaxEnt analysis compared the frequency of presence with kernel data density of each continuous variable. The analysis revealed that canopy height (Xi^2 = 79.545; $p < 0.001$) had the most significant effect on the distribution of Sunda pangolin sleeping sites, followed by habitat class (Xi^2 = 67.11; $p < 0.001$). Significant effects were also observed when variables were analysed in combination (Xi^2 = 28.704; $p < 0.001$).

Fig. 4.12 and **Fig. 4.13** illustrates these relationships. Frequency of observed presence across different habitat types indicates that Sunda pangolins are more likely to use freshwater swamp forests for sleeping sites compared to other habitat types (**Fig. 4.12a**). The kernel density of canopy height, showing a strong correlation between increased canopy height and the frequency of pangolin presence (**Fig. 4.12b**). The kernel density of slope indicating that areas with lower slopes are more frequently used (**Fig. 4.12c**). The kernel density of elevation, indicating that elevation has a minimal effect on the distribution of sleeping sites (**Fig. 4.12d**).

The probability ratio output (PRO) analysis provided additional insights into the factors influencing Sunda pangolin sleeping site selection. For each environmental variable, the PRO values indicated the likelihood of occurrences relative to the average. Values above the threshold (PRO >1) indicating a higher likelihood of a site being used as a sleeping site. The PRO analysis showed the effect response of sleeping sites based on two critical variables: habitat type and canopy height. The analysis revealed that freshwater swamp forests (habitat class 6) had the highest PRO value (**Fig.4.13a**).

Other habitat types, severely degraded areas (habitat class 1), dry lowland forests (habitat class 2), peat swamp forests (habitat class 4), seasonal freshwater swamps (habitat class 5), and underproductive oil palm (habitat class 10), showed PRO values ranging 0.5 to 1, indicating likelihood of being used as sleeping sites. Conversely, habitat class 9 (oil palm with good canopy) had the lowest PRO value (PRO < 0.5), indicating that these areas are least likely to be used as sleeping sites. Habitat classes 3 (limestone forest), 7 (swamp), and 8 (cleared areas/young oil palm) were not represented in the analysis, indicating these habitats are the least likely to be used as sleeping sites.

The PRO values for canopy height demonstrated a positive relationship, with a higher probability of sleeping sites use as canopy height increases (**Fig. 4.13b**). The highest PRO value was observed when the canopy height exceeded 20 m, reinforcing the importance of tall vegetation in the selection of sleeping sites.

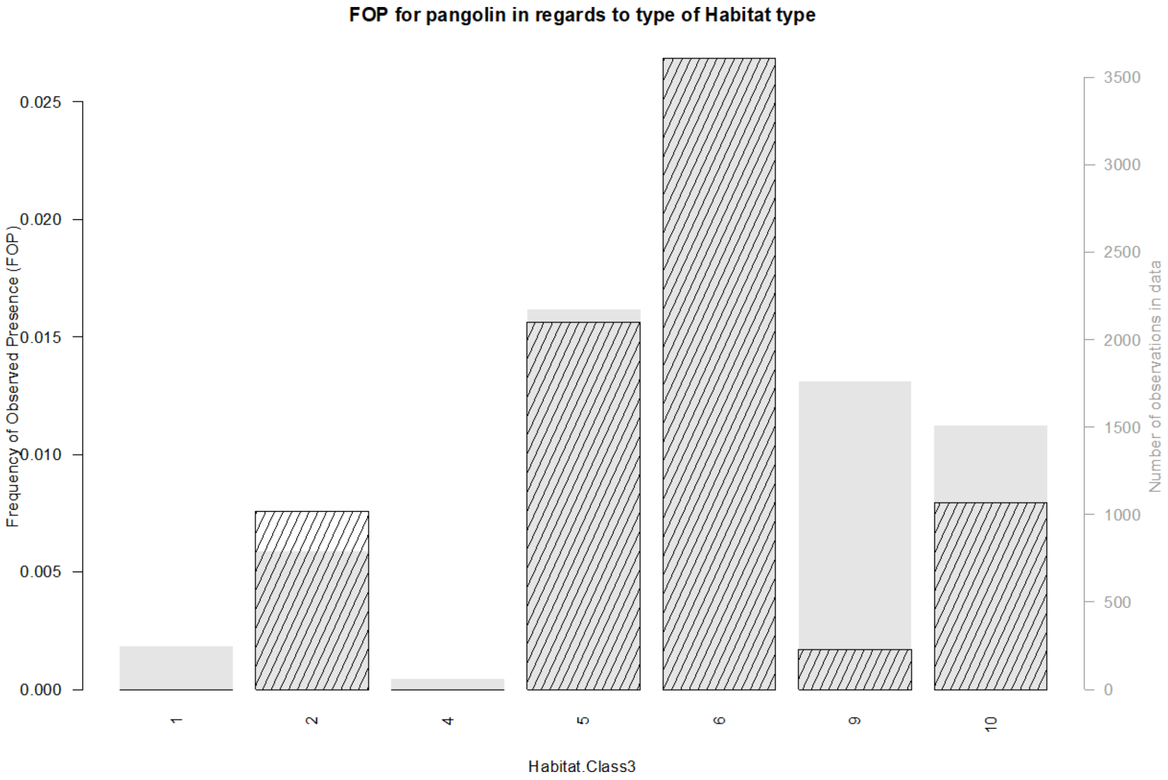

Fig. 4.12a: Frequency of observed presence (FOP) of Sunda pangolins and density of different values within each environmental variable. Habitat class is categorised as the number of observations of each type of habitat: [1] severely degraded areas, [2] dry lowland forest, [3] limestone forest, [4] peat swamp forest, [5] seasonal freshwater swamp, [6] freshwater swamp forest, [7] swamp, [8] cleared areas/young oil palm, [9] oil palm with good canopy, and [10] underproductive oil palm (Guerrero-Sanchez et al., 2021).

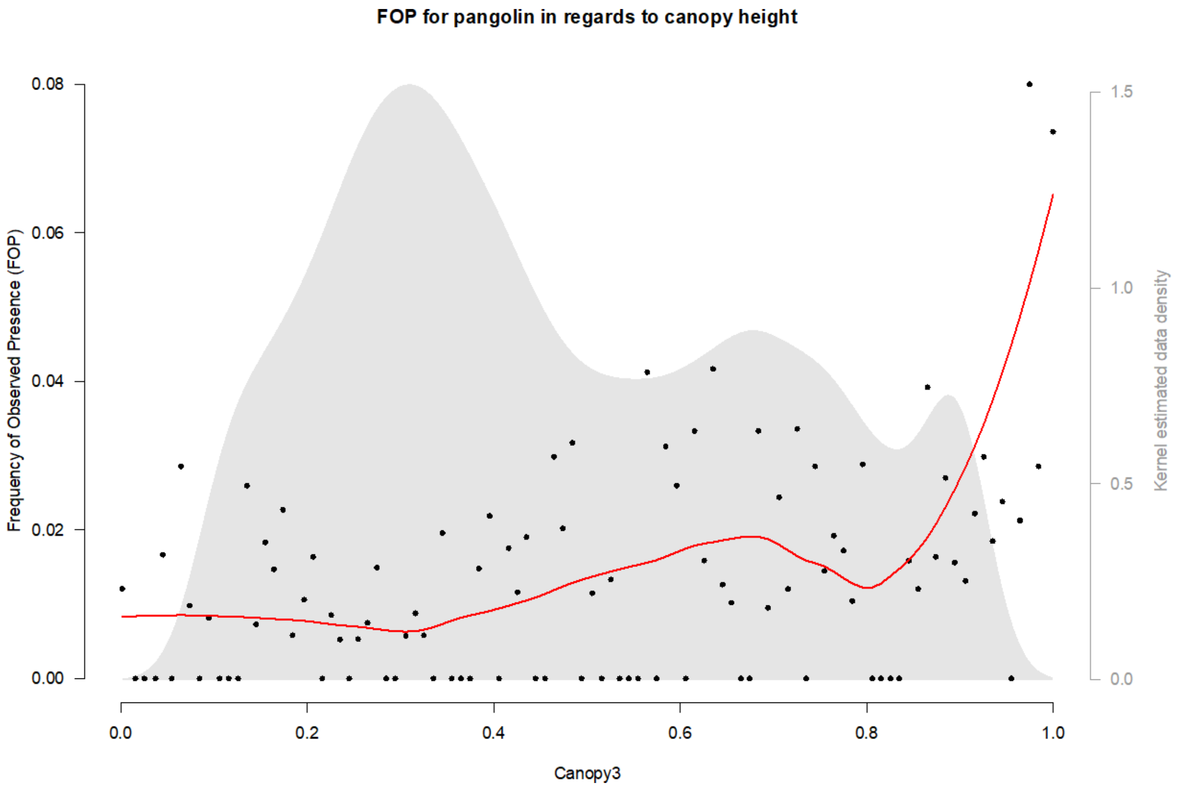

Fig. 4.12b: Kernel density plot comparing canopy height to the frequency of observed presence (FOP) of Sunda pangolins. The grey area represents the kernel density of canopy height, while the black points indicate the observed presence of pangolins within the study area. The red line shows the smoothed trend of the FOP in relation to canopy height.

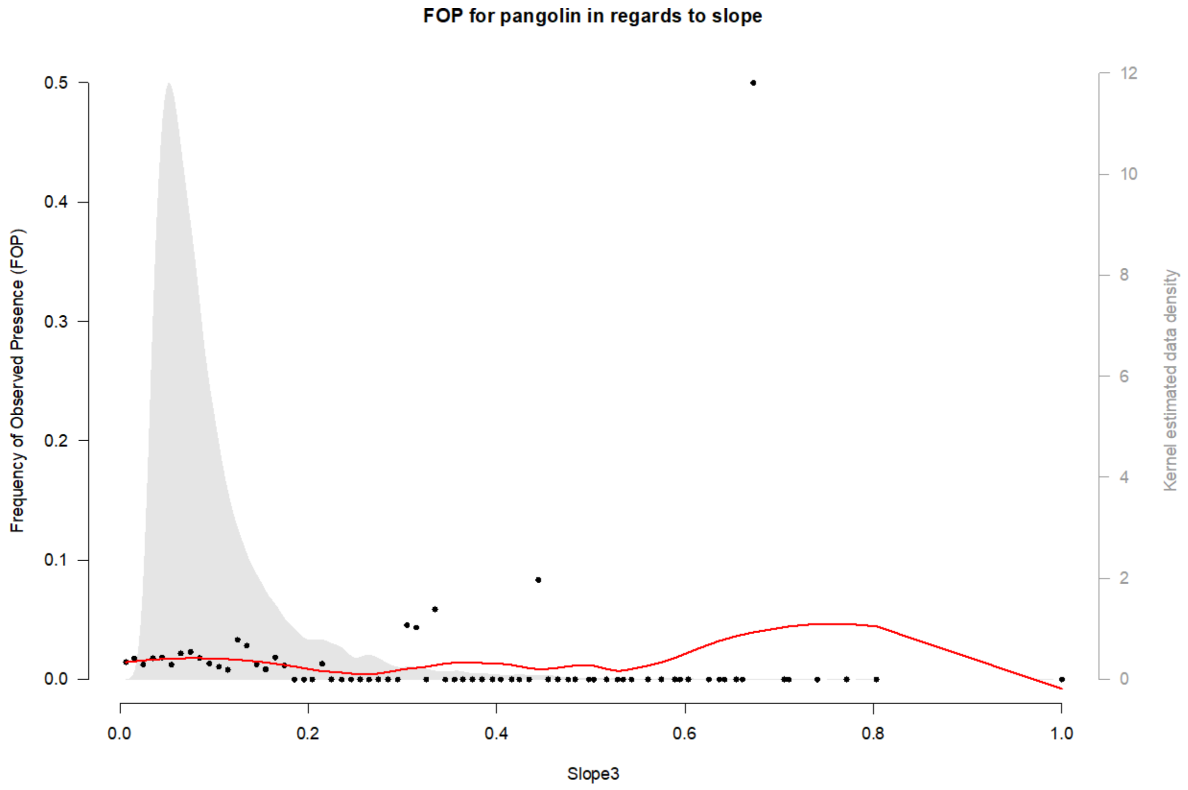

Fig. 4.12c: Kernel density plot comparing slope to the frequency of observed presence (FOP) of Sunda pangolins. The grey area represents the kernel density of slope, while the black points indicate the observed presence of pangolins within the study area. The red line shows the smoothed trend of the FOP in relation to slope.

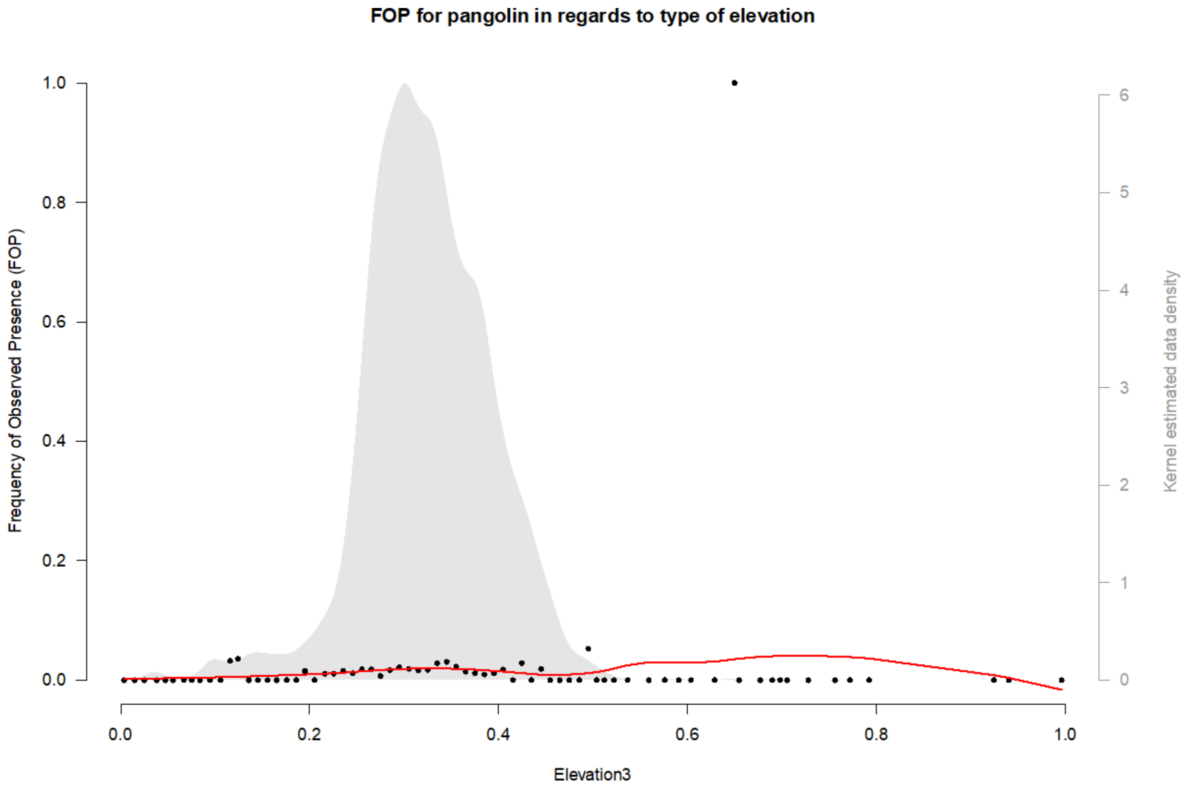

Fig. 4.12d: Kernel density plot comparing elevation to the frequency of observed presence (FOP) of Sunda pangolins. The grey area represents the kernel density of elevation, while the black points indicate the observed presence of pangolins within the study area. The red line shows the smoothed trend of the FOP in relation to elevation.

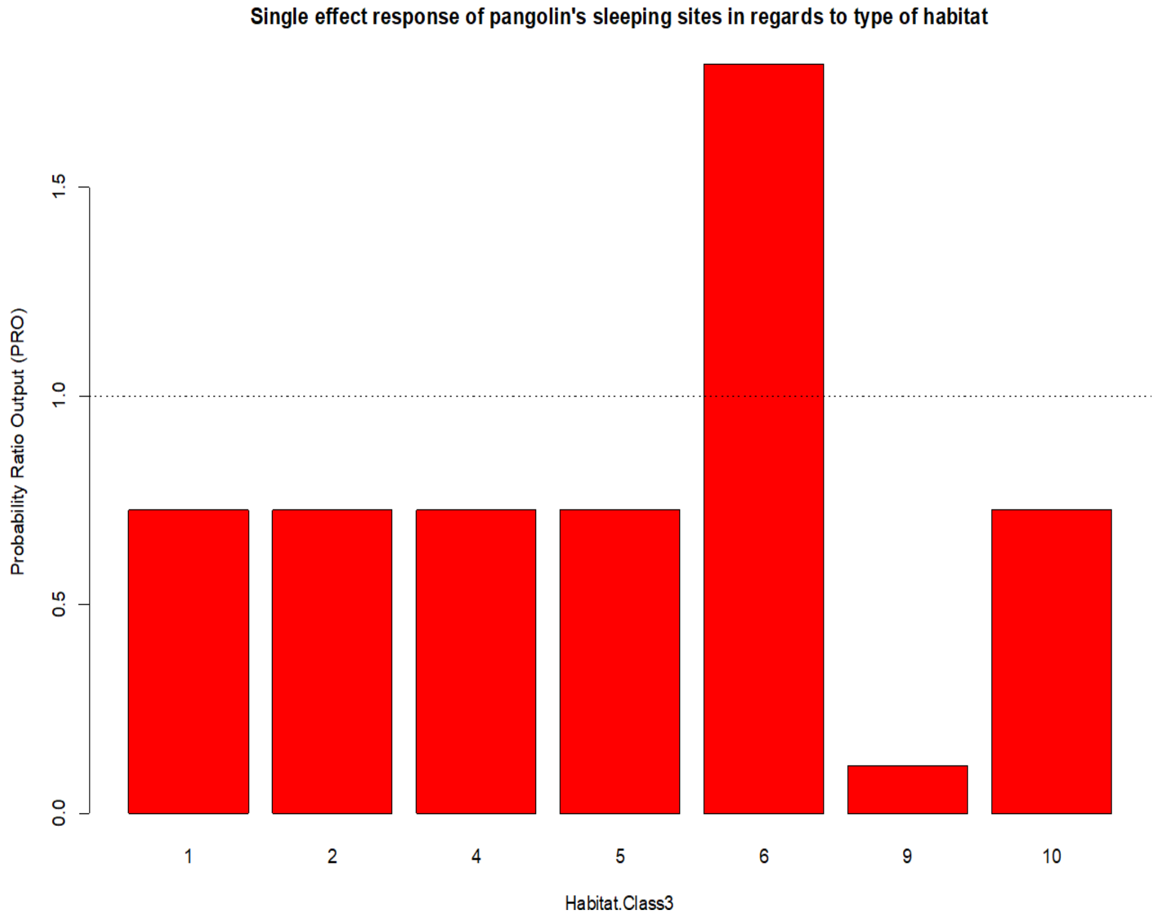

Fig. 4.13a: The effect response of Sunda pangolin sleeping sites based on habitat type. The plot shows the probability ratio output (PRO) for each habitat, where a value above 1 indicates a higher probability of occurrence. Habitat class is categorised as the number of observations of each type of habitat: [1] severely degraded areas, [2] dry lowland forest, [3] limestone forest, [4] peat swamp forest, [5] seasonal freshwater swamp, [6] freshwater swamp forest, [7] swamp, [8] cleared areas/young oil palm, [9] oil palm with good canopy, and [10] underproductive oil palm (Guerrero-Sanchez et al., 2021).

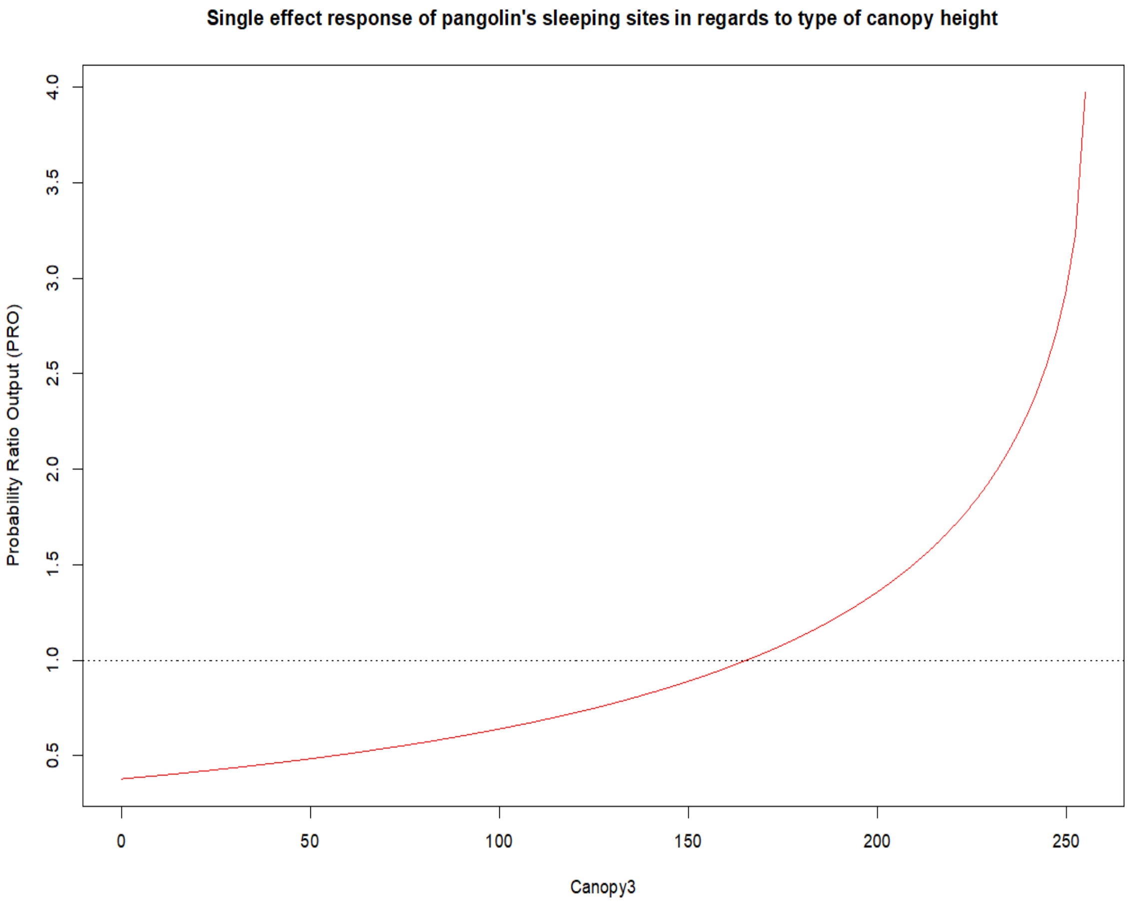

Fig. 4.13b: The effect response of Sunda pangolin sleeping sites based on canopy height. The plot shows the probability ratio output (PRO) for canopy height, value above 1 indicates a higher probability of occurrence.

