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RESEARCH ARTICLE

Sundaic elephants prefer habitats on the periphery of protected areas

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Abstract

1. Protected areas (PAs) are a cornerstone of global conservation strategies. PAs, however, are not equally effective for all threatened taxa, and it is important to understand taxa-specific effectiveness of PAs networks.
2. In this study, we evaluate the role of the PAs network on the protection of Asian elephants *Elephas maximus* and their habitats in Southeast Asia's Sundaic region. Since Asian elephants tend to prefer secondary forests or forest gaps, we predicted that PAs would not represent the species preferred habitats. We conducted the most comprehensive analysis of Asian elephant space and habitat use to date through home range estimations and step selection function analyses using over 600,000 Global Positioning System locations from 102 different elephants from Peninsular Malaysia and Borneo.
3. Our results revealed important similarities in the habitat use of elephants in both regions, with both females and males in Peninsular Malaysia and Sabah preferring secondary forest, forest gaps and areas of regrowth and new plantations.
4. Our results supported our prediction that PAs do not represent Asian elephants' preferred habitats, since for most of the elephants, more than half of their ranges were outside PAs and the probability of selection values for both sexes in both geographical areas were lower inside than outside the PAs.
5. *Synthesis and applications*. Our analysis suggests that conservation strategies need to acknowledge that the long-term survival of Asian elephants in the Sundaic region relies on our capacity to promote human–elephant coexistence at the boundaries of PAs. We advocate that Asian elephant conservation

strategies should be based on the following three key points: (1) large PAs with core areas where elephants can find safety and potentially survive in the long term; (2) promoting connectivity among PAs using a system of wildlife corridors; and (3) effective human–elephant conflict management outside PAs.

KEYWORDS
boundaries, buffer, edge, *Elephas maximus*, probability of selection, protected areas, Southeast Asia, Sundaland

1 | INTRODUCTION

Protected areas (PAs) are a cornerstone of global conservation strategies for safeguarding biodiversity, ecological integrity and endangered species (Pacifici et al., 2020). The amount of land allocated as PAs or Other Effective Conservation Measures has grown to reach 16.8% of the global land surface in 2021 (UNEP-WCMC et al., 2021), and there are ongoing international negotiations to expand this coverage to 30% by 2030 under the Post-2020 Global Biodiversity Framework of the Convention of Biological Diversity (Xu et al., 2021). While crucial for the maintenance of global diversity and ecosystem services, this ambitious goal will not be equally effective for all threatened taxa (Tyrrell et al., 2020); hence, it is important to understand taxa-specific effectiveness of PAs networks.

PAs, however, are considered necessary but not sufficient to halt mammal population declines (Pacifici et al., 2020), and this is particularly true for wide-ranging taxa such as terrestrial megafauna (Ripple et al., 2016). Terrestrial megafauna often come into conflict with people in human-dominated landscapes outside PAs, and this is one of the main causes of mortality in such populations (Nyhus, 2016). Furthermore, terrestrial megafauna populations are unlikely to survive in small and isolated reserves alone, and do not always prefer the habitat provided by PAs because they are attracted to food resources provided by secondary forests or human-dominated landscapes (Evans et al., 2018; Volenec & Dobson, 2020). In this context, PAs borders may become attractive sinks for megafauna species, with important influence on their populations (Woodroffe & Ginsberg, 1998).

Most terrestrial megafauna have faced dramatic range contraction in historical times (Mahmood et al., 2021), with around 60% of the world's largest carnivores and herbivores classified as threatened with extinction based on the IUCN Red List (Ripple et al., 2014, 2015, 2016). This situation is particularly critical in the Sundaic region, a global hotspot for biodiversity (Myers et al., 2000) and threatened terrestrial megafauna (Ripple et al., 2016). Habitat loss is one of the major threats to megafauna conservation, and vast forest loss, fragmentation and degradation have taken place in the region in recent decades (Namkhan et al., 2021) because of logging, commodity-crop plantations (e.g. oil palm, rubber and lightwood), and smallholder agriculture (Hughes, 2017). It is estimated that ~50% of the region's original forest remains and less of 10% of it is formally protected (Hughes, 2017). One of the most iconic Sundaic species is the Asian Elephant *Elephas maximus*, the largest terrestrial animal in Asian ecosystems, where they play important and unique ecological functions (e.g. Campos-Arceiz & Blake, 2011).