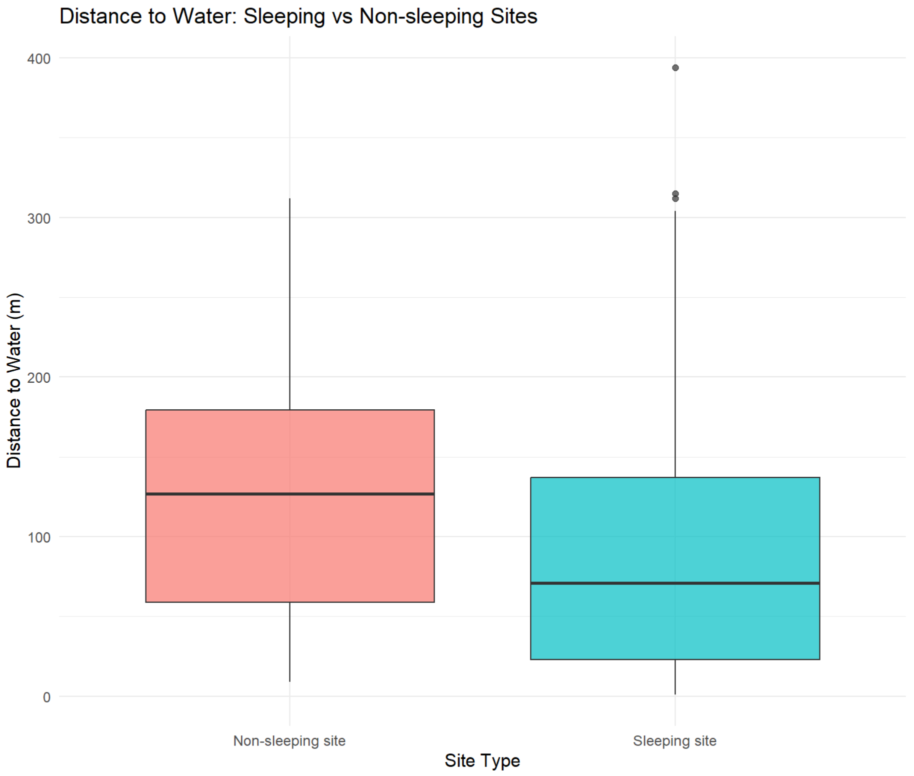

Fig. 4.13c: Boxplot comparing the distance to water between sleeping sites (n=241) and non-sleeping sites (n=288) used by Sunda pangolins in the LKWS. Sleeping sites were, on average, located closer to water than non-sleeping sites. The horizontal line within each box represents the median, the box spans the interquartile range (IQR), and whiskers extend to 1.5 × IQR. Dots above the whiskers represent outliers.

The analysis (**Fig. 4.13c**) showed that sleeping sites were, on average, significantly closer to water sources (mean=91.4 m, SD=82.1) than non-sleeping sites (mean=127.3 m, SD=76.9; Welch's t-test, $p < 0.001$; Wilcoxon rank sum test, $p < 0.001$). Despite this statistical difference, the effect size was relatively small (mean difference=36 m) and both sleeping and non-sleeping sites occurred within short distances of water bodies, reflecting the overall abundance of water in the floodplain landscape. Elevation and ground cover showed no significant influence on sleeping site selection.

The predictive model developed using the MaxEnt algorithm highlighted key areas within the Lower Kinabatangan Wildlife Sanctuary (LKWS) and its surroundings that are likely to be suitable for Sunda pangolin sleeping sites. **Fig. 4.14** shows the predicted probability of suitable locations for Sunda pangolin sleeping sites, represented as PRO of occurrence. The model indicates a clear preference for forested areas, particularly those with dense canopy cover and freshwater swamp habitats.

The spatial representation of these predicted probabilities within the LKWS was shown in **Fig. 4.15**. The brighter (red) shaded areas indicate higher probabilities of occurrence, suggesting that these regions are more likely to be used by Sunda pangolins as sleeping sites. Conversely, the darker (blue) shaded areas represent lower probabilities, indicating that these areas are less suitable for sleeping site selection. The model's AUC value of 0.725 further validates its performance, reflecting a good ability to predict suitable sleeping sites based on the environmental variables considered.

The map **(Fig. 4.14)** illustrates the predicted probability of suitable locations for Sunda pangolin sleeping sites generated through MaxEnt, with values presented as probability ratios (PRO) of occurrence.

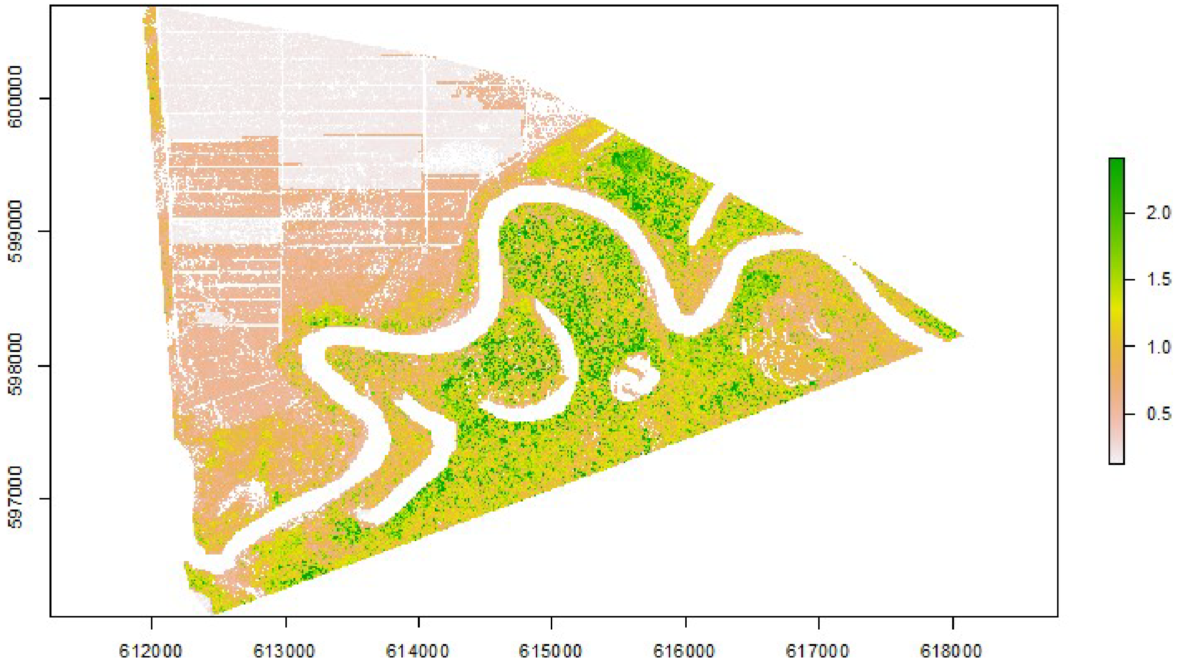

Fig. 4.14: Predicted probability of suitable occurrences for Sunda pangolin sleeping sites. The x-axis represents the Easting coordinates, while the y-axis represents the Northing coordinates. The colour gradient indicates the probability ratio output (PRO) of occurrence, with green representing higher probabilities, yellow indicating moderate probabilities, and brown/white showing lower probabilities.

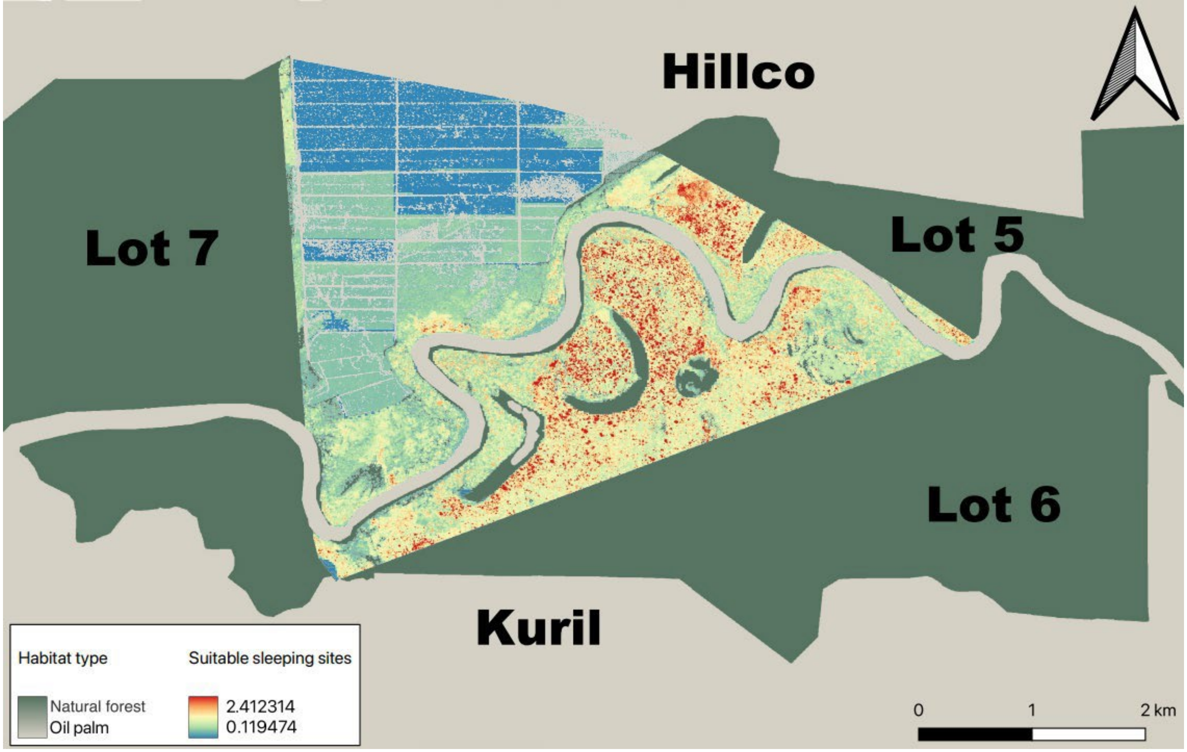

Fig. 4.15: Spatial representation of the predicted probability of suitable sleeping sites for Sunda pangolins in the LKWS and its surrounding areas. The map shows habitat types, with natural forest represented in dark grey and oil palm plantations in light grey. The suitability of sleeping sites is indicated by a colour scale, where red denotes areas with a high probability of occurrence, yellow indicates moderate probability, and blue represents low probability.

4.4 Discussion

The Sunda pangolin is a critically endangered species facing multiple threats, including habitat loss, fragmentation, and poaching (Challender et al., 2014; Chong et al., 2020). The species' survival is intrinsically linked to healthy forested areas with adequate tree cover, as they require this environment for shelter and feed exclusively on ants and termites (Chong et al., 2020). The findings presented in Chapter 2 of this thesis revealed that the Sunda pangolin population in Sabah is primarily distributed within natural forest habitats, which serve as essential strongholds for the species.

While the LKWS in Sabah, Malaysia, is highlighted as a critical habitat for the Sunda pangolins, it is important to recognise that direct encounters and sightings of pangolins were limited during the study. This paucity of encounters reflects the inherent difficulties in studying a species that is naturally elusive, nocturnal, and often resides in dense forest cover, rather than an indication of the habitat’s unsuitability.

Despite these challenges, the ecological characteristics of the LKWS, such as its extensive forest cover, presence of old-growth trees, and availability of suitable feeding resources (Abram and Ancrenaz, 2017), strongly suggest that it provides a vital refuge for Sunda pangolins. The results of this study, while limited by the number of direct pangolin encounters, align with broader ecological understanding and emphasise the importance of protecting such habitats.

Therefore, while we must exercise caution in making definitive statements based on the limited field data, the findings contribute to a growing body of evidence that the LKWS plays a crucial role in the conservation of Sunda pangolins. Continued research and monitoring are needed to further substantiate this role, but the available evidence supports the sanctuary's significance as a key habitat for the species.

To effectively protect and conserve the Sunda pangolin population in the LKWS, it is crucial to understand the physical and spatial characteristics of their sleeping sites, as well as the environmental variables that influence their distribution. This study addressed these issues by detailing the characteristics of sleeping sites used by Sunda pangolins within the sanctuary and identifying the key environmental factors affecting their distribution. The insights gained from this study into the species’ habitat requirements and preferences are invaluable for guiding the development of effective conservation strategies aimed at protecting this critically endangered species.

4.4.1 Physical and spatial characteristics of sleeping sites

This study represents a crucial advancement in understanding the microhabitat preferences of Sunda pangolins by providing detailed insights into the physical and spatial characteristics of their sleeping sites. Prior to this research, there was a significant gap in knowledge regarding the species' microhabitat use, which posed challenges to the development of effective conservation strategies. The findings from this study, particularly the identification of key variables such as tree height, diameter at breast height (DBH), presence of hollows, and vine coverage, offer a valuable foundation for future research and conservation efforts aimed at protecting Sunda pangolins in the LKWS and adjacent oil palm plantations.

The species demonstrated a clear preference for taller, larger, living trees with hollows covered by vines as their preferred sleeping sites. These specific physical characteristic, tree height, DBH, presence of hollows, and vine coverage were associated with the selected sleeping sites, emphasising their importance in the microhabitat preferences of Sunda pangolins. These aligns with previous findings by Lim and Ng (2007, 2008), which highlighted the significance of large trees with hollows for the species' habitat use. In addition to trees, the study found that Sunda pangolins in the LKWS also utilised other structures, including burrows, hollow logs, and grassland, as well as some unidentified structures that were inaccessible due to flooding. The unknown structures observed during the study could potentially belong to one of the identified sleeping site types, such as trees, burrows, or hollow logs. However, due to factors like flooding or inaccessibility at the time of observation, these structures could not be conclusively identified.

The diversity in sleeping site selection among Sunda pangolins indicates that they can utilise a range of microhabitats, from large trees with hollows and vine coverage to burrows, hollow logs, and even grasslands. This flexibility in habitat use may reflect their ability to adapt to varying environmental conditions. Specifically, in the face of habitat degradation and fragmentation, where preferred large trees may become less available, Sunda pangolins might increasingly rely on alternative structures for shelter. This adaptability could be crucial for their survival in increasingly altered landscapes, where traditional forest habitats are being lost or transformed into agricultural lands (oil palm plantations or urban areas). By using a wider range of sleeping sites, Sunda pangolins may be able to maintain their populations in fragmented or degraded environments, thereby enhancing their resilience to habitat changes.

This study found that the number of hollows in a tree was positively associated with the likelihood of use by Sunda pangolins as sleeping sites. Trees with multiple hollows may offer more versatile and secure options, increasing their suitability as refuges. While this study did not directly measure the abundance or interconnectedness of tree hollows, a field observation during attempted re-tagging showed a pangolin using multiple hollow entrances to evade capture. This anecdotal observation supports the idea that hollows can enhance security, but systematic assessment was beyond the scope of this study. Previous research shows that tree hollows form slowly, often taking centuries in natural forests (Haslem et al., 2012; McLean et al., 2015). This slow formation rate highlights the importance of conserving large, old trees that are more likely to contain hollows. Tree hollows are declining due to habitat loss and fragmentation, which reduces the availability of large and old trees with cavities (Gibbons et al., 2008; Ranius et al., 2009), and this shortage of hollows may limit hollow-dependent species populations such as the Sunda pangolin (Lindenmayer et al., 2012a).

The presence of lianas or vines in sleeping trees was found to be important in determining the sleeping sites of Sunda pangolins. Lianas, a type of climbing plant, produce abundant foliage (Schnitzer and Bongers, 2002) and are known to provide important resources for animals, thus likely shaping the evolution of arboreal lifestyles (Emmons and Gentry, 1983; Kilgore et al., 2010). Field observations revealed that Sunda pangolins used vines to climb trees and move from one tree to another, and were also observed sleeping beneath dense liana foliage, which provided the species with effective cover and protection. Lianas are often more abundant in older, structurally complex forests (Schnitzer and Carson, 2010), therefore the conservation of such forests is important for maintaining suitable microhabitat and refuges for Sunda pangolins in the LKWS and Sabah.

The results of the habitat use model indicated that the distance of sleeping sites to water sources, elevation, and ground cover were insignificant in determining the microhabitat preferences of Sunda pangolins in the LKWS. These variables were initially included in the study to explore all potential factors that could influence sleeping site selection. However, the lack of significance may be attributed to the relatively uniform elevation distribution and limited variation in ground cover types in the study area, primarily due to seasonal flooding affecting ground cover availability. The analysis of distances to water revealed that sleeping sites were, on average, located closer to water than non-sleeping sites **(Fig. 4.13c)**. While this result was statistically significant, the ecological importance may be limited given the abundance of water bodies in the study area, including the Kinabatangan River, oxbows and tributaries. The relatively narrow range of distances observed suggests that water is readily available across the landscape, which may reduce its role as a strong determinant of sleeping site selection. Nevertheless, the slight tendency for sleeping sites to be nearer to water could reflect opportunistic use of areas that offer both structural cover and easy access to resources associated with riparian zones.

The LKWS has experienced significant fragmentation and degradation due to human activities such as logging and, notably, the establishment of monoculture oil palm plantations (Estes et al., 2012; Abram et al., 2014). The Lower Kinabatangan is primarily used for agriculture and other non-forestry purposes (Abram et al., 2014). This has led to a mosaic of land uses within the Lower Kinabatangan, including dry lowland forests, semi-inundated forests, grasslands, and swamp forests (Estes et al., 2012; Abram et al., 2014). The ongoing and often unregulated land conversion to agricultural use further worsens habitat loss and fragmentation in the area (Stark et al., 2017). In this study, the use of non-forested habitats such as oil palm plantations as sleeping sites was recorded only among translocated individuals. This suggests that such use may reflect the challenges of release into new environments rather than clear evidence of species-wide adaptation to agricultural landscapes. While this behaviour highlights the risks translocated pangolins may face in fragmented and human-modified areas, further research with larger samples of resident individuals is needed before drawing conclusions about pangolin adaptation at the species level.

Given the fragmented and degraded state of the forest in the LKWS and its surrounding oil palm plantations, the findings of this study highlight critical insights into the adaptability and habitat preferences of Sunda pangolins, particularly in the context of conservation translocation. The study revealed distinct differences between resident and translocated pangolins in their sleeping site selection. Resident pangolins exclusively utilised forest habitats, selecting large, tall trees with hollows as their primary sleeping sites, emphasising their dependence on undisturbed natural forests. Conversely, translocated pangolins showed a broader range of sleeping site selections, including frequent use of oil palm plantations. Because only translocated individuals used oil palm trees and mainly in the months immediately post-release, this is interpreted as use out of necessity during exploratory movement, not evidence of species-level adaptation.

However, the use of oil palm plantations raises significant concerns due to the increased exposure to human activities. Field observations documented translocated pangolins sleeping in exposed locations, such as behind the flanges of oil palm trees or on the crowns, where they could be easily detected by plantation workers. This vulnerability is particularly alarming given reports of active hunting and illegal trade of pangolins within these plantations (Azhar et al., 2013; Panjang et al., 2024). Radio tracking combined with camera traps was essential in revealing these behaviours and risks, which would otherwise remain undetected, thereby strengthening the conservation implications of this study.

These results emphasise the importance of carefully selecting release sites for translocated pangolins, ensuring that they are placed in habitats where the risk of human conflict is minimised. While the use of oil palm plantations by translocated pangolins may suggest some resilience, it also highlights the urgent need for conservation strategies that extend beyond restoration of natural forests within LKWS alone. In heavily modified landscapes like the LKWS, working with oil palm plantation holders to implement wildlife-friendly practices and reduce threats will be just as critical as protecting and restoring remaining forest patches. The integration of sleeping site data from both resident and translocated pangolins in this study reinforces the necessity of preserving old-growth forests with large, hollow trees, while also promoting coexistence strategies in plantation areas.

The habitat and sleeping site analyses conducted in this study found that the likelihood of finding Sunda pangolin sleeping sites in oil palm plantations was higher than in forest habitats, based on the analysis of resident and translocated pangolins. However, it is important to note that the resident pangolins only used sleeping sites in forest habitats. While translocated pangolins were observed using sleeping sites in both forest and oil palm habitats, this behaviour may reflect a lack of available alternatives rather than a true preference. The use of oil palm plantations may indicate the pangolins' need to adapt to suboptimal environments when suitable forested areas are scarce. This adaptation should not be misinterpreted as an indication that oil palm plantations are suitable habitats for the species. Instead, it emphasises the importance of conserving and restoring natural forests to provide the optimal conditions necessary for their survival.

The observation that translocated pangolins utilised sleeping sites in oil palm plantations is more likely a response to limited habitat options in their release environment. Unlike resident pangolins, which consistently selected forested habitats, translocated individuals may have been forced to use suboptimal sites in plantations due to the limited availability of forest habitats in the surrounding areas. Translocated pangolins' use of oil palm plantations may therefore reflect a temporary adjustment to challenging conditions, rather than a true habitat preference. Further research is needed to understand whether these individuals eventually establish preferences like those of resident pangolins or continue to adapt to suboptimal conditions.

Given that natural forests with old-growth trees are crucial for Sunda pangolins, the use of oil palm plantations by translocated individuals likely reflects the challenges they face in adapting to degraded habitats. These findings highlight the importance of protecting and restoring natural forests. However, further research would be needed to confirm this hypothesis. The observed use of non-tree sleeping sites in plantations likely reflects the scarcity of suitable tree sites with hollows, rather than a true preference for non-tree sites. In forest habitats, where suitable trees are more abundant, pangolins may prefer tree-based sleeping sites due to the greater protection they offer.

Additionally, tree sleeping sites may provide better protection from predators and other threats compared to non-tree sleeping sites (Hamilton, 1982; Franklin et al., 2007, 2007a, 2007b). In the forest habitat, resident pangolins may have a more established territory and therefore have easier access to tree sleeping sites, while translocated pangolins may be exploring new areas and therefore more likely to use non-tree sleeping sites. In oil palm plantations, the absence of large, old trees with hollows significantly limits the availability of suitable tree-based sleeping sites. This likely forces pangolin to use alternative, less secure sites, such as the bases of oil palms or other structures, which may increase their vulnerability to threats.

This study provided valuable insights into the sleeping site selection of Sunda pangolins, but the data were limited by the scope of the study area and the number of individuals tracked. Future research should focus on larger sample sizes, longer monitoring periods, and the inclusion of additional habitat variables to better understand the species' habitat preferences and adaptability. Such research could provide more definitive answers to questions about the impact of habitat availability and quality on sleeping site selection.

Another possibility is that translocated pangolins might be trying to return to their original habitat, as has been observed in other animals (Rogers, 1992). This study did not conduct specific movement analyses to investigate homing behaviour due to the limited size of the dataset. While homing behaviour has been documented in various species, including insects (Mandal, 2018), birds (Schiffner et al., 2018), reptiles

(Guerrero-Sanchez et al., 2021) and mammals (Toplicanec et al., 2022), further research with a larger dataset would be necessary to explore this behaviour in Sunda pangolins. Future studies could apply movement analyses and models to better understand the potential homing instincts of Sunda pangolins and their implications for conservation strategies.

While translocated pangolins were observed using sleeping sites in oil palm habitats, this does not necessarily indicate successful adaptation to these new environments. Rather, their use of oil palm plantations may reflect a lack of suitable forested alternatives in the immediate vicinity. The translocated individuals might be compelled to use these suboptimal habitats temporarily, driven by the need to find shelter while potentially still searching for more suitable environments. Further research is required to determine whether this behaviour represents a true adaptation or a temporary coping mechanism in response to habitat loss.

In this study, both resident and translocated pangolins were observed utilising a variety of sleeping sites beyond the more commonly documented tree-based locations, including hollow logs, burrows, and grasslands. These observations highlight the species' ability to exploit a wide range of microhabitats for sleeping. While resident pangolins predominantly used forest habitats for sleeping, translocated pangolins demonstrated a broader range of habitat use and show greater behavioural flexibility. Despite this flexibility, the suitability of oil palm plantations as long-term habitats remains questionable. While these areas may provide ample access to prey, as ant populations in oil palm plantations are abundant and diverse (Alamsari, 2014; Hasan et al., 2023), they also suffer from reduced ant species richness (Fayle et al., 2010). This reduction in species richness and the lack of structural complexity compared to natural forests could limit the long-term viability of these habitats for Sunda pangolins.

Field observations confirmed that pangolins used oil palm trees and non-tree-based sites (e.g., grasses, bushes, burrows) as sleeping sites. Pangolins have been observed sleeping behind fronds or on top of the crown of tall oil palm trees, which are well hidden. Additionally, they have been found utilising grasses, bushes, and burrows as sleeping sites within the plantations. This behaviour mirrors that of other mammals in the study area, such as the common palm civet (*Paradoxurus hermaphroditus*), Malay civet (*Viverra tangalunga*), and leopard cat (*Prionailurus bengalensis*), which have been documented utilising oil palm plantations for sleeping, foraging, and breeding (Evans et al., 2016; Wilson, 2022). Although these locations may provide temporary cover, they also leave pangolins more exposed to detection by people working in plantations. Thus, while plantations can function as suboptimal refuges, they simultaneously increase vulnerability to poaching, highlighting a trade-off between accessibility and safety.

Despite the potential for Sunda pangolins to adapt to non-forested habitats such as oil palm plantations, the primary threats to their survival in these areas remain human-related. These threats include direct hunting and poaching by plantation workers, who may capture pangolins for their high market value in illegal wildlife trade. Additionally, the presence of feral dogs in plantation areas poses a significant risk, as these dogs been known to attack and injure Sunda pangolins (Chong et al., 2020; Panjang et al., 2024). Therefore, it is imperative to consider these specific threats and develop targeted conservation strategies, such as increasing anti-poaching patrols, educating plantation workers about wildlife protection, and managing feral dog populations, to mitigate the risks and ensure the continued survival of this endangered species.

4.4.2 Environmental variables that influence distribution

The MaxEnt model showed that habitat types and canopy height were significant environmental variables affecting the distribution of sleeping sites for Sunda pangolins. Habitat types refer to the broad vegetation categories present in the study area. The results indicate that forested areas, particularly the lowland freshwater swamp forest association (i.e., freshwater swamp forest) in LKWS, were the most likely areas for Sunda pangolins to use as sleeping sites. Peat swamp forests and seasonal freshwater swamps, also associated with the lowland freshwater swamp forest, were also identified as suitable habitats. In addition, dry lowland forests and severely degraded forest were likely suitable habitats for Sunda pangolin sleeping site use. The results also suggested that Sunda pangolins may adapt to non-forested areas such as oil palm plantations with good canopy cover, even underproductive ones.

Forested wetlands in Malaysia, including peat swamp forests, freshwater swamp forests, and riparian forests, cover an area of approximately 4.39 million ha (Ministry of Natural Resources and Environment, 2014). Freshwater swamp forests in Malaysia cover only 2.5% of the country's total forested wetland area, making them relatively scarce. In this study, PRO analysis indicated that freshwater swamp forests had the highest likelihood of being used as sleeping sites by Sunda pangolin, suggesting that these habitats may play an important role locally in the LKWS. Further research is needed to determine whether this pattern holds across other landscapes in Malaysia.

In Sabah, the lowland freshwater swamp forest association is considered a critical habitat for Sunda pangolins, with the freshwater swamp forest being particularly important among the three subtypes. However, these habitats are facing significant threats, with only 33% (23,500 ha) of freshwater swamp forests, 36% (42,000 ha) of peat swamp forests, and a mere 17% (43,000 ha) of seasonal freshwater swamp forests remaining from their original distributions (Abram and Ancrenaz, 2017). This highlights the urgent need for conservation efforts to protect and restore these habitats, as they are essential for the survival of the Sunda pangolin population in Sabah.

The freshwater swamp forest can be found in the Lower Kinabatangan region where this study was conducted. The Lower Kinabatangan floodplain is Sabah's largest and most important wetland (Boonratana, 2000; Abram and Ancrenaz, 2017). Since approximately 23% (more than 9,000 ha) of the Lower Kinabatangan freshwater swamp forests are in private or unalienated land (outside protected areas), conservation efforts should prioritize safeguarding these forests to ensure the survival of the Sunda pangolin population in the areas. To prioritise the safeguarding of freshwater swamp forests, conservation efforts should focus on securing legal protection for remaining unprotected areas, promoting sustainable land-use practices that prevent further degradation; and restoring degraded swamp forests through reforestation and habitat management initiatives. Collaboration with local communities and stakeholders will also be essential in implementing these conservation strategies effectively.

The lowland freshwater swamp forest, characterised by its seasonally flooded conditions, often for more than six months a year, and its formation in backwater swamps with poorly drained soil (Abram and Ancrenaz, 2017), offers unique environmental conditions that may influence the Sunda pangolin’s choice of sleeping sites. The extended flooding periods could lead to the development of specific vegetation structures, such as tall, large trees with extensive buttress roots, which are preferred by Sunda pangolins for sleeping. Additionally, this forest type may support abundant food sources, such as ants and termites, that are critical to the pangolins' diet (Lim and Ng, 2008; Chong et al., 2020). Observation in the field documented sleeping sites in areas with tree species, including *Shorea spp.*, *Ficus spp.* and *Eusideroxylon spp.,* which are commonly found in lowland dipterocarp forests (Ministry of Primary Resources and Tourism, 2022). These factors suggest that the specific environmental and structural features of lowland freshwater swamp forests contribute to their suitability as preferred sleeping habitats for Sunda pangolins.

Additionally, these types of forests have epiphytes, and climbers are abundant (Ministry of Primary Resources and Tourism, 2022), contributing to the structural complexity of the habitat, which may enhance their suitability as sleeping sites for Sunda pangolins. The swamp forests in the study area likely to maintain high level of humidity and moisture due to high rainfall and high temperature (Posa et al., 2011).

These conditions are likely favourable for sustaining populations of insects, particularly ants and termites. This study supports this view, as pangolins were observed frequently using sleeping sites within freshwater swamp forests, indicating that these habitats provide essential resources for the species. In particular, the presence of prey species like ants and termites in these humid environments likely contributes to their use as sleeping sites by Sunda pangolins. This study recorded the use of degraded forest areas as sleeping sites by translocated pangolins, demonstrating the species' capacity to persist in such landscapes. This aligns with findings by Lim and Ng (2008) in Singapore, further suggesting that Sunda pangolins can adapt to fragmented and degraded forests. Therefore, degraded forests should also be considered in conservation strategies, as they may still provide crucial habitat features necessary for the survival of the species.

Conservation strategies for the Sunda pangolin should not only focus on forested areas, but also consider the occasional use of non-forested habitats, as suggested by the findings of this study. For example, in the Lower Kinabatangan, where habitat fragmentation is a significant issue, translocated Sunda pangolins were observed utilising oil palm plantations as alternative habitats. Furthermore, the MaxEnt model revealed that underproductive oil palm plantations with good canopy cover may provide some level of suitability. While these areas are clearly suboptimal compared to forested areas, their inclusion in landscape scale planning may help reduce risks in fragmented habitats.

Borneo has undergone significant land conversion to accommodate the cultivation of oil palm plantations. In Sabah alone, the area of land used for oil palm cultivation amounts to approximately 1.43 million ha (Abram et al., 2014). This industry plays a major role in the region's economy and has notable environmental and socio-economic impacts. The Kinabatangan floodplain, being the largest of its kind in Sabah, provides a particularly conducive environment for the growth of oil palm (Abram and Ancrenaz, 2017). However, studies have indicated that the expansion of oil palm plantations threatens the local wildlife and their habitats in Sabah (Hearn et al., 2018; Lim et al., 2019; Abram et al., 2022; Guharajan et al., 2022). Thus, while acknowledging the importance of the oil palm industry in Malaysia, it is crucial to consider the impact of such plantations on the surrounding environment and wildlife, including the Sunda pangolin.

In the context of oil palm plantations, underproductive oil palm refers to trees nearing the end of their productive lifespan or suffering from poor health, resulting in low yield (Henson et al., 2008; Abram et al., 2014; Corley and Tinker, 2015; Woittiez et al., 2017). Despite their reduced productivity, these trees, if they have dense canopy cover, may still provide suitable habitat for wildlife, including Sunda pangolins. In this study, translocated pangolins were observed using oil palm trees, often hiding behind fronds or sleeping on top of the crowns, suggesting that tall trees with abundant foliage may offer effective cover from natural predators. The association between sleeping and foraging sites in oil palm plantations is critical for understanding habitat use. Although termite species richness is lower in oil palm plantations compared to primary forests (Fayle et al., 2010; Keng and Rahman, 2012), termites tend to be found near deadwood and stacked fronds, which are more common in older or poorly managed plantations. Additionally, studies have shown that ground-foraging ants, a prey of Sunda pangolins, are abundant in oil palm plantations, especially in areas with understory vegetation (Hood et al., 2020). Underproductive oil palm plantations, where such vegetation is less frequently removed, may support higher prey availability, making them not only suitable as sleeping sites but also potentially advantageous as foraging grounds.

The vertical extent of the forest canopy, known as canopy height, is an important variable influencing the sleeping site selection of Sunda pangolins. Being semi-arboreal, Sunda pangolins rely on trees for movement and foraging of arboreal insects (Chong et al., 2020), making canopy height a crucial factor in their habitat selection. The MaxEnt analysis conducted in this study revealed that Sunda pangolins preferred sleeping sites in areas with higher canopy heights of up to 20 m, suggesting that taller trees may provide more suitable microhabitats for the species. Tree height was identified as one of the most significant physical characteristics in Sunda pangolin sleeping site selection.

The preference for taller trees can be explained ecologically by considering the various advantages that taller trees provide. Taller trees typically offer greater structural complexity, which can provide enhanced cover and protection to Sunda pangolins from predators (Lim and Ng, 2008), particularly in areas where the forest canopy is dense. Additionally, the increased vertical space may offer better access to arboreal prey, such as ants and termites. The canopy layer of taller trees may also be less disturbed by ground-level human activities, allowing pangolins to rest more securely. The increased height of trees may also help regulate microclimatic conditions, such as temperature and humidity (Richter et al., 2022), which could provide a more stable and favourable environment for resting and avoiding overheating or dehydration during the day. Importantly, taller and older trees are also more likely to contain natural hollows (Haslem et al., 2012), which provide secure refuges and further increase their suitability as sleeping sites. Together, these ecological factors make taller trees an ideal choice for sleeping sites in both natural and degraded habitats.

Sunda pangolins are adept climbers equipped with powerful claws and prehensile tails for grasping tree branches while climbing (Chong et al., 2020). Field observations indicate that Sunda pangolins are slow on the ground, making them vulnerable to predators. In contrast, when they are up in the trees, they can move much faster and are protected from predators, making tall trees with high canopy height desirable sleeping sites. This behaviour may explain the low encounter rates of Sunda pangolins on ground camera trapping reported in several studies (Kwaja et al., 2019; Gray et al., 2022), highlighting the importance of using different camera trapping methods such as arboreal camera trapping as suggested by Willcox et al. (2019). This study suggests that understanding the behaviour and habitat preferences of Sunda pangolins can inform research methods and improve species detection. Furthermore, identifying canopy height as a significant variable influencing the sleeping site selection of Sunda pangolins highlights the importance of tall trees and high canopy cover for the conservation of the species.

4.4.2 Observations on Sunda pangolin social behaviour

The study provided valuable insights into the social behaviour of Sunda pangolins, including their interactions with conspecifics and co-existence with other species in sleeping sites. Among the male Sunda pangolins, territorial behaviour was documented, with males competing for dominance over sleeping sites. These incidents were documented using camera traps during the study period.

In the first incident, a translocated pangolin was observed leaving its sleeping site after being attacked by a wild male pangolin, which subsequently took over the sleeping sites. In the second incident, a wild pangolin successfully defended its sleeping site from another wild male. Finally, in the third incident, a wild male pangolin was observed fighting with another male for access to a female pangolin with a baby. The victorious male then mated with the female, illustrating the competitive nature of male interactions, especially for sleeping sites and mating opportunities. These findings, captured through camera trap documentation, provide important insights into the social dynamics of Sunda pangolins, particularly male territoriality and aggression. Previous studies have also reported aggressive interactions between male Sunda pangolins (Lim, 2007; Panjang and Goossens, 2022). While identifying and mapping all male territories at potential release sites is rarely feasible, these observations suggest that translocation planning should consider spacing male releases more widely to help reduce the risk of direct conflict with resident males.

In addition to interactions with other Sunda pangolins, the study documented the co-existence of Sunda pangolins with other species in sleeping sites in Sabah. For example, Sunda pangolins were observed sharing tree holes with bats (Chiroptera) (Panjang and Goossens, 2022), highlighting the shared use of microhabitats by different species. Similarly, Sunda pangolins were found occupying burrows simultaneously with small mammal species, such as Malay badgers (*Mydaus javanensis*), moonrats (*Echinosorex gymnura*), Malayan weasels (*Mustela nudipes*), and common porcupines (*Hystrix brachyura*) (Panjang and Goossens, 2022). These observations suggest that Sunda pangolins may have adapted to coexist with other species in their natural habitats.

Similar observations have been reported for other pangolin species globally, further supporting the idea that pangolins can share sleeping sites with various species. In Central Gabon, for example, the giant pangolin (*Smutsia gigant*ea) has been observed cohabiting with bats (Lehmann et al., 2020). Additionally, other species, such as pythons, monitor lizards (*Varanus sp.*), and tortoises, have been found occupying pangolin sleeping sites in other regions (S. Trageser, unpub. data). These global examples emphasise the adaptability of pangolins to co-exist with a diverse range of species, which may be an important ecological trait that supports their survival in fragmented or degraded habitats.

4.4.3 Implications for conservation and management

The findings of this study have important implications for the conservation and management of Sunda pangolin populations in the study area and beyond. The study highlights the role of freshwater swamp forests, peat swamp forests, and seasonal freshwater swamps as key habitats for Sunda pangolins. As such, these habitats should be prioritised in conservation efforts. Restoration and preservation of these vital forest types, particularly in areas where they are fragmented and degraded, should be a key focus of management strategies.

Additionally, this study found that degraded forests, dry lowland forests, and underproductive oil palm plantations with good canopy cover can also serve as suitable habitats for Sunda pangolins. Therefore, conservation plans should also include the protection and management of these areas, ensuring that habitat quality is maintained or improved.

To ensure the survival of Sunda pangolins, conservation efforts should prioritise the protection and restoration of critical habitats. These forested wetlands must be safeguarded through habitat protection and restoration efforts. Additionally, degraded forests, which have shown potential to support pangolin populations, should be targeted for restoration. Underproductive oil palm plantations, while not ideal, can also be incorporated into conservation plans by promoting better management practices that preserve ground cover and fronds, offering some habitat support for translocated pangolins. Addressing human-related threats, such as illegal hunting and poaching, is essential for protecting pangolin populations, particularly in oil palm plantations. Stricter monitoring, anti-poaching patrols, and awareness campaigns for plantation workers are recommended. Collaboration with local communities and stakeholders will further enhance conservation efforts.

The study underscores the significance of microhabitat preferences for Sunda pangolins, as certain physical and spatial characteristics are critical in the selection of sleeping sites. The results indicate that tall, large living trees with hollows and abundant vine coverage are the preferred sleeping sites for Sunda pangolins, and these habitats are predominantly found in old and mature forests. These findings emphasize the importance of protecting and maintaining natural forests, as they are essential for the survival of Sunda pangolin populations. Furthermore, the ability of Sunda pangolins to use a diverse range of sleeping sites across various habitat types suggests the species' adaptability and resilience to habitat fragmentation and degradation.

The study highlights the need for targeted conservation efforts that prioritise microhabitat features critical to Sunda pangolin survival. Specifically, the protection of tall, large living trees with multiple hollows and abundant vine coverage should be a focal point, as these structures serve as essential sleeping sites for the species. Conservation strategies should prioritise maintaining mature forest stands with trees that provide hollows and vine cover, as these features were consistently associated with sleeping site use in this study.

In areas with habitat degradation or fragmentation, management plans should emphasise the preservation of key microhabitat features, even within non-forest environments like degraded lands or oil palm plantations. Since oil palm trees are typically cut and replaced every 25 years, strategies should prioritise the retention of older trees with dense canopies until the end of their productive lifespan, as they can provide temporary refuge for Sunda pangolins. Additionally, maintaining forest patches within plantations and protecting High Conservation Value (HCV) areas can help preserve critical microhabitats, such as trees with hollows, vine coverage, and ground cover. These conservation efforts ensure that even in altered landscapes, essential microhabitat features are available to support the survival and persistence of Sunda pangolins across a range of environments.

In light of the frequent rescues and confiscations of Sunda pangolins in recent years, it is important to consider ex-situ conservation strategies for the species, including the design of captive environments based on their microhabitat preferences found in their natural habitats. Unfortunately, many Sunda pangolins kept in rescue facilities or animal zoos have experienced high rates of stress and injury and have died in captivity (Save Vietnam Wildlife, unpubl. data; Sabah Wildlife Department, unpubl. data.). Therefore, it is crucial to provide a suitable captive environment that mimics the natural habitat of Sunda pangolins, which may increase their chances of survival and eventual release back into the wild. By doing so, ex-situ conservation efforts can complement the protection and conservation of natural habitats for Sunda pangolins.

Based on the findings of this study, captive environments for Sunda pangolins should replicate the key microhabitat features identified in their natural habitat. Specifically, the inclusion of tall, large structures with artificial hollows is crucial, as the species prefers sleeping sites in such trees. Providing these features in captivity can offer refuge and reduce stress, mimicking their natural sleeping behaviour. Additionally, since vines and other climbing structures play an important role in their habitat, incorporating dense vine-like structures or climbing frames within enclosures can support the natural climbing tendencies of pangolins, helping them feel more secure and promoting healthier behaviour.

Although ground cover (e.g., grasses, bushes) was not found to be a significant factor in the selection of sleeping sites, maintaining diverse substrates such as soil, leaves, and grasses in captive environments could still be beneficial. These natural elements provide enrichment, reducing stress and encouraging exploration. Furthermore, controlling the humidity and temperature to replicate the conditions of swampy or forested environments is essential, as Sunda pangolins thrive in moist, temperate conditions. Together, these recommendations can help improve the survival rates of pangolins in captivity and support their eventual release into the wild.

The findings of this study have important implications for the design of future research methodologies for Sunda pangolins. The elusive, rare, and nocturnal nature of the species historically made them difficult to detect in their natural habitat (Kwaja et al., 2019). However, this study has provided valuable insights into their ecology and behaviour, highlighting the importance of employing multiple methods to study Sunda pangolins. The study recommends the use of GPS and VHF tracking, ground and arboreal camera trapping, diurnal and nocturnal surveys, and community interviews to collect data on the species. Collaboration with other researchers to maximize data through the collection of by-catch camera trap data of Sunda pangolins is also recommended. The implementation of these research methodologies will improve our understanding of the species and help to inform effective conservation measures.

Although the study provided valuable insights into the microhabitat preferences of Sunda pangolins, there are limitations that should be considered. The study was conducted in a single geographic area, which limits its applicability to other regions. Additionally, the findings are based on a small sample of resident and translocated pangolins in the LKWS, and as such, the results reflect the specific conditions of this location rather than the entire population. Future research could collect more detailed data on individual movements and habitat use across various geographic regions to provide a more comprehensive understanding of Sunda pangolins distribution and habitat preferences. Furthermore, research should focus on post-release monitoring, survival rates, and investigating the physicochemical characteristics of sleeping sites to inform conservation efforts and captive breeding programmes for the species.

Overall, this study emphasises the importance of understanding the habitat requirements and preferences of Sunda pangolins for effective conservation and management planning. By incorporating this information into conservation strategies, we can help ensure the persistence of Sunda pangolin populations in the study area and beyond.

Chapter 5: General Discussion

Global biodiversity has been depleted due to natural ecosystem destruction and degradation (Pereira et al., 2010; Rands et al., 2010), an accelerating trend, particularly in tropical regions (Hansen et al., 2013). The Sunda pangolin (*Manis javanica*), which has been historically understudied and poorly understood in its response to these changes, has been significantly impacted by habitat loss and fragmentation (Kwaja et al., 2019; Chong et al., 2020). Due to these behaviours, the Sunda pangolin, a rare, elusive, and nocturnal species, has proven difficult to study using conventional methods (Kwaja et al., 2019; Willcox et al., 2019; Chong et al., 2020). However, with advanced scientific technologies such as camera traps and radio trackers, it is now possible to collect data on rare and elusive species, such as the Sunda pangolin, which can help us understand their behaviours and predict their responses in a fragmented or changing habitat. These findings are critical for informing conservation efforts to protect this species.