Asian elephants were widely distributed throughout tropical Asia but are now endangered and live in highly fragmented landscapes (Williams et al., 2020). Three subspecies of Asian elephants occur in the Sundaic region: *E. m. indicus* in the Malay Peninsula, *E. m. borneensis* in northeast Borneo and *E. m. sumatranus* in Sumatra (Sharma et al., 2018). Due to their extensive spatial requirements and foraging behaviour, elephants use forest edges and human-dominated landscapes and, inevitably, come into conflict with people in the landscapes where they occur (de la Torre et al., 2021; Evans et al., 2020). Human–elephant conflict (HEC) is a grave conservation and social problem throughout the Asian elephant range (Shaffer et al., 2019). In this context, the Asian elephant is an appropriate model species for understanding the relevance of PAs and their borders for the conservation of endangered megafauna.

Furthermore, Asian elephants' responses to PAs and their habitats are likely to differ between sexes. Elephant males and females are highly dimorphic and exhibit sexually distinct behaviours (de la Torre et al., 2021; de Silva & Wittemyer, 2012). Females and their calves form matrilineal groups, a strategy likely to improve offspring survival through intra-group cooperation and by choosing habitats suitable for the infants. Males are usually solitary or form loose associations with other males or female herds (Vidya & Sukumar, 2005), and can embrace high-risk-high-gain foraging strategies which may have positive effects on their reproductive fitness but may result in conflict with people (Srinivasaiah et al., 2019; Sukumar & Gadgil, 1988). Understanding Asian elephant sex-specific responses to PAs is key to develop evidence-based strategies for elephant conservation and to reduce the burden of HECs for local communities. HEC incidents include crop raiding, property damage and attacks to people (de la Torre et al., 2021).

In this study, we evaluate the role of PAs on the protection of Asian elephants and their habitats in the Sundaic region. Since Asian elephants tend to prefer areas of disturbed vegetation such as forest gaps, secondary forests and other forms of early-succession vegetation (de la Torre et al., 2019; Evans et al., 2018), and since most of terrestrial PAs in this region encompass areas with mature forest, we predicted that PAs do not represent the species preferred habitats. Specifically, our objectives were to (1) assess elephants' space use within and outside the PAs, (2) evaluate elephant habitat preferences in PAs and at different distances from their borders, and (3) compare these preferences by sex and across two geographical areas in the Sundaic region, Peninsular Malaysia and the Malaysian state of Sabah in Borneo. With these analyses, we illustrate the importance of defining new conservation strategies for megafauna protection in disturbed human-dominated landscapes. Information provided by this study will contribute to understand the role of PAs and other land use and tenure systems for the conservation of elephants in the Sundaic region. Finally, we provide recommendations to wildlife managers and decision-makers on how to improve the protection and species' management at a regional scale.

2 | MATERIALS AND METHODS

2.1 | Study area

This study focused on two Asian elephant populations, one in Peninsular Malaysia and one in Sabah, Borneo. Elephants in Peninsular Malaysia occur within three Managed Elephant Ranges (MERs; Figure 1), covering an area of ~73,100 km^2 where wild elephants are expected to roam in the foreseeable future (PMDWNP, 2013). The estimated wild Asian elephant population in Peninsular Malaysia is ~1500 individuals (Saaban et al., 2011). The terrain in Peninsular Malaysia's MERs is hilly, with several mountain ranges in a north–south alignment and an altitudinal range from sea level to a maximum of 2187 m. The natural vegetation is dominated by lowland dipterocarp, hill dipterocarp and montane forest, and other land uses include cash crops, mainly oil palm and rubber plantations.

Sabah's elephants roam in three MERs which include the forested areas of central, southern and eastern Sabah (Figure 1). Elephant habitat in Borneo is largely represented by continuous and connected forest, although there are two important barriers, which isolate elephants in the Lower Kinabatangan Range (eastern Sabah) and Tabin Range (southern Sabah), both of which are surrounded by extensive oil palm plantations (Sabah Wildlife Department, 2020). Sabah's central block comprises less disturbed forest with rugged and hilly terrain with a maximum elevation range of ~2500 m a.s.l. Sabah's total elephant population is estimated to be not larger than 1000–1500 individuals (Sabah Wildlife Department, 2020).