5.1 Summary of findings

Chapter 2 of this thesis revealed that the greatest potential distribution of Sunda pangolins in Sabah, Malaysia, is found in the natural forests, primarily in the central and southwestern areas. The study found that the predicted distribution of the species was significantly associated with moderate-high condition forest, specifically in lowland forests. Habitat suitability was highest in and near the forest but decreased in areas closer to urbanisation and at higher elevations. The lack of previous research on Sunda pangolin distribution makes this study critical to understanding the species' habitat preferences. The study stressed that Sunda pangolins depend on forested areas and are forced to roam outside their natural habitats due to habitat loss and fragmentation. Although the species is adaptable and can occupy various habitat types, pangolins found outside of natural habitats, such as in agricultural areas and urban areas, are more vulnerable to poaching due to their high value in the illegal wildlife trade (Lim and Ng, 2008; Chong et al., 2020; Panjang and Goossens, 2022).

Chapter 2 also emphasises that nearly all available Sunda pangolin habitats in Sabah are accessible to poaching activities due largely to the network of roads and logging trails from oil palm plantations that connect to nearby towns and remote forests (Wong and Linkie, 2013; Brodie et al., 2015). As a result, protecting and maintaining Sabah's remaining forests is critical, as they are the last stronghold for the Sunda pangolin population. Although this study did not specifically investigate social science aspects, and only focused on the ecological aspects of habitat use and distribution, effective conservation of the species will require a multifaceted approach, including education and outreach efforts to reduce poaching and illegal wildlife trade.

Despite the long study period and the use of multiple methods to detect Sunda pangolins, encounter rates in the study area were low, as described in **Chapter 3** of this thesis. In global camera trapping analyses, similar patterns were observed for other pangolin species (Kwaja et al., 2019). This study emphasises the importance of continuing to study Sunda pangolins using multiple methods, including previously untested methods such as extensive arboreal camera trapping, to improve detection. As more Sunda pangolins are encountered and rescued opportunistically, networking and collaboration with stakeholders will be critical (Sabah Wildlife Department, unpubl. data).

Chapter 3 demonstrated that resident Sunda pangolins have smaller, well-established home ranges within forested areas. Home range sizes were influenced by the availability of suitable sleeping sites and proximity to water sources. Interestingly, the home ranges reported in this study were larger than those documented on a small island (Lim and Ng, 2007, 2008), where limited availability of sleeping sites may have contributed to the smaller ranges observed in island populations (Nascimento et al., 2011). Male Sunda pangolins also exhibited territorial behaviour (Lim and Ng, 2007; Chong et al., 2020), which may further limit dispersal and contribute to smaller home ranges. Conversely, translocated Sunda pangolins showed larger ranges following release, which resulted in more extensive exploratory movement patterns compared to the resident pangolins, who were more settled and showed slower, steady movement. This study highlights the need for careful consideration of suitable release sites in translocation programmes and the importance of post-release monitoring to ensure the long-term success of these efforts.

Chapter 4 of this thesis highlights the specific habitat requirements of Sunda pangolins for suitable sleeping sites: tall, larger living trees with hollows and abundant vines commonly found in old and mature forests. The potential distribution of Sunda pangolins predicted in **Chapter 2** was found to be influenced by the selection of suitable sleeping sites. Both resident and translocated Sunda pangolins were found to use various sleeping site types, with translocated individuals exhibiting greater adaptability and occupying a wider range of sleeping sites, including those in oil palm plantations.

The study predicted that the distribution of sleeping sites for Sunda pangolins is influenced by habitat types and canopy height, with freshwater swamp forests having the greatest potential distribution of sleeping sites. Taller trees were found to be one of the important physical characteristics of sleeping sites, influencing the potential distribution of sleeping sites in forested and non-forested areas. **Chapter 4** delves into the microhabitat level associated with natural forests, as revealed in **Chapter 2**. Additionally, the chapter reveals interesting social behaviours which are not commonly observed in the wild, including interactions with conspecifics and co-existence with other species. Furthermore, the chapter emphasises that the findings from the analysis of natural habitats provide valuable insights for designing suitable captive environments. Given the increasing number of Sunda pangolins being rescued and confiscated by authorities, creating captive environments that mimic key features of their natural sleeping sites, could improve the welfare of pangolins in captivity and enhance their chances of successful reintroduction into the wild.

5.2 Limitations and recommendations for future work

This thesis offers a comprehensive investigation of Sunda pangolins' ecology and conservation needs, the first detailed study of this species in Sabah, Malaysia Borneo. This study provides novel insights into the largely unstudied ecology of this mammal by examining habitat suitability, home range, movement behaviour, and microhabitat preferences. However, this study, like all scientific research, has limitations that can be addressed in future studies.

While the low encounter rates of Sunda pangolins in the study area present certain limitations, the data collected in this study still provide valuable insights into habitat use and sleeping site preferences. Although the encounter rate may limit applicability of some findings, such as home range estimations, the consistency across multiple detection methods suggests that results are representative of key population trends within the study area. Future research could further improve sample sizes and accuracy by employing innovative methods like arboreal camera trapping and environmental DNA (Willcox et al., 2019), which could enhance understanding of the species' ecological traits and behaviour.

The present study focused solely on a single study area in Sabah, Malaysia, and thus may not represent the broader range of Sunda pangolin populations across Southeast Asia. As Sunda pangolins inhabit a variety of habitats and regions, caution should be exercised when applying these findings to other areas. Further research in diverse geographic areas would help develop a more comprehensive understanding of Sunda pangolin ecology and conservation needs in different environments. This could reveal factors driving variation in Sunda pangolin behaviour across different populations and inform region-specific conservation strategies.

The study incorporated direct methods, including camera traps and transect surveys, to gather data on Sunda pangolins. While these methods did not result in direct detections of Sunda pangolins, they were part of the overall monitoring approach. The challenges of detecting this elusive, nocturnal species are well-known, and the low detection probability in dense forests can limit the effectiveness of these methods (Roberts, 2011; Kolowski et al., 2021). Additionally, radio telemetry was used to track pangolin movements, which provided valuable insights into their behaviour and home range. However, radio telemetry was constrained by factors such as signal loss in dense vegetation and the logistical challenges of conducting long-term tracking in remote areas. Despite the use of multiple methods and a long-term study period, these limitations emphasise the need for careful interpretation of the study's findings.

While this study did not incorporate models assessing potential impacts of climate change on Sunda pangolin habitat suitability and distribution, it prioritised immediate threats such as habitat fragmentation, poaching, and illegal wildlife trade, which are currently the most pressing concerns for pangolin conservation in Sabah. These threats are driven by human activities, including habitat encroachment and the accessibility of remaining pangolin populations via logging roads and plantations, which significantly increase the species' vulnerability. As such, the study focused on habitat suitability and accessibility, aiming to inform immediate conservation actions that could help to protect pangolins from illegal trade and habitat loss.

It is acknowledged that climate change is an important factor that could further affect habitat availability and quality for Sunda pangolins in the long term. Climate change is a global phenomenon that can significantly impact biodiversity (Bellard et al., 2012; Yu et al., 2023), particularly in tropical regions (Tagliari et al., 2021), where species may have limited ability to adapt to changing environmental conditions. Changes in temperature, rainfall patterns, and extreme weather events can all affect the distribution and quality of habitats, potentially leading to range shifts or declines in population abundance (Coumou and Rahmstorf, 2012; Coumou et al., 2013; Holland and Bruyère, 2014; Anonymous, 2020). While some models predict a potential increase in suitable habitat for Sunda pangolins due to climate change (Xian et al., 2020), this may not lead to positive outcomes for their populations due to the sensitivity of Sunda pangolins to temperature changes (Save Vietnam Wildlife, unpubl. data) and other ecological disruptions. Therefore, future research could integrate climate change models to complement the ongoing efforts to mitigate current threats, ensuring that conservation planning accounts for both immediate and long-term environmental changes.

5.3 Implications for Sunda pangolin conservation in Sabah

5.3.1 Habitat

The study has demonstrated that Sunda pangolins in Sabah are dependent on natural forest habitats and the stronghold for the remaining Sunda pangolin populations, especially those containing suitable sleeping sites, which were found to be predominantly tall, large, living trees with hollows and abundant vines. The habitat suitability analysis conducted in Chapter 2 suggests that natural forests in Sabah, specifically lowland forests in central and southwestern areas, are the most suitable habitats for Sunda pangolins. This highlights the urgent need for conservation initiatives to protect and maintain these critical habitats to ensure the species' survival in Sabah. The potential distribution of suitable habitats for Sunda pangolins predicted in this study is also influenced by physical and spatial characteristics of the habitat, such as the presence of taller trees, large living trees and tree hollows, which provides important insights for conservation planning. Thus, in addition to protecting natural forest habitats, conservation efforts should also focus on restoring degraded or fragmented habitats to enhance the availability of suitable sleeping sites and foraging opportunities for Sunda pangolins. Lim and Ng (2008) reported that the Sunda pangolin could survive in the degraded forests in Singapore if conservation efforts were in place. Restoration efforts can be implemented by introducing suitable tree species that can persist (Butterfield et al., 2016) and creating wildlife corridors to connect fragmented forest habitats (Graves et al., 2007; Liu et al., 2018;). Such restoration efforts may also benefit other forest-dependent species in the area.

Furthermore, habitat fragmentation and degradation due to human activities, such as logging and agriculture, were identified as the threats to the survival of Sunda pangolins in Sabah (Chong et al., 2020). Therefore, it is crucial to implement effective management plans and sustainable land-use practices that prioritize the conservation of forested habitats in Sabah. These efforts should also incorporate the involvement of local communities and stakeholders to ensure that conservation initiatives are sustainable in the long term (Brown, 2003; White et al., 2005).

5.3.2 Population monitoring

The low encounter rates of Sunda pangolins observed in the study highlight the challenges of monitoring this elusive species. While this research primarily focused on habitat selection and movement patterns, the difficulty in detecting pangolins highlights the need for long-term and systematic population monitoring. Methods such as camera trapping and GPS/radio telemetry, which were employed in this study, proved effective in tracking individuals, but their limitations in detecting elusive and low-density populations were evident. These limitations emphasise the importance of exploring innovative approaches for population monitoring, such as using drones, eDNA analysis, acoustic sensors or thermal imaging (Pfleger et al., 2016; Dema et al., 2019; Willcox et al., 2019; Zhang et al., 2020) to increase detection rates and improve accuracy in population assessments.

In degraded or fragmented habitats where natural nesting sites are scarce, the implementation of artificial ‘nest boxes’ as sleeping and breeding sites could be a viable strategy to support and monitor pangolin populations. Although this study did not directly assess nest box use, the identification of key sleeping site characteristics, such as tree hollows, suggests that providing artificial nesting structures could help to mitigate habitat loss. However, designing effective nest boxes would require detailed physical information on natural sleeping sites, such as temperature, humidity, and substrate, to closely match the environmental conditions pangolins prefer. Additionally, it is important to note that sleeping and nesting sites may have different requirements, which future studies should clarify. Similar efforts with hornbills in Kinabatangan have demonstrated the potential of nest boxes to support species in fragmented landscapes

(Vercoe et al., 2021). Future research could test the effectiveness of nest boxes for Sunda pangolins, using occupancy rates to monitor population trends and reproductive success in areas where natural nesting sites are limited.

In addition to detection methods, collecting demographic and reproductive data is essential for understanding population dynamics and informing conservation efforts. While this study provided some insights into movement patterns and sleeping site preferences, further research is needed to gather comprehensive data on life history traits, breeding areas, and reproductive success. This information could be crucial in developing targeted management strategies to restore key habitats, mitigate threats like poaching, and ensure the long-term survival of Sunda pangolins in Sabah. (Grande et al., 2009; Robinson et al., 2014; Dahlgren et al., 2016).

5.3.3 Translocation as a conservation tool

Translocation has been increasingly used as a conservation tool for threatened and endangered species (Griffith et al., 1989; Parker, 2008), including Sunda pangolins (Gray et al., 2022). While this study did not directly assess the outcomes of translocation efforts, the findings on habitat use, home range size, and sleeping site selection can inform translocation practices for Sunda pangolins. For example, the observed differences in habitat use between resident and translocated pangolins suggest that the success of translocations may depend on factors such as the availability of suitable sleeping sites and the connectivity of forested habitats. This emphasises the importance of carefully selecting release sites that provide adequate habitat and resources to support translocated individuals.

Additionally, the potential risks of human-wildlife conflicts, such as poaching and road collisions, should be considered when selecting release sites for translocated pangolins. Monitoring translocated individuals is essential to assess their movements, survival, and adaptation to new environments. The results of this study suggest that long-term evaluations of translocation outcomes are necessary to ensure habitat suitability and connectivity over time, as well as to identify potential risks such as poaching or human-wildlife conflicts.

Although translocation can be a valuable tool in pangolin conservation, it should complement, not replace, habitat protection and restoration efforts (Towns and Williams, 1992). Translocation also poses risks, such as the potential spread of diseases or genetic mixing between local populations (Laikre et al., 2010; Aiello et al., 2014). Therefore, best practices for translocation should be followed, including health screening of translocated individuals and genetic assessments to minimise negative impacts on local populations (Benjamin et al., 2007; Kock et al., 2010).

Additionally, the study highlights the need for further research to evaluate the effectiveness of translocation as a conservation tool for Sunda pangolins, particularly in relation to its impacts on their social behaviour and population dynamics. Successful translocation efforts require strong collaboration and coordination among government agencies, conservation organisations, and local communities. Working together at all levels enhances the effectiveness of these initiatives and fosters local support for conservation. Involving local communities in translocation initiatives can build engagement and local capacity and encourage the coexistence of humans and wildlife (Chazdon et al., 2020). Moreover, the study emphasises the importance of developing standardised protocols for the translocation of Sunda pangolins and ensuring that best practices are implemented and lessons learned are shared among conservation practitioners.

5.5.4 Awareness and education

The success of Sunda pangolin conservation in Sabah ultimately depends on raising public awareness and education. The complex nature of poaching and illegal trade necessitates a comprehensive approach that addresses the social, economic, and cultural factors that underlie these activities (Pratt et al., 2004; Duffy and St John, 2013). A multi-pronged strategy could include awareness-raising campaigns targeted at key audiences, such as traditional medicine practitioners and consumers of pangolin products, to promote the value of protecting the species and alternatives to pangolin-based products (Crudge et al., 2016). Education can also play a vital role in conservation efforts, particularly in the involvement of local communities in conservation activities. Conservation education in schools and outreach programmes can help foster stewardship and ownership of Sunda pangolins and their habitats, motivating local communities to participate in conservation efforts (Fisman, 2010; Tidball and Krasny, 2011).

Moreover, involving local communities in habitat restoration and monitoring can provide an opportunity for capacity building and empowerment, promoting a sense of shared responsibility for the protection of Sunda pangolins (Ahmad et al., 2021). Collaboration between government agencies, NGOs, and local communities is crucial for effective conservation planning and action (Brown, 2003; White et al., 2005). Building partnerships and fostering cooperation between different groups can help to leverage resources, share knowledge and expertise, and promote the implementation of conservation initiatives (Berdej and Armitage, 2016; Sandwith et al., 2021). This collaborative approach can create a shared vision for the protection of Sunda pangolins in Sabah and ensure the success of conservation efforts for this unique and threatened species.

5.3.5 Animal Use

Although this study primarily focused on the ecological aspects of Sunda pangolins, including their habitat preferences and the impacts of habitat degradation, it is essential to consider the broader socio-cultural context in which pangolins are used. Research into ethnozoological knowledge, particularly the traditional use of pangolins in medicine, can complement ecological studies by offering valuable insights into human-wildlife interactions that influence conservation outcomes. While this study explored pangolin sleeping site preferences and habitat use, understanding the human dimension, such as how local communities use and value pangolins, is equally important in creating effective conservation strategies.

By integrating both ecological data and ethnozoological knowledge, conservationists can develop a more holistic approach to pangolin conservation. Engaging with traditional healers, medicinal practitioners, and local communities can enhance efforts to protect Sunda pangolins, especially in regions where the illegal wildlife trade poses a significant threat. Conservation strategies informed by both scientific and traditional knowledge can help mitigate threats to pangolins while promoting sustainable use practices that align with the cultural beliefs of local communities.

5.4 Conclusion

Understanding the habitat requirements, movement patterns, and behaviour of Sunda pangolins in Sabah is essential for effective conservation planning and management. However, the species' survival is currently threatened by habitat loss and fragmentation, poaching, and illegal wildlife trade. Therefore, urgent action is needed to protect and restore their remaining natural habitats, monitor their populations, and raise public awareness and education. The findings of this study provide important insights into the ecology and conservation needs of Sunda pangolins, highlighting the strong dependence on natural forest habitats with suitable sleeping sites. In particular, wild pangolins primarily utilised sleeping sites in forested areas, while translocated individuals used both forested and non-forested sites, suggesting the importance of suitable release sites in translocation programmes. Effective conservation strategies must be tailored to the specific needs and challenges of Sunda pangolin populations in different regions, focusing on protecting and restoring natural habitats, monitoring populations using a variety of methods, implementing successful translocation programmes, and raising public awareness and education. The implementation of such strategies is crucial for the survival of this elusive and threatened species in Sabah and beyond.

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Appendix 1: Additional home range estimation results

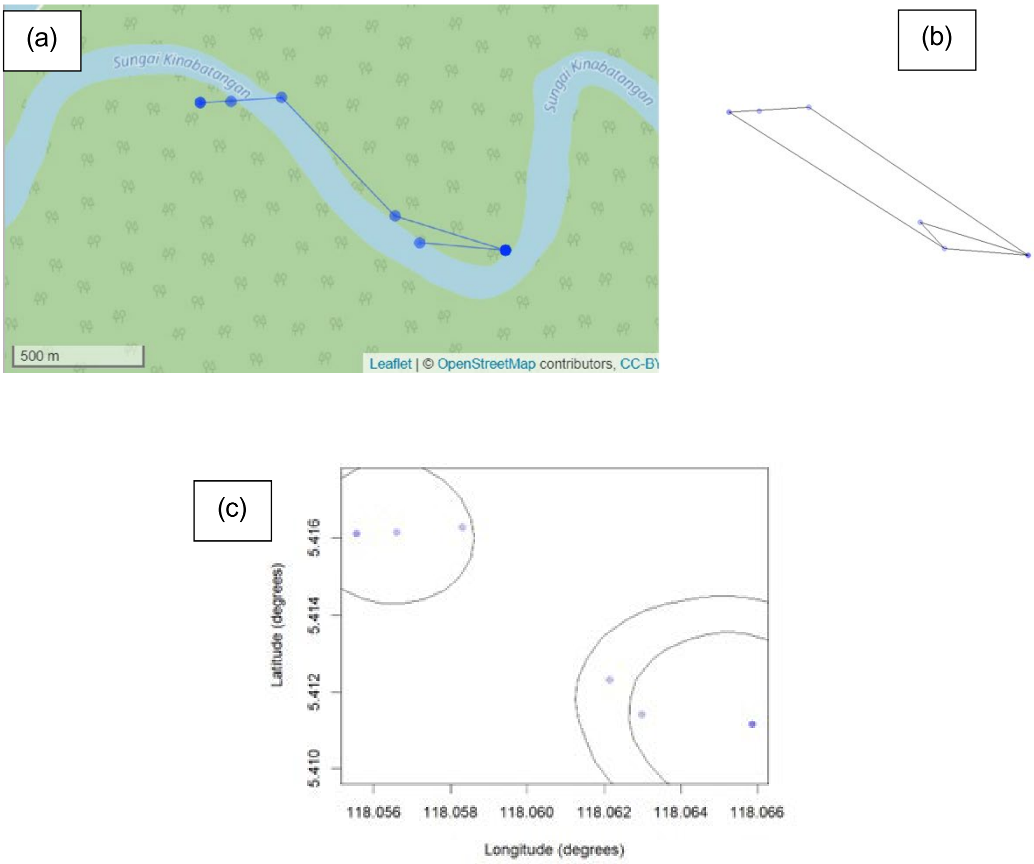


Fig. 3.20: **(a)** shows the GPS location points of Anggun, plotted on a map of the study area, **(b)** displays the graph of MCP estimates, and **(c)** shows the graph of KDE estimates for Anggun.

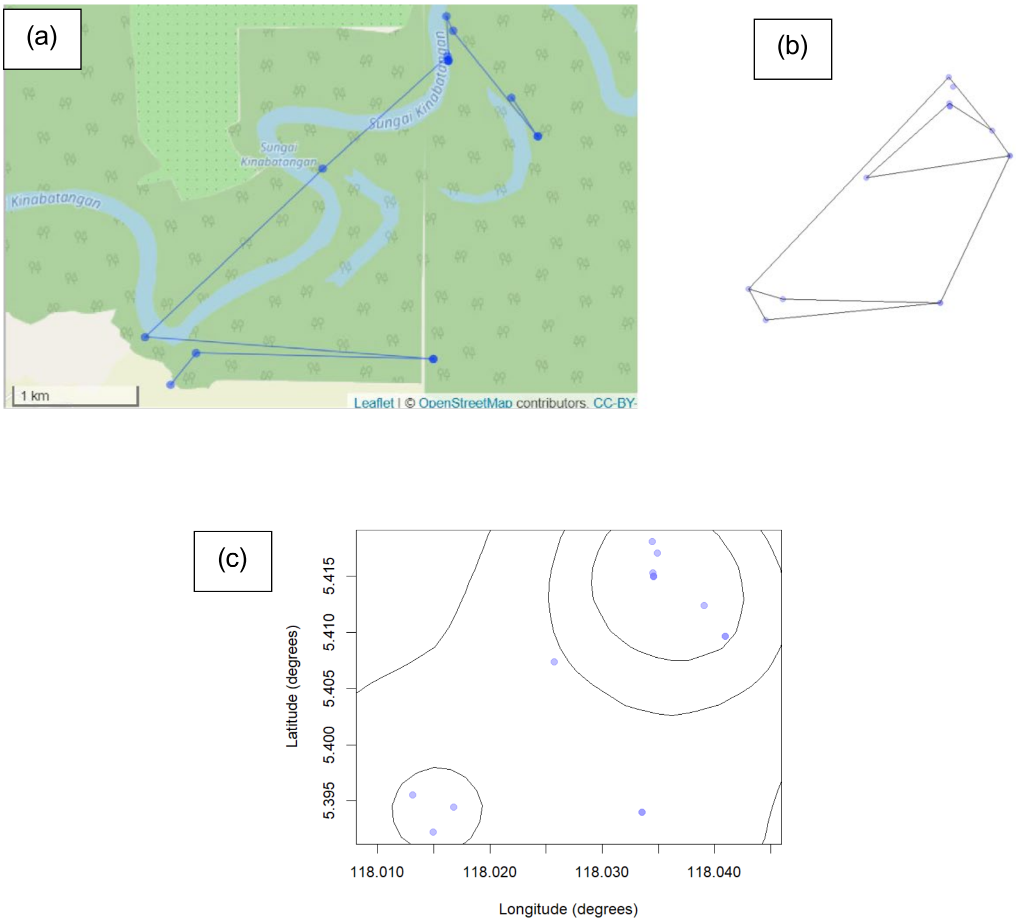


Fig. 3.21: **(a)** shows the GPS location points of Gagah, plotted on a map of the study area, **(b)** displays the graph of MCP estimates, and **(c)** shows the graph of KDE estimates for Gagah.

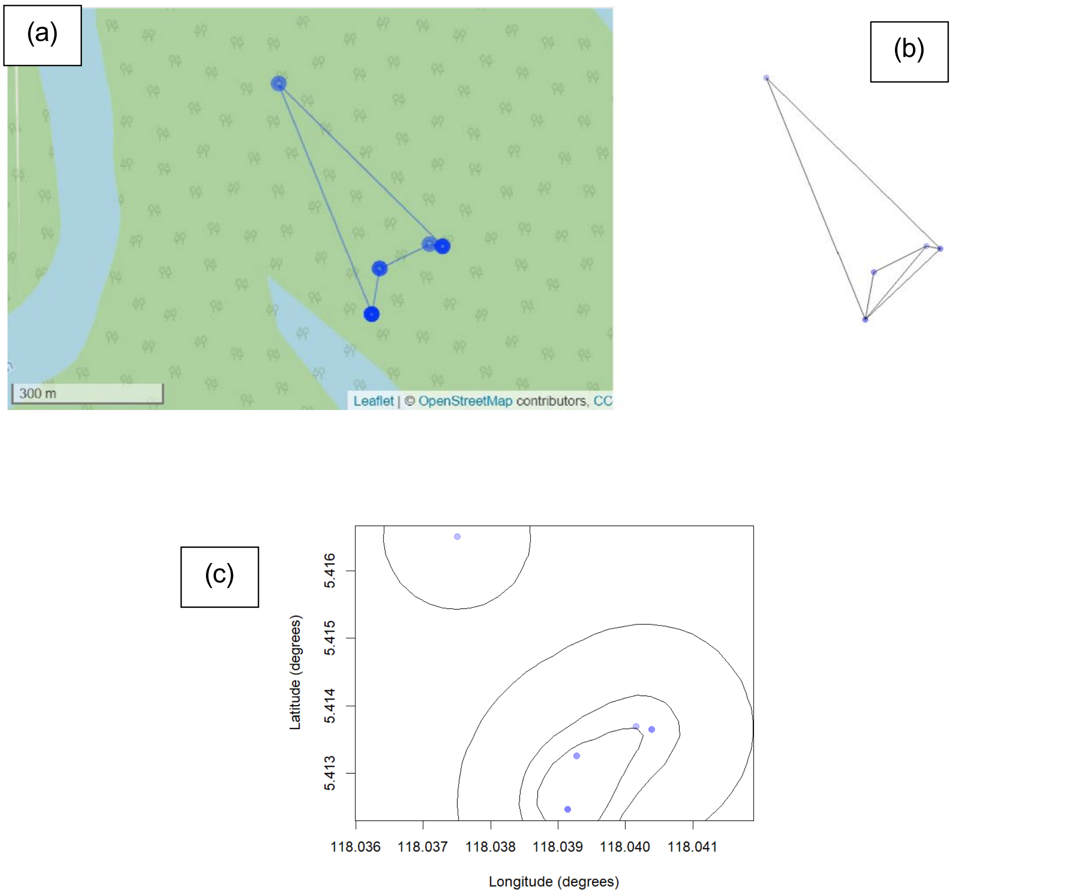


Fig. 3.22: **(a)** shows the GPS location points of Gagah, plotted on a map of the study area, **(b)** displays the graphs of MCP estimates, and **(c)** shows the graphs of KDE estimates for Gagah.

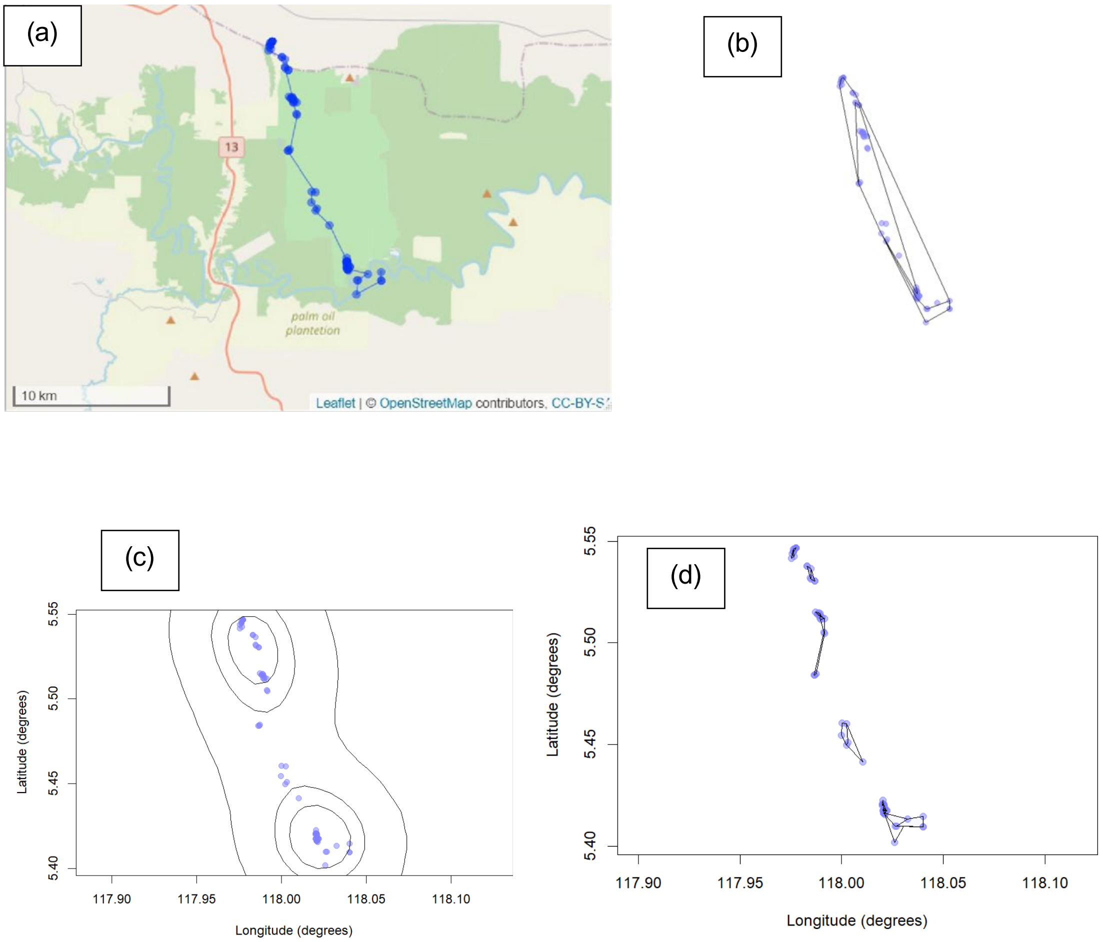


Fig. 3.23: **(a)** shows the GPS location points of Pesona, plotted on a map of the study area, **(b)** shows the graph of MCP estimates, **(c)** shows the graph of KDE estimates, and 3.3o (d) shows the graph of LoCoH estimates for Pesona.

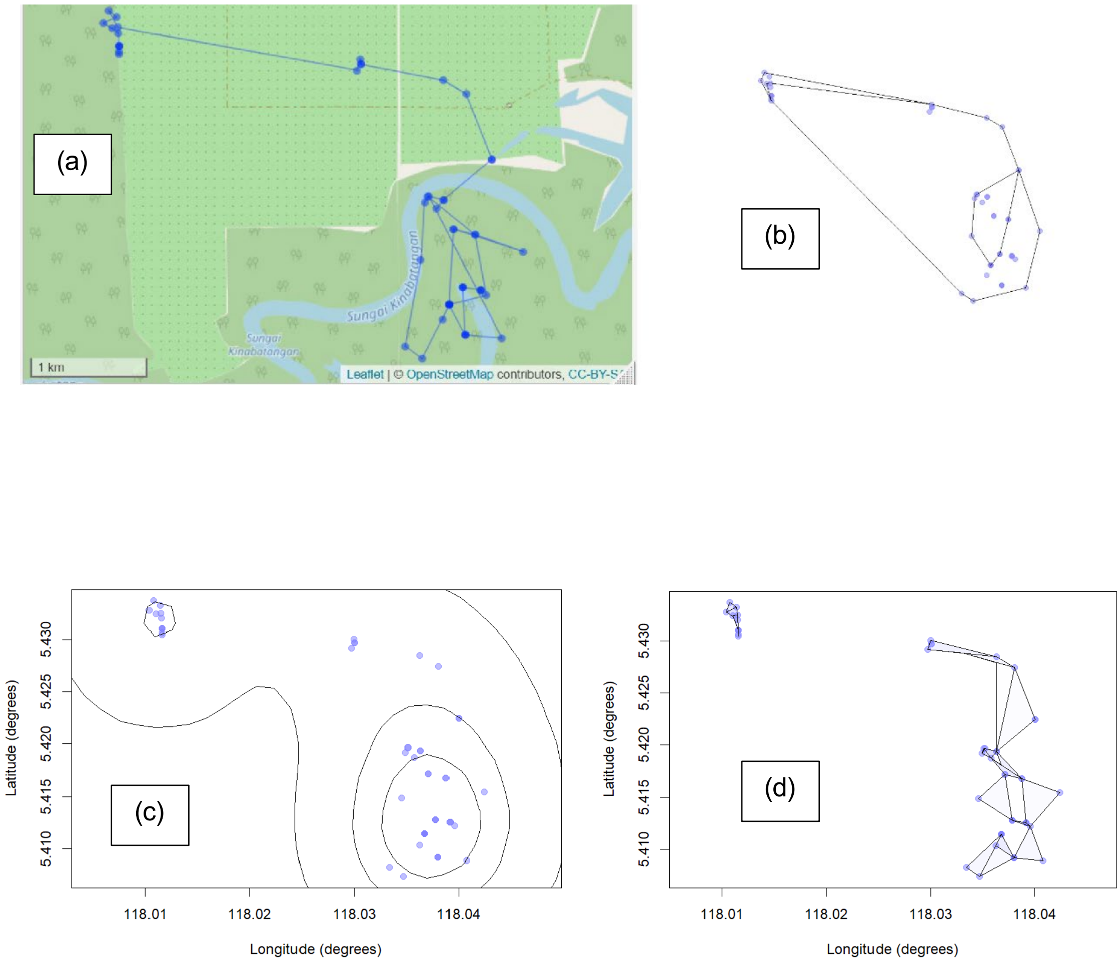


Fig. 3.24: **(a)** shows the GPS location points of Suka, plotted on a map of the study area, **(b)** shows the graph of MCP estimates, **(c)** shows the graph of KDE estimates, and **(d)** shows the graph of LoCoH estimates for Suka.

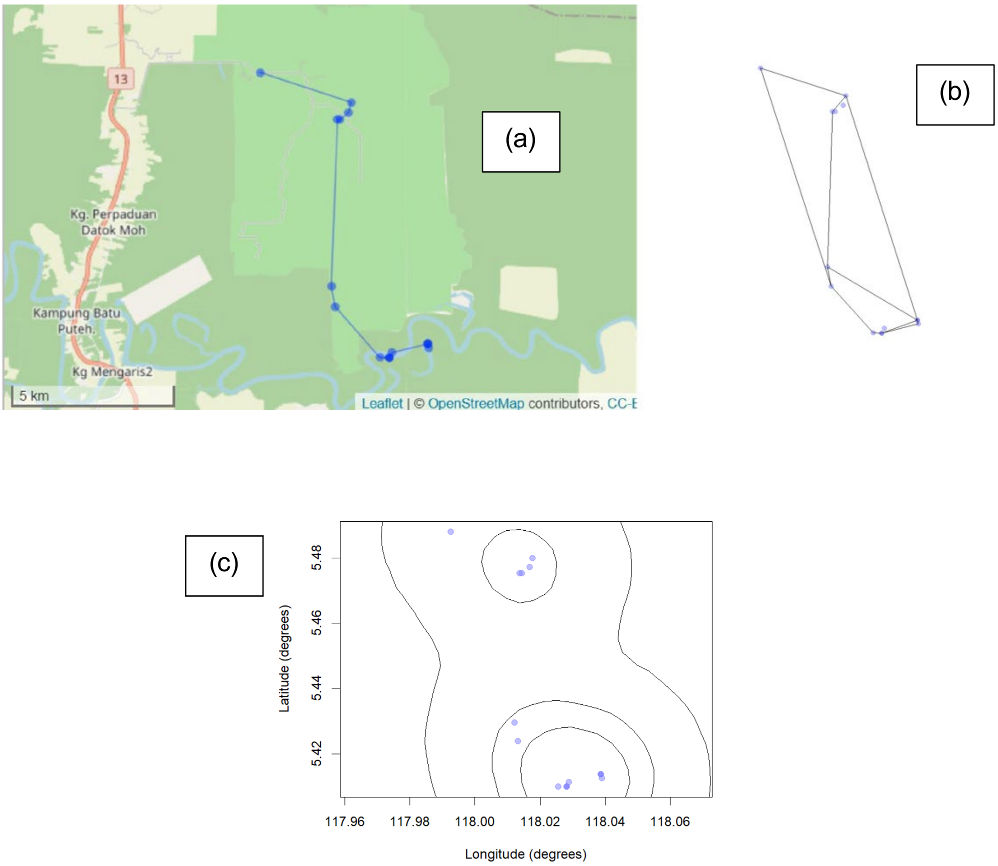


Figure 3.25: **(a)** shows the GPS location points of Tuah, plotted on a map of the study area, **(b)** displays the graph of MCP estimates, and **(c)** shows the graph of KDE estimates for Tuah

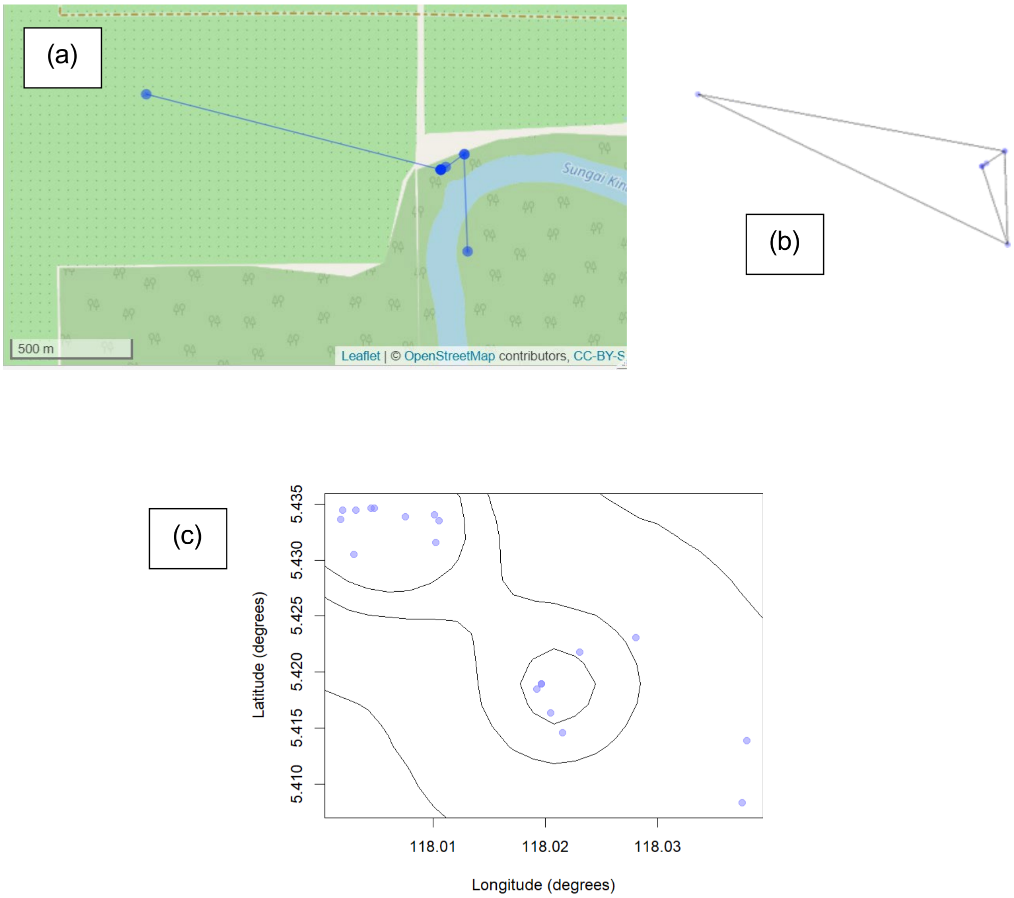
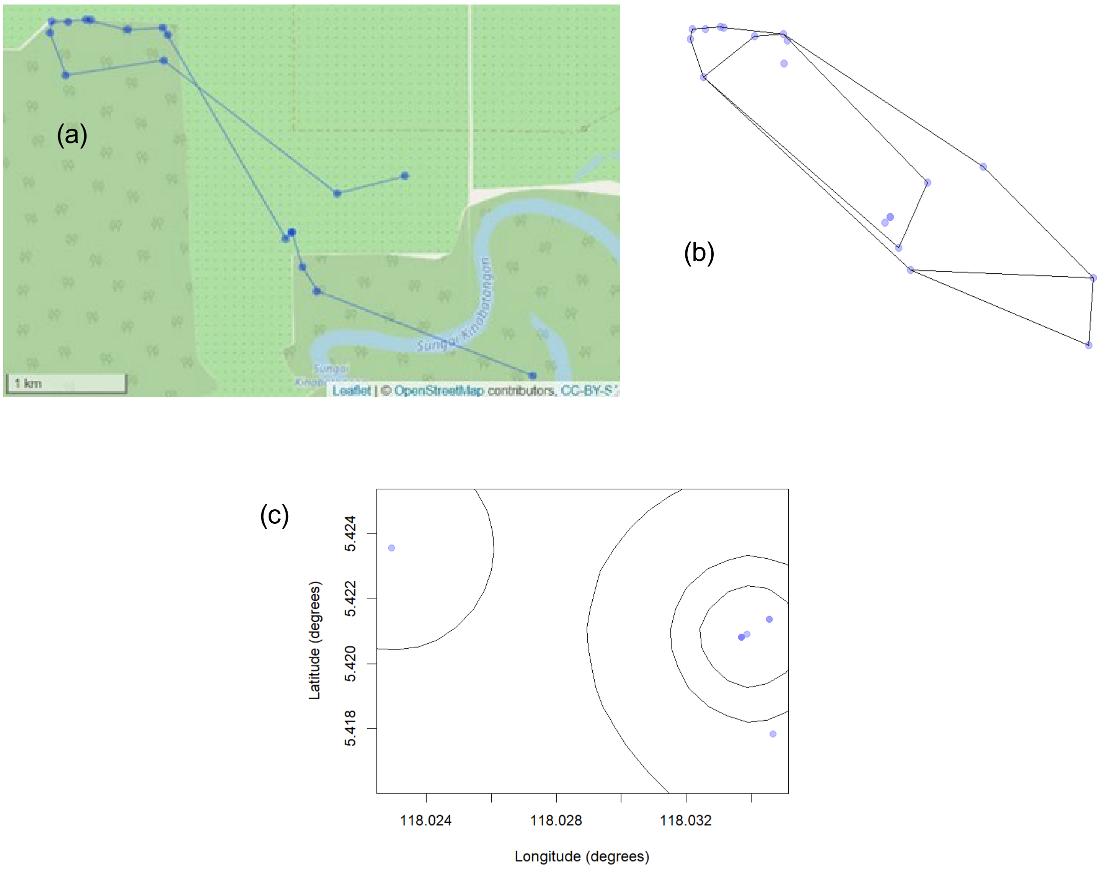
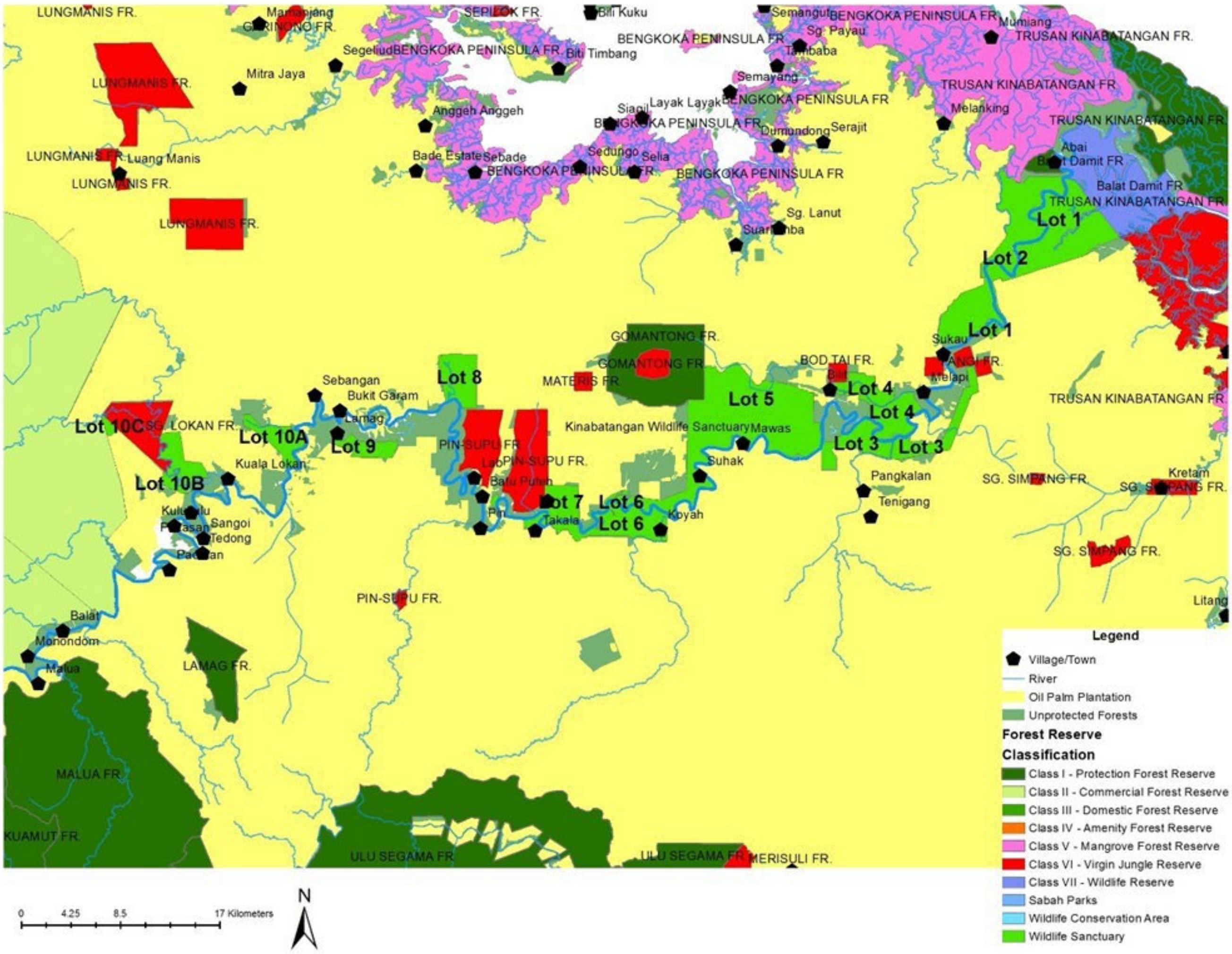