Using the extents of the MER in both Peninsular Malaysia and Sabah, we extracted the areas that are formally protected according to the World Database of PAs (UNEP-WCMC, IUCN, 2021). In the case of Sabah, we included a buffer of 32 km around the MERs, since elephants roam outside these MERs. This distance threshold was established according to the radius of the home range areas exhibited by the elephants in Sabah. Peninsular Malaysia's MERs encompass 99 PAs of different protection categories, covering a total area of 15,897 km^2. Sabah's MERs encompass 113 PAs, with total extension of 12,218 km^2. It is important to note that the PA terminology is not consistent between Sabah and Peninsular Malaysia, with Forest Reserves encompassing different protection categories (details in Appendix S1). In our analysis, in both cases for Sabah and Peninsular Malaysia, we only used the Forest Reserves included in the World Database of PAs, which are the Forest Reserves of restricted use or for protection, and we excluded all the Forest Reserves that are exploited for logging or other kind of production (i.e. Commercial and Production Forest Reserves).

2.2 | Movement data

For Peninsular Malaysia, we used Global Positioning System (GPS) telemetry data of 47 elephants monitored between 2011 and 2018, including 16 resident (10 females and 6 males) and 31 translocated (6 females and 27 males) individuals with a total of 191,648 fixes. For Sabah, we used data of 55 elephants monitored between 2010 and 2020, including 35 resident (32 females and 3 males) and 20 translocated (5 females and 15 males) individuals with a total of 427,013 fixes. By 'translocated' we refer to elephants relocated from HEC areas to PAs; while 'resident' elephants were individuals sedated, collared and released at the same location within a few hours.

All animal handling was carried out in accordance with the current laws of Malaysia and the Standard Operation Procedures on Animal Capture, Anaesthesia and Welfare of the Peninsular Malaysia's Department of Wildlife and National Parks, and the Sabah Wildlife Department (see Appendix S2). Research and animal handling permits to collar elephants were granted either by Peninsular Malaysia's Department of Wildlife and National Parks (permit #JPHL%TN[IP]: 80-4/2) or by the Sabah Wildlife Department. Elephant captures and collaring operations were supervised by veterinarian officers from the relevant government departments. In both regions, we used Inmarsat and Iridium satellite GPS collars from Africa Wildlife Tracking, programmed to record a location every one (n = 19), two (n = 69) or four (n = 16) hours. We used the data from both translocated and non-translocated elephants in our analyses.

2.3 | Elephant home ranges inside and outside PAs

To evaluate the importance of PAs in relation to elephants' space use, we estimated their home ranges using the Kernel Density Estimator (KDE) at the 95% and 50% of the utilization distribution using ADEHABITATHR (Calenge, 2013) for R (R Core Team, 2022). We then calculated the percentage of each home range and core area (95% and 50% respectively) within PAs and compared these percentages between sexes and regions using a zero-inflated beta regression with GAMLSS in R (Stasinopoulos & Rigby, 2007).