Figure 3.26: **(a)** shows the GPS location points Wira's first release, plotted on a map of the study area, **(b)** displays the graph of MCP estimates of Wira's first release, and **(c)** shows the graph of KDE estimates of Wira's first release



Supplementary Figure 3.27: **(a)** shows the GPS location points of Wira’s second release, plotted on a map of the study area, **(b)** displays the graph of MCP estimates of Wira’s second release, and **(c)** shows the graph of KDE estimates of Wira’s second release

Appendix 2: Map of the Lower Kinabatangan Wildlife Sanctuary (LKWS), Sabah, Malaysia



Appendix 3: Scripts of data analysis

Chapter 3: Home range and movement of the Sunda pangolin in the highly fragmented Lower Kinabatangan landscape

Home range analysis

```
#### Pangolin home range analysis ####

# Set working directory ####

setwd("F:/Spatial course archive")

setwd("D:/PhD Thesis/Chapter 3/PANGOLIN HOME RANGE ANALYSIS")


# Activate a load of libraries... ####

#  install.packages("adehabitatHR")

library(sp)

library(adehabitatHR)

library(deldir)

library(ade4)

library(adehabitatMA)

library(adehabitatLT)

library(CircStats)

library(MASS)

library(boot)

library(rgdal)


# Read in the data ####

dframe1 = read.csv('galaknew.csv', stringsAsFactors = T)  # Choose a csv file to read in, e.g. Galak the pangolin

dframe1


# Renaming coordinates data as lat and long

dframe1$lat <- dframe1$y
```

```
dframe1$long <- dframe1$x


# Plot the GPS points ####
plot(dframe1$lat ~ dframe1$long, asp=1,
     xlab="Longitude (degrees)",
     ylab="Latitude (degrees)")


# Join the dots!
lines(dframe1$lat ~ dframe1$long, col="light grey") # Connected the GPS points in sequence


# Check the global location using a "Leaflet" interactive map ####
library(leaflet)
median(dframe1$lat, digits=5)  # identify the median Lat and Long
median(dframe1$long, digits=5)


# Create the map tile
map1 <- leaflet() %>% setView(lng = 118.0379, lat = 5.41513, zoom = 14) # Galak
map1


# Add the point locations
map1 %>% addTiles()%>%addCircles(data = dframe1, lat = ~ lat, lng = ~ long)%>%
  addScaleBar(position=c("bottomleft"),
              options=scaleBarOptions(maxWidth=200,imperial=FALSE,metric=TRUE))


# repeat but join the dots with lines
map1 %>% addTiles()%>%addCircles(data = dframe1, lat = ~ lat, lng = ~ long)%>%
  addPolylines(data = dframe1, lat = ~ lat, lng = ~ long, weight=1)%>%
  addScaleBar(position=c("bottomleft"),
```

```
        options=scaleBarOptions(maxWidth=200,imperial=FALSE,metric=TRUE))

# animated movement

#### Home range analysis: data preparation ####

# Remove any rows with missing latitude or longitude
dframe1 <- dframe1[!is.na(dframe1$long) & !is.na(dframe1$lat),]
length(dframe1$id)

# Retain long and lat
library(sp)
data.sp <- dframe1[, c("id", "long", "lat")]
data.sp
coordinates(data.sp) <- c("long", "lat")
data.sp

# Add the coordinate reference system / projection, and turn the dataframe into a spatial points object
coord.dec = SpatialPoints(data.sp, proj4string=CRS("+proj=longlat"))
coord.dec  # Decimal coordinates

# Plot the decimal coordinates
plot(coord.dec, pch=19,
   col=rgb(0.5, 0.5, 1, 0.5),
   xlab="Longitude (degrees)",
   ylab="Latitude (degrees)",
   asp=1) # plot the coordinates with an aspect-ratio of 1
box()
```

```
# add the distribution centroid

points(median(dframe1$lat) ~ median(dframe1$long), col="red", cex=2)


# Calculate home range statistics ####

library(adehabitatHR)

# Minimum Convex Polygon method ####


# 100% MCP

myMCP <- mcp(coord.dec, percent=100)      # Edit the percent to get different % MCPs


plot(myMCP,add=T)


# 95% MCP

myMCP <- mcp(coord.dec, percent=95)


plot(myMCP,add=T)


# 50% MCP

myMCP <- mcp(coord.dec, percent=50)


plot(myMCP,add=T)


# Calculating the area of the home range: ####

# To do this, we need to convert the decimal coordinates into UTC coordinates

# Transform the decimal coordinates into UTM coordinates

coord.UTM <- spTransform(coord.dec, CRS("+init=epsg:32650"))     # epsg 32650 is the
         regional code for Borneo

coord.UTM  # UTM coordinates
```

```
plot(coord.UTM, pch=19, col=rgb(0.5, 0.5, 1, 0.5)) # Plot the UTM coordinates


library(adehabitatHR)
myMCP <- mcp(coord.UTM, percent=100,     # Edit the percent to get different % MCPs
             unin = "m", unout ="km2")
plot(myMCP,add=T)
myMCP  # note area of MCP, in Km^2


myMCP <- mcp(coord.UTM, percent=95,     # Edit the percent to get different % MCPs
            unin = "m", unout ="km2")
plot(myMCP,add=T)
myMCP  # note area of MCP, in Km^2


myMCP <- mcp(coord.UTM, percent=50,     # Edit the percent to get different % MCPs
            unin = "m", unout ="km2")
plot(myMCP,add=T)
myMCP  # note area of MCP, in Km^2


# Create a home range kernel using the "href" method
?kernelUD
kernel.href <- kernelUD(coord.dec,  h = "href")


# Plot the decimal coordinates and add home range kernel
plot(dframe1$lat ~ dframe1$long, asp=1,
     pch=19, col=rgb(0.5, 0.5, 1, 0.5),
     ylim=c(5.405, 5.425),
     xlab="Longitude (degrees)",
```

```
    ylab="Latitude (degrees)")


myKernel <- getverticeshr(kernel.href, percent=95) # Edit the percent to get different % MCPs

plot(myKernel,add=T)


myKernel <- getverticeshr(kernel.href, percent=50) # Edit the percent to get different % MCPs

plot(myKernel,add=T)


myKernel <- getverticeshr(kernel.href, percent=25) # Edit the percent to get different % MCPs

plot(myKernel,add=T)


# calculating kernel areas in Km^2 from the UTM coordinates

kernel.href <- kernelUD(coord.UTM,  h = "href")

kernel.area(kernel.href, percent = c(25, 50, 95),

          unin = c("m"),

          unout = c("km2"), standardize = FALSE)


# Create a home range using the LoCoH method ####

?LoCoH # The functions LoCoH.k, LoCoH.r, and LoCoH.


# Fixed k LoCoH method

# The convex hull for each point is constructed from the (k-1) nearest neighbors to that point. Hulls are merged together from smallest to largest based on the area of the hull.


# Plot the decimal coordinates

plot(dframe1$lat ~ dframe1$long, asp=1,

    pch=19, col=rgb(0.5, 0.5, 1, 0.5),
```

```
     # ylim=c(5.405, 5.425),
     xlab="Longitude (degrees)",
     ylab="Latitude (degrees)")


# k=5
myHR <- LoCoH.k(coord.dec, k=5,
        duplicates="random")
plot(myHR, col=rgb(0.5,0.5,1, 0.01), add=T)


# Use UTM coords to obtain area of LoCoH
myHR <- LoCoH.k(coord.UTM, k=5, unin = "m",
                unout = "km2",
                duplicates="random")
plot(myHR)
max(myHR$area) # combined area of individual polygons


# k=10
myHR <- LoCoH.k(coord.dec, k=10,
                duplicates="random")
# Plot the decimal coordinates
plot(dframe1$lat ~ dframe1$long, asp=1,
     pch=19, col=rgb(0.5, 0.5, 1, 0.5),
     # ylim=c(5.405, 5.425),
     xlab="Longitude (degrees)",
     ylab="Latitude (degrees)")


plot(myHR, col=rgb(0.5,0.5,1, 0.01), add=T)
```

```
# Use UTM coords to obtain area of LoCoH
myHR <- LoCoH.k(coord.UTM, k=10, unin = "m",
            unout = "km2",
            duplicates="random")
plot(myHR)
max(myHR$area)

#Adding the river location
river.lat <- c(5.415284, 5.414506, 5.413872, 5.413241, 5.412713, 5.412099,
           5.411593, 5.411337, 5.410999, 5.410715, 5.410383, 5.410171,
           5.410000, 5.410011, 5.410006, 5.410108, 5.410182, 5.410275,
           5.410348, 5.410429, 5.410518, 5.410581, 5.410630, 5.410492,
           5.409366, 5.410034, 5.408433, 5.407522, 5.406959, 5.406538,
           5.405745)
river.long   <-   c(118.034676,    118.034684,    118.034688,    118.034556,    118.034355,
         118.034171,
            118.033888, 118.033522, 118.033128, 118.032769, 118.032172, 118.031433,
            118.030706, 118.029445, 118.028382, 118.027702, 118.027081, 118.026417,
            118.025967, 118.025444, 118.024785, 118.024134, 118.022765, 118.022629,
            118.022407, 118.023530, 118.024424, 118.025361, 118.026075, 118.026565)

#print length of each vector
length(river.lat)
length(river.long)

#pad shortest vector with NA's to have same length as longest vector
length(river.lat) <- length(river.long)

#create data frame using vectors as columns
```

```
df <- data.frame(river.lat=river.lat, river.long=river.long)


#view resulting data frame
df


river.coords <- data.frame(river.long, river.lat)
lines(river.coords, lwd=2)


# other LoCoH methods ####
?LoCoH.r


# Fixed r method ####
# Local hulls formed from all points within a specified distance (r)
#  of each root point


myHR <- LoCoH.r(coord.dec,  r=0.001,
             duplicates="random")
plot(dframe1$lat ~ dframe1$long, asp=1,
   pch=19, col=rgb(0.5, 0.5, 1, 0.5),
   # ylim=c(5.405, 5.425),
   xlab="Longitude (degrees)",
   ylab="Latitude (degrees)")


plot(myHR, col=rgb(0.5,0.5,1, 0.01), add=T)


# adaptive LoCoH method ####
# Create convex hulls from the maximum number of nearest neighbours
#   such that the sum of their distances is less than or equal to this parameter
```

```
myHR <- LoCoH.a(coord.dec,  a=0.1,
            duplicates="random")

plot(dframe1$lat ~ dframe1$long, asp=1,
    pch=19, col=rgb(0.5, 0.5, 1, 0.5),
    # ylim=c(5.405, 5.425),
    xlab="Longitude (degrees)",
    ylab="Latitude (degrees)")

plot(myHR, col=rgb(0.5,0.5,1, 0.01), add=T)

# Adding the river location (not used)

# line defining the south bank of the Kinabatangan river associated with Galak's boundary
river.lat <- c(5.410556, 5.409965, 5.411489, 5.413848, 5.417857, 5.419525,
            5.420229, 5.420245, 5.419099, 5.417928, 5.416053,
            5.413590, 5.411906, 5.411319, 5.410928, 5.411341,
            5.411575, 5.411716, 5.412138, 5.413825, 5.415771,
            5.416476, 5.416780, 5.416938, 5.416938, 5.416661,
            5.416310)
river.long <- c(118.024386, 118.030924, 118.033869, 118.034725, 118.034319,
         118.034953,
            118.036390, 118.037877, 118.041102, 118.042846, 118.044285,
            118.045223, 118.045661, 118.046253, 118.047928, 118.048068,
            118.048422, 118.048936, 118.049315, 118.050058, 118.050763,
            118.051358, 118.052205, 118.053866, 118.054901, 118.055820,
            118.056413)
river.coords <- data.frame(river.long, river.lat)
lines(river.coords, lwd=2)
```

```
# Calculating overlap between two home ranges, e.g. Galak and Pesona

# Read in the data ####
galak = read.csv('galakdata.csv', stringsAsFactors = T) # Choose a csv file to read in
pesona = read.csv('pesonadata.csv', stringsAsFactors = T) # Choose a csv file to read in

# Renaming coordinates data as lat and long
galak$lat <- galak$y
galak$long <- galak$x

pesona$lat <- pesona$y
pesona$long <- pesona$x

plot(pesona$lat ~ pesona$long, asp=1, pch=1, col="red")
points(galak$lat ~ galak$long, asp=1, pch=1, col="blue")

# pesona home range
# Remove any rows with missing latitude or longitude
pesona <- pesona[!is.na(pesona$long) & !is.na(pesona$lat),]
# Retain long and lat
library(sp)
pesona.sp <- pesona[, c("id", "long", "lat")]
pesona.sp
coordinates(pesona.sp) <- c("long", "lat")
pesona.sp

# Add the coordinate reference system / projection, and turn the dataframe into a spatial points object
```

```
pesona.coord.dec = SpatialPoints(pesona.sp, proj4string=CRS("+proj=longlat"))
pesona.coord.dec  # Decimal coordinates


library(adehabitatHR)
# 100% MCP
pesona.MCP <- mcp(pesona.coord.dec, percent=100,       # Edit the percent to get different % MCPs
                unin = "m", unout ="km2")
plot(pesona.MCP, border="red")



# galak home range
# Remove any rows with missing latitude or longitude
galak <- galak[!is.na(galak$long) & !is.na(galak$lat),]


# Retain long and lat
library(sp)
galak.sp <- galak[, c("id", "long", "lat")]
galak.sp
coordinates(galak.sp) <- c("long", "lat")
galak.sp


# Add the coordinate reference system / projection, and turn the dataframe into a spatial points object
galak.coord.dec = SpatialPoints(galak.sp, proj4string=CRS("+proj=longlat"))
galak.coord.dec  # Decimal coordinates


library(adehabitatHR)
# 100% MCP
```

```
galak.MCP <- mcp(galak.coord.dec, percent=100,       # Edit the percent to get different % MCPs
            unin = "m", unout ="km2")
plot(galak.MCP, add=T, border="blue")

# Calculate and plot overlap
library(rgeos)
# ?gIntersection
overlap <- gIntersection(galak.MCP, pesona.MCP)
plot(overlap, add=T, col=rgb(0.5,0.5,0.5, 0.4))

# Convert to UTM coordinates


# galak
galak.coord.UTM <- spTransform(galak.coord.dec, CRS("+init=epsg:32650"))
galak.coord.UTM  # UTM coordinates

library(adehabitatHR)
galak.UTM.MCP <- mcp(galak.coord.UTM, percent=100,     # Edit the percent to get different % MCPs
            unin = "m", unout ="km2")
galak.UTM.MCP  # note area of MCP, in Km^2

# pesona
pesona.coord.UTM <- spTransform(pesona.coord.dec, CRS("+init=epsg:32650"))
pesona.coord.UTM  # UTM coordinates

pesona.UTM.MCP <- mcp(pesona.coord.UTM, percent=100,        # Edit the percent to get different % MCPs
                  unin = "m", unout ="km2")
```

```
pesona.UTM.MCP  # note area of MCP, in Km^2


# Calculate the area of the overlap zone

library(rgeos)

UTM.overlap <- gIntersection(galak.UTM.MCP, pesona.UTM.MCP)


gArea(UTM.overlap)          # in metres^2

gArea(UTM.overlap)/1000000 # in Km2


# Calculating the area of the overlap as a % of each individual's home range


gArea(UTM.overlap) / gArea(galak.UTM.MCP)  # the overlap zone represents 64.0% of
        Galak's home range

gArea(UTM.overlap) / gArea(pesona.UTM.MCP)  # the overlap zone represents 2.4% of
        Galak's home range


#### End ####


#### Modelling distributions using GAMs ####


setwd("F:/Spatial course archive")

setwd

# read in your data

dframe1 = read.csv('berkatnew.csv', stringsAsFactors = T)  # Galak


summary(dframe1)


dframe1$Presence <- 1 # label the locations where the animal was Present as 1

summary(dframe1)
```

```
plot(y ~ x, data=dframe1,
    pch=19,
    col=rgb(0.5, 0.5, 1, 0.5),
    xlab="Longitude (UTM)",
    ylab="Latitude (UTM)",
    asp=1) # plot the coordinates with an aspect-ratio of 1

# Create Pseudo-absences
Pseudo.absences <- expand.grid(id="galak",
                 x = seq(min(dframe1$x), max(dframe1$x), length.out=50),
                 y = seq(min(dframe1$y), max(dframe1$y), length.out=50),
                 Date = "NA", Time = "NA",
                 Presence =0)      # Label the pseudo-absences as "0"

dframe2 <- data.frame(Pseudo.absences)    # Convert the pseudo-absences into a data frame

plot(y ~ x, data=dframe2, pch=19, cex =0.01, asp=1) # Plot the pseudo-absence data
points(y ~ x, data=dframe1,
    pch=19,
    col=rgb(0.5, 0.5, 1, 0.5),
    xlab="Longitude (UTM)",
    ylab="Latitude (UTM)",
    asp=1)

#bind together the two data frames
library(dplyr)
GAM.dframe <- bind_rows(dframe1, dframe2)
```

```
GAM.dframe


# Combine the observations (dframe1) with the pseudo-absences (dframe2)
GAM.dframe <- rbind(dframe1, dframe2)
GAM.dframe
summary(GAM.dframe)


# Model the likelihood of presence across the landscape as a 2-D GAM smoother
library(mgcv)
model1 <- gam(Presence ~ s(x,y,      # smoother s applied to both x and y coordinates, to
          produce a smoothed 2-D "landscape" of likelihood of finding Galak
                      k=-1),  # k= -1 allows the degree of smoothing to be chosen using the cross-
          validation method,
            family=binomial(link="logit"),
            data = GAM.dframe)


summary(model1)


plot(model1) # rough contour plot
points(y~x, data=dframe1, pch=19, col="blue")


# Here is our standard 4-step prediction plotting procedure


pdat <- expand.grid(x = seq(min(dframe1$x), max(dframe1$x), length.out=100),
                y = seq(min(dframe1$y), max(dframe1$y), length.out=100))
pdat


preds <- predict(model1, newdata=pdat, type="response", se.fit=T)
preds
```

```
predframe <- data.frame(pdat, preds)

predframe

summary(predframe$fit)


scale <- predframe$fit / max(predframe$fit)

summary(scale)


plot(y~x, data = predframe, pch=15,  col="white")


points(y~x, data = predframe, pch=15,

      cex= 1.2,                # edit this value to suit your viewer

      col=rgb(0,0,1,scale))  # intensity of blue scaled by likelihood of finding Galak


points(y ~ x,  data = dframe1) #add the locations of the observations


# add the line defining the south bank of the Kinabatangan river for Galak

river.lat <-  c(5.410556, 5.409965, 5.411489, 5.413848, 5.417857, 5.419525,

            5.420229, 5.420245, 5.419099, 5.417928, 5.416053,

            5.413590, 5.411906, 5.411319, 5.410928, 5.411341,

            5.411575, 5.411716, 5.412138, 5.413825, 5.415771,

            5.416476, 5.416780, 5.416938, 5.416938, 5.416661,

            5.416310)

river.long  <-  c(118.024386,  118.030924,  118.033869,  118.034725,  118.034319,
         118.034953,

            118.036390, 118.037877, 118.041102, 118.042846, 118.044285,

            118.045223, 118.045661, 118.046253, 118.047928, 118.048068,

            118.048422, 118.048936, 118.049315, 118.050058, 118.050763,

            118.051358, 118.052205, 118.053866, 118.054901, 118.055820,
```

```
              118.056413)
river.coords <- data.frame(river.long, river.lat)
lines(river.coords, lwd=2)

# Berkat
river.lat <- c(5.415284, 5.414506, 5.413872, 5.413241, 5.412713, 5.412099,
             5.411593, 5.411376, 5.411045, 5.410768, 5.410383, 5.410171,
             5.410000, 5.410011, 5.410006, 5.410108, 5.410182, 5.410275,
             5.410348, 5.410429, 5.410518, 5.410581, 5.410630, 5.410492,
             5.409366, 5.410034, 5.408433, 5.407522, 5.406959, 5.406538, 5.405745)
river.long <- c(118.034676, 118.034684, 118.034688, 118.034556, 118.034355,
          118.034171,
              118.033888, 118.033486, 118.033070, 118.032709, 118.032172, 118.031433,
              118.030706, 118.029445, 118.028382, 118.027702, 118.027081, 118.026417,
              118.025967, 118.025444, 118.024785, 118.024134, 118.022765, 118.022629,
          118.022407, 118.023530, 118.024424, 118.025361, 118.026075, 118.026565)

#print length of each vector
length(river.lat)
length(river.long)

#pad shortest vector with NA's to have same length as longest vector
length(river.lat) <- length(river.long)

#create data frame using vectors as columns
df <- data.frame(river.lat=river.lat, river.long=river.long)

#view resulting data frame
df
```

```
river.coords <- data.frame(river.long, river.lat)

lines(river.coords, lwd=2)


#### End ####
```

Movement pattern analysis

```
##### Script for EMbC algorithm based on: ####
##### "Garriga, J. and Bartumeus, F., The EMbC R-package: quick reference." ####
# Expectation Maximisation Binary Clustering

# Set working directory
setwd("C:/Users/AV laptop/Desktop/Spatial course archive") #Rob's
setwd("D:/PhD Thesis/Chapter 3/Movement strategies/EMBC New") #Elisa's

# Read in the data for each pangolin
Pesona <- read.csv("Pesona.csv")
Pesona
Galak <- read.csv("Galak.csv")
Galak
Anggun <- read.csv("Anggun.csv")
Anggun
Berkat <- read.csv("Berkat.csv")
Berkat
Gagah <- read.csv("Gagah.csv")
Gagah
Oroi <- read.csv("Oroi.csv")
Oroi
Suka <- read.csv("Suka.csv")
Suka
Tuah <- read.csv("Tuah.csv")
Tuah
Wira1 <- read.csv("Wira1.csv")
```

```
Wira1

Wira2 <- read.csv("Wira2.csv")

Wira2


dframe1 <- rbind(Pesona,Anggun,

             Gagah, Oroi, Suka, Tuah, Wira1, Wira2)


head(dframe1)

dframe1


dframe1$Latitude <- dframe1$y

dframe1$Longitude <- dframe1$x


# Basic checking / plotting###

plot(Latitude ~ Longitude, data = dframe1)

plot(Latitude ~ Longitude, data = dframe1, type ="b", asp=1)  # aspect ratio


#Install the packages ####

install.packages("methods")

install.packages("sp")

install.packages("maptools")

install.packages("mnormt")

install.packages("RColorBrewer")

install.packages("rgl")

install.packages("move")

install.packages("EMbC")

install.packages("tmvnsim")
```

```
library(methods)
library(sp)
library(maptools)
library(mnormt)
library(RColorBrewer)
library(rgl)
library(move)
library(tmvnsim)
library(EMbC) #this is the main package
citation("EMbC")

#Import data sets - **analyse individually** #####
dframe1$lat <- dframe1$y
dframe1$long <- dframe1$x

# Convert to DateTime format, e.g. 30/11/2017  17:30:08 ####

Date <- paste((dframe1$Year), dframe1$Month, dframe1$Day, sep="/")
Date

Time <- paste(dframe1$Hour, dframe1$Minute, dframe1$Second, sep=":")
Time

DateTime <- paste(Date, Time, sep=" ")
DateTime
length(DateTime)

DateTime2 <- as.POSIXct(DateTime, tz="GMT")  # MYT
```

```
length(DateTime2)
DateTime2

#extract relevant columns per GPS deployment ####
#
names(dframe1)
dframe2 <- as.data.frame(DateTime2) #have to put as.data.frame here because R thinks it's a matrix so you have to tell it it isn't
dframe2$lon <- dframe1$long
dframe2$lat <- dframe1$lat
dframe2$id <- dframe1$id

dframe2 # view the compiled dataframe
str(dframe2)
summary(dframe2)

# Now start the actual analysis! ####

#To start with pass the data.frame through the "constuctor" clustering algorithm stbc()
?stbc # speed turn binary clustering
mybcp <- stbc(dframe2, info=-1)
mybcp

#Slots contain information related to the binary clustering (e.g. input data, intermediate computations and output data)####
slotNames(mybcp)

#To show the statistics of the clustering run stts () ####
stts(mybcp)
```

```
#Then there are various plots you can run####
#Cluster plot:####
sctr(mybcp)

#labeling profile - temporal series of data and of behaviours labelled ####
#the number of points shown on the graphs/map is the length noted from mybcp <- above
lblp(mybcp)

#chkp is similar to lblp but includes a control variable - e.g. day and night/environmental info
chkp(mybcp)

#fast visualisation of annotated trajectories####
#the number of points shown on the graphs/map is the length noted from mybcp <- above
view(mybcp, lims=c(1, 147))

#You can then create a kml file for more detailed inspections... ####
pkml(mybcp, display=TRUE) #display=TRUE launches google-earth from within R

# Speed and turning angle
# HH = High Velocity, High Turning Angle
# HL = High Velocity, Low Turning Angle
# LH = Low Velocity, High Turning Angle
# LL = Low Velocity, Low Turning Angle

mybcp@dst  # distances between successive points
hist(mybcp@dst,
    main="",
```

```
    xlab="Distance covered (m/day)")   # split histogram by resident/translocated

mybcp@hdg   # heading
hist(mybcp@hdg,
    main="",
    xlab="Heading")

mybcp@spn   # time between fixes?
mybcp@bursted  # FALSE
mybcp@tracks
mybcp@midPoints

mybcp@X
mybcp@U
mybcp@m
mybcp@R
mybcp@P
mybcp@W
mybcp@C
mybcp@A  # behaviour classifications
dframe1$Class <- mybcp@A
mybcp@L

dframe1
names(dframe1)

#### Plotting kernels for each individual pangolin ####
```

```
plot(Latitude ~ Longitude, data = dframe1,
     subset = dframe1$id=="pesona",          # choose your pangolin
     col="white", pch=19,  # colour points by day
     type ="b", asp=1)      # aspect ratio

MySubset <- subset(dframe1,
                   dframe1$id=="pesona" # Pangolin ID
                   & dframe1$Class==3)  # behaviour class
MySubset
?`EMbC-package`

points(Latitude ~ Longitude, data = dframe1,
     col= rgb(1,0.5, 0.5, 0.5), subset=dframe1$Class==3 & dframe1$id=="pesona", pch=19)
            # class 1

# Create the subset for which you want the kernel

# Retain long and lat

library(sp)
data.sp <- MySubset[, c("id", "long", "lat")]
data.sp

coordinates(data.sp) <- c("long", "lat")
data.sp

# Add the coordinate reference system / projection, and turn the dataframe into a spatial
            points object
coord.dec = SpatialPoints(data.sp, proj4string=CRS("+proj=longlat"))
```

```
coord.dec  # Decimal coordinates



# Create a home range kernel

library(adehabitatHR)

# kernel.href <- kernelUD(coord.dec,  h = "href") # href method

# kernel.href <- kernelUD(coord.dec,  h = "LSCV") # LSCV method

kernel.href <- kernelUD(coord.dec,  h = 0.005)  # setting h value manually

#?kernelUD



myKernel <- getverticeshr(kernel.href, percent=50) # Edit the percent to get different % MCPs

plot(myKernel, col=rgb(1,0.5,0.5, 0.3), add=T, border=F)
```

Calculation for Fig. 3.19

```
# Packages
library(dplyr)
library(lubridate)
library(geosphere)

# ---- Load tracking data ----
f <- "tracking_latlon.csv"   # raw GPS data
df <- read.csv(f, stringsAsFactors = FALSE)

# Normalise column names
names(df) <- tolower(names(df))

# Build timestamp
if (all(c("year","month","day") %in% names(df))) {
  hr <- if ("hour"   %in% names(df)) df$hour   else 0
  mn <- if ("minute" %in% names(df)) df$minute else 0
  sc <- if ("second" %in% names(df)) df$second else 0
  df$timestamp <- make_datetime(df$year, df$month, df$day, hr, mn, sc, tz = "UTC")
} else if ("timestamp" %in% names(df)) {
  df$timestamp <- ymd_hms(df$timestamp, tz = "UTC")
} else {
  stop("No time columns found.")
}

# Order by individual and time
df <- df %>% arrange(id, timestamp)

# ---- Step lengths (meters) ----
df_steps <- df %>%
  group_by(id) %>%
```

```
  mutate(step_m = distHaversine(
    p1 = cbind(lag(x), lag(y)),
    p2 = cbind(x, y)
  )) %>%
  ungroup()

# Clean
df_steps <- df_steps %>%
  filter(!is.na(step_m), step_m >= 0) %>%
  mutate(date = as_date(timestamp))

# ---- Daily totals (meters) ----
daily <- df_steps %>%
  group_by(id, date) %>%
  summarise(daily_distance_m = sum(step_m, na.rm = TRUE), .groups = "drop")

# ---- Mean per individual (meters) ----
mean_daily <- daily %>%
  group_by(id) %>%
  summarise(
    DailyDist_mean_m = mean(daily_distance_m, na.rm = TRUE),
    Days_with_data   = n(),
    .groups = "drop"
  )

# Save outputs
write.csv(daily,      "daily_distance_by_id_m.csv", row.names = FALSE)
write.csv(mean_daily, "mean_daily_distance_by_id.csv", row.names = FALSE)

# ---- Load annotated file with Status & Sex ----
# This file must have: id, Status, Sex, DailyDist_mean_m (in meters/day)
data <- read.csv("Daily mean.csv", stringsAsFactors = FALSE)

# Ensure numeric
data$DailyDist_mean_m <- as.numeric(data$DailyDist_mean_m)

# ---- Summaries in meters/day ----
status_summary <- data %>%
  group_by(Status) %>%
  summarise(
    n = n(),
    mean_daily_m = mean(DailyDist_mean_m, na.rm = TRUE),
    sd_daily_m   = sd(DailyDist_mean_m, na.rm = TRUE)
  )

sex_summary <- data %>%
  group_by(Sex) %>%
  summarise(
    n = n(),
    mean_daily_m = mean(DailyDist_mean_m, na.rm = TRUE),
    sd_daily_m   = sd(DailyDist_mean_m, na.rm = TRUE)
  )

print(status_summary)
print(sex_summary)
```

```
# ---- Boxplots (meters/day) ----
boxplot(DailyDist_mean_m ~ Status, data = data,
        main = "Daily Distance by Status",
        ylab = "Mean daily distance (m)",
        col = c("lightblue", "lightgreen"))

boxplot(DailyDist_mean_m ~ Sex, data = data,
        main = "Daily Distance by Sex",
        ylab = "Mean daily distance (m)",
        col = c("pink", "lightgrey"))

# ---- Statistical tests ----
# Status: Welch t-test (small, unequal n)
print(t.test(DailyDist_mean_m ~ Status, data = data))

# Sex: Wilcoxon (small n, non-normal)
print(wilcox.test(DailyDist_mean_m ~ Sex, data = data))

##### END  #######
```

Chapter 4: Habitat use and sleeping site preference of Sunda pangolins in the highly fragmented Lower Kinabatangan landscape

Analysis of sleeping sites and predicting their distribution

```
###Comparison analysis between sleeping and non-sleeping sites###
# Load the CSV file
dframe1 <- read.csv("Sleeping Site Survey Data New - Copy.csv")

# Check the structure of the data
str(dframe1)

# Summary statistics for sleeping sites
summary(dframe1[dframe1$Used == 1, ])

# Summary statistics for non-sleeping sites
summary(dframe1[dframe1$Used != 1, ])

# T-test for Dist.Water
t.test(dframe1$Dist.Water ~ dframe1$Used)

# Chi-square test for Tree
table_tree <- table(dframe1$Tree, dframe1$Used)
chisq.test(table_tree)

# Chi-square test for Hollow presence
table_hollow <- table(dframe1$Hollow, dframe1$Used)
chisq.test(table_hollow)

# Chi-square test for Vines presence
```

```
table_vines <- table(dframe1$Vines, dframe1$Used)
chisq.test(table_vines)

# T-test for DBH
t.test(dframe1$DBH ~ dframe1$Used)

# T-test for Tree Height
t.test(dframe1$Tree.Height ~ dframe1$Used)

# T-test for Elevation
t.test(dframe1$Elevation ~ dframe1$Used)

# T-test for Ground Cover
t.test(dframe1$Ground.Cover ~ dframe1$Used)

# Update vectors for the table with Ground Cover
Variable <- c("Dist.Water", "Tree", "Hollow", "Vines", "DBH", "Tree.Height", "Elevation", "Ground.Cover")
Test_Type <- c("T-test", "Chi-square", "Chi-square", "Chi-square", "T-test", "T-test", "T-test", "T-test")
p_value <- c(0.0008094, 2.292e-07, 0.3064, 0.025, 2.398e-05, 0.0004904, 0.03242, 0.1423) # Replace 0.1423 with the actual p-value for Ground Cover
Mean_Non_Sleeping <- c(127.3056, NA, NA, NA, 0.5645238, 33.82701, 74.55890, 50.72) # Replace 50.72 with the actual mean for non-sleeping sites
Mean_Sleeping <- c(101.8232, NA, NA, NA, 0.6623358, 38.37956, 74.35223, 54.37) # Replace 54.37 with the actual mean for sleeping sites
Interpretation <- c("Significant difference",
                    "Significant association",
                    "No significant association",
                    "Significant association",
                    "Significant difference",
```

```
                "Significant difference",

                "Significant difference (very small)",

                "No significant difference") # Update this based on the Ground Cover results


# Combine into a data frame

results_table <- data.frame(Variable, Test_Type, p_value, Mean_Non_Sleeping,
        Mean_Sleeping, Interpretation)


# View the table

print(results_table)


# Export the table to a CSV file

write.csv(results_table, "Pangolin_Sleeping_Sites_Statistical_Summary.csv", row.names =
        FALSE)


###NEW###


# Load the CSV file

dframe1 <- read.csv("Sleeping Site Survey Data New - Copy.csv")


# Check the structure of the data

str(dframe1)


# Summary statistics for sleeping sites

summary(dframe1[dframe1$Used == 1, ])


# Summary statistics for non-sleeping sites

summary(dframe1[dframe1$Used != 1, ])
```

```
# T-test for Dist.Water (in meters)

t.test(dframe1$Dist.Water ~ dframe1$Used)


# Chi-square test for Tree

table_tree <- table(dframe1$Tree, dframe1$Used)

chisq.test(table_tree)


# Chi-square test for Hollow presence (0 = No hollow, 1 = Has hollow)

table_hollow <- table(dframe1$Hollow, dframe1$Used)

chisq.test(table_hollow)


# Chi-square test for Vines presence (0 = No vines presence, 1 = Minimal vine coverage, 2 = Light vine coverage, 3 = Moderate vine coverage, 4 = Dense vine coverage, 5 = Heavily covered by vines)

table_vines <- table(dframe1$Vines, dframe1$Used)

chisq.test(table_vines)


# T-test for DBH (in meters)

t.test(dframe1$DBH ~ dframe1$Used)


# T-test for Tree Height (in meters)

t.test(dframe1$Tree.Height ~ dframe1$Used)


# T-test for Elevation (in meters)

t.test(dframe1$Elevation ~ dframe1$Used)


# T-test for Ground Cover (in percentage)

t.test(dframe1$Ground.Cover ~ dframe1$Used)
```

```
# Chi-square test for Number of Hollows (0 = No hollow, 1 = One hollow, 2 = Two or more hollows)

table_no_hollows <- table(dframe1$No.Hollows, dframe1$Used)

chisq.test(table_no_hollows)



# Update vectors for the table with Ground Cover and Number of Hollows

Variable <- c("Dist.Water", "Tree", "Hollow", "Vines", "DBH", "Tree.Height", "Elevation", "Ground.Cover", "No.Hollows")

Test_Type <- c("T-test", "Chi-square", "Chi-square", "Chi-square", "T-test", "T-test", "T-test", "T-test", "Chi-square")

p_value <- c(0.0008094, 2.292e-07, 0.3064, 0.025, 2.398e-05, 0.0004904, 0.03242, 0.1423, 0.0724) # Replace 0.0724 with the actual p-value for Number of Hollows

Mean_Non_Sleeping <- c(127.3056, NA, NA, NA, 0.5645238, 33.82701, 74.55890, 50.72, NA) # Replace 0.8407 with the actual mean for non-sleeping sites

Mean_Sleeping <- c(101.8232, NA, NA, NA, 0.6623358, 38.37956, 74.35223, 54.37, NA) # Replace 0.8882 with the actual mean for sleeping sites

Interpretation <- c("Significant difference",

                "Significant association",

                "No significant association",

                "Significant association",

                "Significant difference",

                "Significant difference",

                "Significant difference (very small)",

                "No significant difference",

                "No significant association") # Update this based on the Number of Hollows results



# Combine into a data frame

results_table <- data.frame(Variable, Test_Type, p_value, Mean_Non_Sleeping, Mean_Sleeping, Interpretation)



# View the table
```

```
print(results_table)


# Export the table to a CSV file

write.csv(results_table, "Pangolin_Sleeping_Sites_Statistical_Summary.csv", row.names =
          FALSE)


#Sleeping Site Analysis for Resident Pangolins


# Load necessary libraries

library(dplyr)

library(car)

library(boot)

library(ggplot2)


# Load the data

data <- read.csv("SS resident.csv")


# Fit the logistic regression model without Ground.Cover

model <- glm(Used ~ DBH + factor(No.Hollows) + Dist.Water + Elevation + factor(Vines) +
          Tree.Height,

           data = data, family = binomial)


# Check the VIF values for the remaining variables

vif_values <- vif(model)

print(vif_values)


# Extract adjusted GVIF^(1/(2*Df)) values if available

vif_adjusted <- vif_values[, "GVIF^(1/(2*Df))"]
```

```
# Bootstrap to get VIF confidence intervals
vif_func <- function(formula, data, indices) {
  d <- data[indices,] # allows boot to select sample
  fit <- glm(formula, data = d, family = binomial)
  vif_vals <- vif(fit)[, "GVIF^(1/(2*Df))"]
  return(vif_vals)
}

# Perform the bootstrap
vif_boot <- boot(data = data, statistic = vif_func, R = 1000, formula = Used ~ DBH + factor(No.Hollows) + Dist.Water + Elevation + factor(Vines) + Tree.Height)

# Extract VIF confidence intervals
vif_ci_lower <- sapply(1:length(vif_adjusted), function(i) boot.ci(vif_boot, type = "perc", index = i)$percent[4])
vif_ci_upper <- sapply(1:length(vif_adjusted), function(i) boot.ci(vif_boot, type = "perc", index = i)$percent[5])

# Calculate CI Increased and Tolerance values
ci_increased <- vif_adjusted / sqrt(vif_ci_lower * vif_ci_upper)
tolerance <- 1 / vif_adjusted
tolerance_ci_lower <- 1 / vif_ci_upper
tolerance_ci_upper <- 1 / vif_ci_lower

# Combine results into a data frame
vif_df <- data.frame(
  Term = rownames(vif_values),
  VIF = vif_adjusted,
  VIF_95CI_Lower = vif_ci_lower,
  VIF_95CI_Upper = vif_ci_upper,
```

```
  CI_Increased = ci_increased,
  SE_Tolerance = tolerance,
  Tolerance_95CI_Lower = tolerance_ci_lower,
  Tolerance_95CI_Upper = tolerance_ci_upper
)

# Print the VIF and tolerance table
print(vif_df)

# Perform Likelihood Ratio Tests (LRT) for each term in the model
lrt_results <- drop1(model, test = "Chisq")

# Print the results
print(lrt_results)

### Plotting Section ###

# Ensure dplyr and ggplot2 packages are loaded
library(dplyr)
library(ggplot2)

# Remove rows with NA or infinite values in DBH
cleaned_data <- data %>%
  filter(!is.na(DBH) & is.finite(DBH))

# 1. DBH vs. Likelihood of Being Used
model_dbh <- glm(Used ~ DBH, data = cleaned_data, family = binomial)
plot_data_dbh <- data.frame(
```

```
  DBH = seq(min(cleaned_data$DBH), max(cleaned_data$DBH), length.out = 100)
)
plot_data_dbh$Likelihood <- predict(model_dbh, newdata = plot_data_dbh, type = "response")
conf_intervals_dbh <- predict(model_dbh, newdata = plot_data_dbh, type = "link", se.fit = TRUE)
plot_data_dbh$Lower_CI <- plogis(conf_intervals_dbh$fit - 1.96 * conf_intervals_dbh$se.fit)
plot_data_dbh$Upper_CI <- plogis(conf_intervals_dbh$fit + 1.96 * conf_intervals_dbh$se.fit)

ggplot() +
  geom_jitter(data = cleaned_data, aes(x = DBH, y = Used), width = 0.05, height = 0.05, alpha = 0.3, color = "blue") +
  geom_line(data = plot_data_dbh, aes(x = DBH, y = Likelihood), color = "red", linewidth = 1) +
  geom_ribbon(data = plot_data_dbh, aes(x = DBH, ymin = Lower_CI, ymax = Upper_CI), fill = "red", alpha = 0.2) +
  labs(x = "DBH (m)", y = "Likelihood of being used") +
  theme_minimal() +
  ggtitle("DBH vs. Likelihood of Being Used")

# 2. Presence of Hollow vs. Likelihood of Being Used (Dot Plot with Error Bars)
# Fit a logistic regression model including Hollow presence
model_hollow <- glm(Used ~ factor(No.Hollows), data = cleaned_data, family = binomial)

# Create a data frame with all possible hollow presence scores
plot_data_hollow <- data.frame(
  No.Hollows = factor(0:2, levels =c(0, 1, 2))
)

# Predict likelihood and calculate confidence intervals for each hollow presence score
```

```
plot_data_hollow$Likelihood <- predict(model_hollow, newdata = plot_data_hollow, type =
        "response")
plot_data_hollow$SE <- predict(model_hollow, newdata = plot_data_hollow, type = "link",
        se.fit = TRUE)$se.fit
plot_data_hollow$Lower_CI <- plogis(qlogis(plot_data_hollow$Likelihood) - 1.96 *
        plot_data_hollow$SE)
plot_data_hollow$Upper_CI <- plogis(qlogis(plot_data_hollow$Likelihood) + 1.96 *
        plot_data_hollow$SE)


# Plot Hollow Presence vs. Likelihood of Being Used
ggplot(plot_data_hollow, aes(x = No.Hollows, y = Likelihood)) +
geom_point(size = 3, color = "black") +
  geom_errorbar(aes(ymin = Lower_CI, ymax = Upper_CI), width = 0.2, color = "black") +
  labs(x = "Hollow Presence", y = "Likelihood of being used") +
  ylim(0.0, 1.0) +  # Set the y-axis limits from 0.0 to 1.0
  theme_minimal() +
  ggtitle("Hollow Presence vs. Likelihood of Being Used")


# 3. Presence of Vines vs. Likelihood of Being Used (Dot Plot with Error Bars)


# Convert Vines to a factor with levels 1 to 5 since 0 is not present
data$Vines <- factor(data$Vines, levels = 1:5)


# Remove rows with NA or infinite values in DBH
cleaned_data <- data %>%
  filter(!is.na(DBH) & is.finite(DBH))


# Fit the logistic regression model including Vine Score
model_vines <- glm(Used ~ factor(Vines), data = cleaned_data, family = binomial)
```

```
# Create a data frame with all possible vine scores, ensuring the levels match the model
plot_data_vines <- data.frame(
  Vines = factor(1:5, levels = levels(cleaned_data$Vines))
)

# Predict likelihood and calculate confidence intervals for each vine score
plot_data_vines$Likelihood <- predict(model_vines, newdata = plot_data_vines, type = "response")
plot_data_vines$SE <- predict(model_vines, newdata = plot_data_vines, type = "link", se.fit = TRUE)$se.fit
plot_data_vines$Lower_CI <- plogis(qlogis(plot_data_vines$Likelihood) - 1.96 * plot_data_vines$SE)
plot_data_vines$Upper_CI <- plogis(qlogis(plot_data_vines$Likelihood) + 1.96 * plot_data_vines$SE)

# Plot Vine Score vs. Likelihood of Being Used
ggplot(plot_data_vines, aes(x = Vines, y = Likelihood)) +
geom_point(size = 3, color = "black") +
  geom_errorbar(aes(ymin = Lower_CI, ymax = Upper_CI), width = 0.2, color = "black") +
  labs(x = "Vine Score", y = "Likelihood of being used") +
  ylim(0.0, 1.0) +  # Set the y-axis limits from 0.0 to 1.0
  theme_minimal() +
  ggtitle("Vine Score vs. Likelihood of Being Used")

# 4. Tree height vs. Likelihood of Being Used
# Assuming cleaned_data has been prepared with NA values removed
# Fit the logistic regression model including Tree Height
model_tree_height <- glm(Used ~ Tree.Height, data = cleaned_data, family = binomial)

# Create a new data frame for plotting, varying Tree.Height while keeping other variables constant
```

```
plot_data_tree_height <- data.frame(
  Tree.Height = seq(min(cleaned_data$Tree.Height), max(cleaned_data$Tree.Height), length.out = 100)
)


# Predict the likelihood of being used based on the model
plot_data_tree_height$Likelihood <- predict(model_tree_height, newdata = plot_data_tree_height, type = "response")


# Add confidence intervals for the predictions
conf_intervals_tree_height <- predict(model_tree_height, newdata = plot_data_tree_height, type = "link", se.fit = TRUE)
plot_data_tree_height$Lower_CI <- plogis(conf_intervals_tree_height$fit - 1.96 * conf_intervals_tree_height$se.fit)
plot_data_tree_height$Upper_CI <- plogis(conf_intervals_tree_height$fit + 1.96 * conf_intervals_tree_height$se.fit)


# Create the scatterplot with fitted regression line
ggplot() +
  geom_jitter(data = cleaned_data, aes(x = Tree.Height, y = Used), width = 0.05, height = 0.05, alpha = 0.3, color = "blue") +
  geom_line(data = plot_data_tree_height, aes(x = Tree.Height, y = Likelihood), color = "red", linewidth = 1) +
  geom_ribbon(data = plot_data_tree_height, aes(x = Tree.Height, ymin = Lower_CI, ymax = Upper_CI), fill = "red", alpha = 0.2) +
  labs(x = "Tree Height (m)", y = "Likelihood of being used") +
  theme_minimal() +
  ggtitle("Tree Height vs. Likelihood of Being Used")


# Calculate means for DBH, Hollow, Vines, and Tree Height
means <- cleaned_data %>%
  summarise(
```

```
    Mean_DBH = mean(DBH, na.rm = TRUE),
    Mean_No_Hollows = mean(as.numeric(as.character(No.Hollows)), na.rm = TRUE),
    Mean_Vines = mean(as.numeric(as.character(Vines)), na.rm = TRUE),
    Mean_Tree_Height = mean(Tree.Height, na.rm = TRUE)
  )

# Print the means
print(means)

# Calculate the mean likelihood for each level of No.Hollows
mean_likelihood_hollows <- plot_data_hollow %>%
group_by(No.Hollows) %>%
  summarise(Mean_Likelihood = mean(Likelihood))

# Print the means for No.Hollows
print(mean_likelihood_hollows)

# Calculate the mean likelihood for each level of Vines
mean_likelihood_vines <- plot_data_vines %>%
group_by(Vines) %>%
  summarise(Mean_Likelihood = mean(Likelihood))

# Print the means for Vines
print(mean_likelihood_vines)

# Calculate the mean for Elevation
mean_elevation <- mean(data$Elevation, na.rm = TRUE)
```

```
# Print the mean elevation
print(mean_elevation)

###Sleeping site analysis for translocated pangolins###

# Load necessary libraries
library(dplyr)
library(car)
library(boot)
library(ggplot2)

# Load the data
data <- read.csv("SS translocated.csv")

# Fit the logistic regression model excluding Elevation
model <- glm(Used ~ DBH + factor(No.Hollows) + Dist.Water + factor(Vines) + Tree.Height
           + factor(Habitat.Category),
             data = data, family = binomial)

# Check for aliased coefficients in the model
alias_info <- alias(model)
print(alias_info)

# If no aliasing issues, proceed with VIF calculation
if (is.null(alias_info$Complete)) {
  vif_values <- vif(model)
  print(vif_values)

  # Extract adjusted GVIF^(1/(2*Df)) values if available
```

```
vif_adjusted <- vif_values[, "GVIF^(1/(2*Df))"]

# Bootstrap to get VIF confidence intervals
vif_func <- function(formula, data, indices) {
  d <- data[indices,] # allows boot to select sample
  fit <- glm(formula, data = d, family = binomial)
  vif_vals <- vif(fit)[, "GVIF^(1/(2*Df))"]
  return(vif_vals)
}

# Perform the bootstrap
vif_boot <- boot(data = data, statistic = vif_func, R = 1000, formula = Used ~ DBH +
        factor(No.Hollows) + Dist.Water + factor(Vines) + Tree.Height +
        factor(Habitat.Category))

# Extract VIF confidence intervals
vif_ci_lower <- sapply(1:length(vif_adjusted), function(i) boot.ci(vif_boot, type = "perc",
        index = i)$percent[4])
vif_ci_upper <- sapply(1:length(vif_adjusted), function(i) boot.ci(vif_boot, type = "perc",
        index = i)$percent[5])

# Calculate CI Increased and Tolerance values
ci_increased <- vif_adjusted / sqrt(vif_ci_lower * vif_ci_upper)
tolerance <- 1 / vif_adjusted
tolerance_ci_lower <- 1 / vif_ci_upper
tolerance_ci_upper <- 1 / vif_ci_lower

# Combine results into a data frame
vif_df <- data.frame(
  Term = rownames(vif_values),
```

```
    VIF = vif_adjusted,
    VIF_95CI_Lower = vif_ci_lower,
    VIF_95CI_Upper = vif_ci_upper,
    CI_Increased = ci_increased,
    SE_Tolerance = tolerance,
    Tolerance_95CI_Lower = tolerance_ci_lower,
    Tolerance_95CI_Upper = tolerance_ci_upper
  )

  # Print the VIF and tolerance table
  print(vif_df)

  # Perform Likelihood Ratio Tests (LRT) for each term in the model
  lrt_results <- drop1(model, test = "Chisq")
  print(lrt_results)
} else {
  print("There are aliased coefficients. Consider simplifying the model further.")
}

###NEW###

# Load necessary libraries
library(dplyr)
library(car)
library(boot)
library(ggplot2)

# Load the data
```

```
data <- read.csv("SS translocated.csv")

# Fit the logistic regression model with Habitat.Category and DBH
model <- glm(Used ~ DBH + factor(Habitat.Category), data = data, family = binomial)

# Check for aliased coefficients in the model
alias_info <- alias(model)
print(alias_info)

# If no aliasing issues, proceed with VIF calculation
if (is.null(alias_info$Complete)) {
  vif_values <- vif(model)
  print(vif_values)

  # Bootstrap to get VIF confidence intervals
  vif_func <- function(formula, data, indices) {
    d <- data[indices,] # allows boot to select sample
    fit <- glm(formula, data = d, family = binomial)
    vif_vals <- vif(fit)
    return(vif_vals)
  }

  # Perform the bootstrap
  vif_boot <- boot(data = data, statistic = vif_func, R = 1000, formula = Used ~ DBH +
        factor(Habitat.Category))

  # Extract VIF confidence intervals
  vif_ci_lower <- sapply(1:length(vif_values), function(i) boot.ci(vif_boot, type = "perc", index
        = i)$percent[4])
```

```
  vif_ci_upper <- sapply(1:length(vif_values), function(i) boot.ci(vif_boot, type = "perc", index
          = i)$percent[5])


  # Calculate CI Increased and Tolerance values

  ci_increased <- vif_values / sqrt(vif_ci_lower * vif_ci_upper)

  tolerance <- 1 / vif_values

  tolerance_ci_lower <- 1 / vif_ci_upper

  tolerance_ci_upper <- 1 / vif_ci_lower


  # Combine results into a data frame

  vif_df <- data.frame(

    Term = names(vif_values),

    VIF = vif_values,

    VIF_95CI_Lower = vif_ci_lower,

    VIF_95CI_Upper = vif_ci_upper,

    CI_Increased = ci_increased,

    SE_Tolerance = tolerance,

    Tolerance_95CI_Lower = tolerance_ci_lower,

    Tolerance_95CI_Upper = tolerance_ci_upper

  )


  # Print the VIF and tolerance table

  print(vif_df)


  # Perform Likelihood Ratio Tests (LRT) for each term in the model

  lrt_results <- drop1(model, test = "Chisq")

  print(lrt_results)

} else {

  print("There are aliased coefficients. Consider simplifying the model further.")
```

```
}


# 1. DBH vs likelihood of sleeping site use


# Fit the logistic regression model for DBH
model_dbh <- glm(Used ~ DBH, data = data, family = binomial)
# Generate a sequence of DBH values for prediction
plot_data_dbh <- data.frame(
  DBH = seq(min(data$DBH, na.rm = TRUE), max(data$DBH, na.rm = TRUE), length.out = 100)
)


# Predict likelihood of use based on DBH
plot_data_dbh$Likelihood <- predict(model_dbh, newdata = plot_data_dbh, type = "response")


# Calculate confidence intervals
conf_intervals_dbh <- predict(model_dbh, newdata = plot_data_dbh, type = "link", se.fit = TRUE)
plot_data_dbh$Lower_CI <- plogis(conf_intervals_dbh$fit - 1.96 * conf_intervals_dbh$se.fit)
plot_data_dbh$Upper_CI <- plogis(conf_intervals_dbh$fit + 1.96 * conf_intervals_dbh$se.fit)


# Plotting DBH vs. Likelihood of Being Used
ggplot() +
  geom_jitter(data = data, aes(x = DBH, y = Used), width = 0.05, height = 0.05, alpha = 0.3, color = "blue") +
  geom_line(data = plot_data_dbh, aes(x = DBH, y = Likelihood), color = "red", linewidth = 1) +
  geom_ribbon(data = plot_data_dbh, aes(x = DBH, ymin = Lower_CI, ymax = Upper_CI), fill = "red", alpha = 0.2) +
  labs(x = "DBH (m)", y = "Likelihood of Being Used") +
```

```
theme_minimal() +

ggtitle("DBH vs. Likelihood of Being Used")
```

Habitat vs likelihood of sleeping site use

```
# Fit the logistic regression model for habitat category

model_habitat <- glm(Used ~ factor(Habitat.Category), data = data, family = binomial)


# Create a data frame for prediction

plot_data_habitat <- data.frame(Habitat.Category = c(0, 1))


# Predict likelihood of use based on habitat category

plot_data_habitat$Likelihood <- predict(model_habitat, newdata = plot_data_habitat, type = "response")


# Calculate confidence intervals

conf_intervals_habitat <- predict(model_habitat, newdata = plot_data_habitat, type = "link", se.fit = TRUE)

plot_data_habitat$Lower_CI <- plogis(conf_intervals_habitat$fit - 1.96 * conf_intervals_habitat$se.fit)

plot_data_habitat$Upper_CI <- plogis(conf_intervals_habitat$fit + 1.96 * conf_intervals_habitat$se.fit)


# Convert Habitat.Category back to labels

plot_data_habitat$Habitat <- factor(plot_data_habitat$Habitat.Category, labels = c("Forest", "Plantation"))


# Plotting Habitat vs. Likelihood of Being Used (Dot plot with error bars)

ggplot(plot_data_habitat, aes(x = Habitat, y = Likelihood)) +

geom_point(size = 4, color = "black") +

  geom_errorbar(aes(ymin = Lower_CI, ymax = Upper_CI), width = 0.2, color = "black", size = 1) +

  labs(x = "Habitat Type", y = "Likelihood of Being Used") +

  ylim(0.0, 1.0) +  # Set the y-axis limits from 0.0 to 1.0
```

```
  theme_minimal() +

  ggtitle("Likelihood of Sleeping Site Use in Forest vs. Plantation")


# Calculate the mean likelihood of being used for each habitat type

mean_likelihood_by_habitat <- aggregate(Likelihood ~ Habitat.Category, data =
        plot_data_habitat, FUN = mean)


# Print the results

print(mean_likelihood_by_habitat)


# Calculate the overall mean DBH

mean_dbh <- mean(data$DBH, na.rm = TRUE)


# Print the mean DBH

print(mean_dbh)
```

Species distribution modelling (SDM) analysis

```
###MiaMaxEnt Package###

library(sp)
library(rgdal)
library(raster)
library(maptools)
library(datasets)
library(GISTools)
library(RColorBrewer)
library(spatstat)
library(lgcp)
library(MIAmaxent)
library(adehabitatHS)
library(ggfortify)
library(PCAmixdata)
library(FactoMineR)
library(factoextra)
library(smacof)
library(bootstrap)
library(sf)
library(ggplot2)
library(dplyr)

###Create a folder with the following content:
# A folder called ContVar, which will contain the ccontinous rasters "Canopy height" and "Forest width"
# A folder called CatVat, which will contain the categorical raster "Habitat class"
```

```
# The .csv files with the primates locations (one file for each species), with the coordinates in UTM.


###### Select the source #########

setwd("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New")#Direct to the folders that contains the necessary files

list.files("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New")#List the files contained in the folder


setwd("D:/PhD Thesis/Chapter 4/Pangolin Project/raster_files_Elisa-20221210T192440Z-001_2/raster_files_Elisa/Pangolins_Sleeping Sites_MiaMAXENT")

list.files("D:/PhD Thesis/Chapter 4/Pangolin Project/raster_files_Elisa-20221210T192440Z-001_2/raster_files_Elisa/Pangolins_Sleeping Sites_MiaMAXENT")


##### Verify the information of each raster. Extent,Projection and Resolution must be the same in all the ratsers #######


Canopy<-raster("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/ContV/Canopy3.asc")

proj4string(Canopy)<- CRS("+proj=utm +zone=50 +datum=WGS84 +units=m +no_defs +ellps=WGS84 +towgs84=0,0,0")

Canopy


Elev<-raster("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/ContV/Elevation3.asc")

proj4string(Elev)<- CRS("+proj=utm +zone=50 +datum=WGS84 +units=m +no_defs +ellps=WGS84 +towgs84=0,0,0")

Elev


Slope<-raster("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/ContV/Slope3.asc")

proj4string(Slope)<- CRS("+proj=utm +zone=50 +datum=WGS84 +units=m +no_defs +ellps=WGS84 +towgs84=0,0,0")
```

```
Slope



HabType<-raster("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/CatV/Habitat_Class3.asc")

proj4string(HabType)<- CRS("+proj=utm +zone=50 +datum=WGS84 +units=m +no_defs +ellps=WGS84 +towgs84=0,0,0")

extent(HabType)<-c(611931.3, 618087, 596110.3, 600702)

res(HabType)<-1.99988

HabType



#### Visualize the GPS locations, select any raster file as background #######



OaEV1 <- raster("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/ContV/Canopy3.asc")

OaPO <- read.csv("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New//Locations.csv")#You will have to run one model per  species seapareately

plot(OaEV1, legend=TRUE, ylim=c(592000,700000))

points(OaPO$X, OaPO$Y, pch = 20, cex = 0.5, col = 'blue')

OaPO



#####MAXENT STARTS HERE######

##### Gather the information needed for the analysis ######



OvAllData <- readData(# Put everything together


        occurrence="/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/Locations.csv",# File with the GPS locations of the target species

  contEV="/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/ContV",  #Folder containing the raster files with CONTINUOUS values

  catEV="/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/CatV",  #Folder containing the raster files with CATEGORICAL values
```

```
  maxbkg=10000,PA=FALSE)

str(OvAllData) #Read the content of the new data frame (RV= number of occurrences [GPS locations])

OvAllData #RV=NA translates as "Abscences" or zero. As Maxent works as only presence model, locations (RV) without presence are recoderd as NA



###### Visualize the Frequency of Observed Presence (FOP; dots and red line) in relation with the weight of each Environmental varable value (grey area)

OvAll_Canopy_FOP <- plotFOP(OvAllData, "Canopy3",# Make sure that the name of the raster file is the same that is given by R. The point between words replaces the space

                    ranging=TRUE, main="FOP for pangolin in regards to canopy height")# Verify the name of the species is correct

OvAll_Slope_FOP <- plotFOP(OvAllData, "Slope3",# Make sure that the name of the raster file is the same that is given by R. The point between words replaces the space

                    ranging=TRUE,main="FOP for pangolin in regards to slope")# Verify the name of the species is correct

OvAll_Elevation_FOP <- plotFOP(OvAllData, "Elevation3",# Make sure that the name of the raster file is the same that is given by R. The point between words replaces the space

                    ranging=TRUE,main="FOP for pangolin in regards to type of elevation") # Verify the name of the species is correct; as this is a categorical variable, grey bars show how much of each category exist in the study area, while dashed bars show the frequency of observed presence.

OvAll_Habitat_FOP <- plotFOP(OvAllData, "Habitat.Class3",# Make sure that the name of the raster file is the same that is given by R. The point between words replaces the space

                    ranging=TRUE,main="FOP for pangolin in regards to type of Habitat type") # Verify the name of the species is correct; as this is a categorical variable, grey bars show how much of each category exist in the study area, while dashed bars show the frequency of observed presence.

##Call the list of data where the plots came from

OvAll_Canopy_FOP

OvAll_Slope_FOP

OvAll_Elevation_FOP

OvAll_Habitat_FOP

?deriveVars
```

```
#### Create a series of transformations of each Environmental Variable to create Derivated
        Variables, using the Maxent algortihm


OvAllDataDVs <- deriveVars(OvAllData,#c("L", "M", "D", "HF", "HR", "T", "B")

        transformtype = c("L","M","D","HF","HR","T","B"),algorithm =
        "maxent",write=FALSE)# If you need to write the outcome, you should specify the
        directory using the function "dir=", and name add the name of a new folder

summary(OvAllDataDVs) #General summary of the outcome

summary(OvAllDataDVs$dvdata) #The list of environmental variables tested and the
        number of transformations for each one of them

summary(OvAllDataDVs$transformations) # List of transformations tested for each
        environmental variable


#### Visualize and compare the outcomes of the transformations using Chi square test

OvAllHSDVselect <- selectDVforEV(OvAllDataDVs$dvdata, test= c("Chisq"),

                    alpha = 0.001, algorithm = "maxent",quiet = TRUE, write=TRUE,


        dir="/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/Outcomes")#
        The outcome is saved as a series of .csv files (one for each variable)

                                        #within a sub- folder called "selectDVforEV" within
        a folder called "Outcomes+spp.name";

                                        #R will create the folder for you, in the directory
        you want and with the name you want.

                                        #Just make sure you have one "outcome" folder
        for each species.


summary(OvAllHSDVselect$dvdata)


### Identify the Enviionmental Variables that are determinant for the distribution of the target
        species

OvAllEVselect<-selectEV(OvAllHSDVselect$dvdata,alpha=0.001,

                algorithm ="maxent",interaction=TRUE,write=TRUE,


        dir="/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/Outcomes")#
        The outcome is saved as a unique .csv file
```

```
                                   #within a sub- folder called "selectEV" within a folder
        called "Outcomes+spp.name";

                                   #R will create the folder for you, in the directory you
        want and with the name you want.

                                   #Just make sure you have one "outcome" folder for
        each species.


summary(OvAllEVselect$dvdata)

OvAllEVselect$selectedmodel$formula#Here, you will get the formula to run the model


#plot(OvAllEVselect$selection$round, OvAllEVselect$selection$Dsq, xlab="Round",
        ylab="Dsq")


#### Create a new model for the species distribution using the relevant variables, using the
        Maxent algorithm

OvAllModel<-chooseModel(OvAllHSDVselect$dvdata,

                formula("~Canopy3 + Habitat.Class3"), #use the names of the raster files that
        were identified in the formula

                  algorithm = "maxent") # Make sure the name of the independent variables
        coincide with the names of the previous raster file


OvAllModel


##### Create plots of response of the occurrence in relation to the variable tested

plotResp(OvAllModel, OvAllDataDVs$transformations,"Habitat.Class3", main="Single effect
        response of pangolin's sleeping sites in regards to type of habitat")

plotResp(OvAllModel, OvAllDataDVs$transformations,"Canopy3",main="Single effect
        response of pangolin's sleeping sites in regards to type of canopy height")


#### Create a predictive raster for species distribution

OvAllEVfiles <-
        c(list.files("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/ContV"
        ,full.names=TRUE),
```

```
    list.files("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/CatV",full.names=TRUE)

)

EVstack <- raster::stack(OvAllEVfiles)

names(EVstack) <- gsub(".asc", "", basename(OvAllEVfiles))

OvAllPreds <- projectModel(model = OvAllModel,

                    transformations = OvAllDataDVs$transformations,

                    data = EVstack)

OvAllPreds


plot(log2(OvAllPreds$output + 1)) #Log2 transformation of the predictive values; This image gives you a much better visualization.




##### Export the predictive raster as .tif file


raster::writeRaster(log2(OvAllPreds$output+1),"/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/Pred_model.tif") #The file will be saved in the same folder taht was called at the begining of the script




##### Test the Area Under the Curve (AUC) to validate the model. Values under 2 are acceptable

OvAllPA <- readData(


    occurrence="/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/Locations.csv",

  contEV="/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/ContV",

  catEV="/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/CatV",

  PA = FALSE, XY = TRUE)
```

```
head(OvAllPA)

tail(OvAllPA)


presences <- OvAllPA[OvAllPA$RV==1, ]

points(presences$x, presences$y, pch = 20, cex = 0.5, col = 'red')


testAUC(model = OvAllModel, transformations = OvAllDataDVs$transformations,

       data = OvAllPA)


##### Transform the predictive raster in a .csv file with the probability of occurrence of the species in each pixel

Pred<-raster("/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/Pred_model.tif") #Call the .tif file created before

proj4string(Pred)<-CRS("+proj=utm +zone=50 +datum=WGS84 +units=m +no_defs +ellps=WGS84 +towgs84=0,0,0")

Pred

x<-rasterToPoints(Pred)

#x

write.csv(x,"/Users/sergioguerrero/Documents/Students/Elisa_Pangolins/New/Pred_model.csv") #A .csv file is created and saved in the same folder
```

Calculations for Fig. 4.13c

```
# Load libraries
library(dplyr)
library(ggplot2)

# Load your CSV
data <- read.csv("sleeping_sites_distance.csv")

# Inspect data
head(data)
str(data)

# Summary by site type
data %>%
  group_by(Type) %>%
  summarise(
```

```
    n = n(),
    mean_dist = mean(DistWater, na.rm = TRUE),
    sd_dist = sd(DistWater, na.rm = TRUE),
    median_dist = median(DistWater, na.rm = TRUE)
  )

# Boxplot for visualisation
ggplot(data, aes(x = Type, y = DistWater, fill = Type)) +
  geom_boxplot(alpha = 0.7) +
  theme_minimal() +
  labs(title = "Distance to Water: Sleeping vs Non-sleeping Sites",
       x = "Site Type", y = "Distance to Water (m)") +
  theme(legend.position = "none")

# T-test (if normal distribution assumption reasonable)
t_test_result <- t.test(DistWater ~ Type, data = data)
print(t_test_result)

# Non-parametric alternative: Wilcoxon test
wilcox_result <- wilcox.test(DistWater ~ Type, data = data)
print(wilcox_result)
```