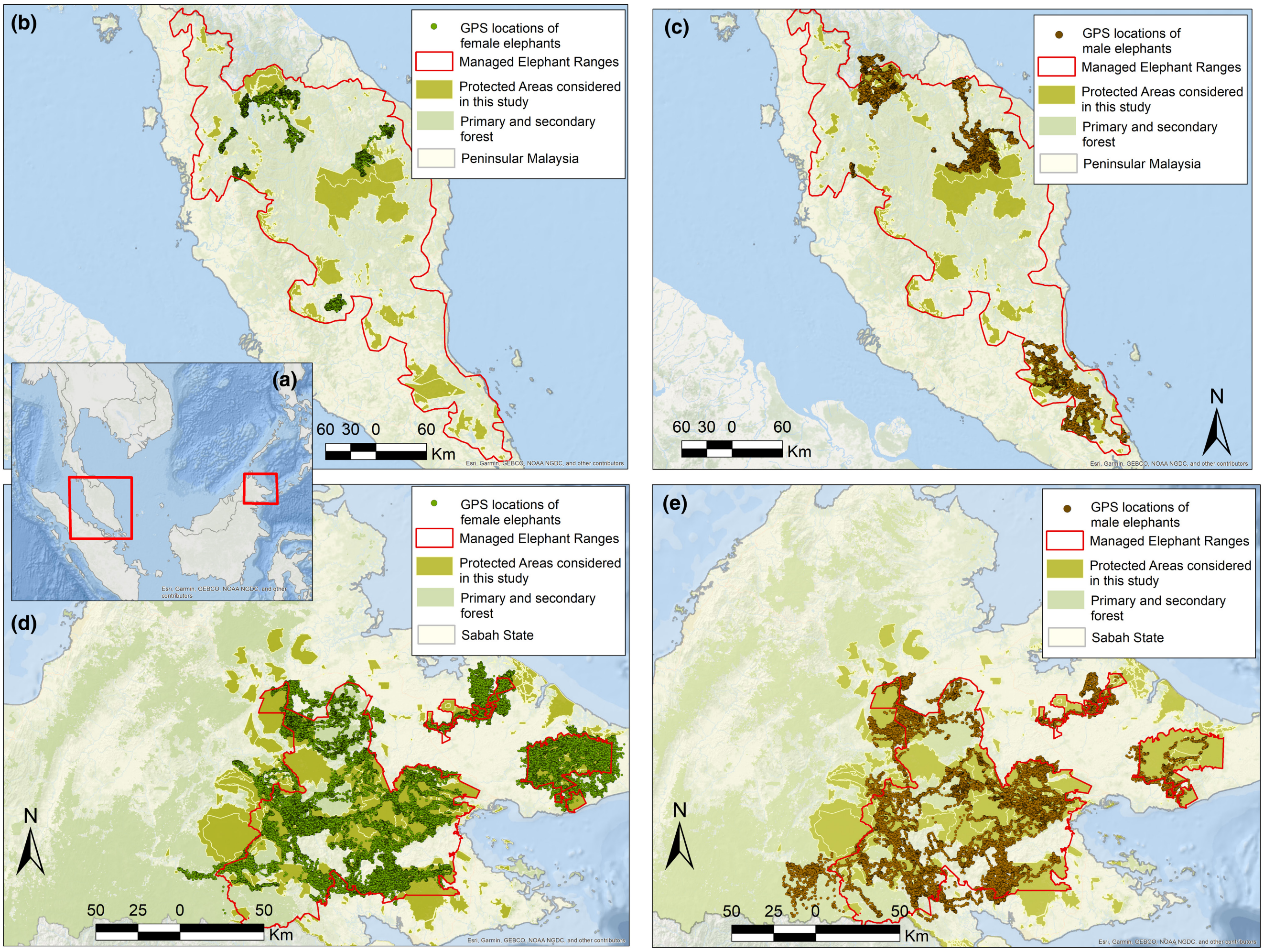

FIGURE 1 Study area in Peninsular Malaysia and Sabah, northern Borneo. (a) Red boxes indicate the location of Peninsular Malaysia and Sabah in South-East Asia. (b) and (c) include the complete extension of the managed elephant ranges (MERs), protected areas (PAs), and the Global Positioning System (GPS) locations of females and males, respectively, for Peninsular Malaysia. (d) and (e) include the complete extension of the MERs, PAs and the GPS locations of females and males, respectively, for Sabah

2.4 | Environmental covariates

We compiled a geospatial dataset which included variables associated with the land use (e.g. proportion of primary forest) and distance to forest and plantation (oil palm and rubber) boundaries, as well as terrain covariates (elevation and slope) (Table S1). We also included in this dataset the Tasselled Cap Wetness Index (hereafter 'wetness') that captures important information about the vegetation, forest structure and/or moisture content to evaluate if elephant habitat use is related to wetness and moisture content of the natural and cultivated vegetation. This covariate is a proxy of the forest quality, and its values reflect changes in vegetation structure. To evaluate the influence of anthropogenic activities, we used the mean of nightlight and distance to main roads covariates (see Table S1 for details, sources of, and treatments to the spatial covariates). All these explanatory variables were represented as raster layers at a 30 m resolution.

2.5 | Habitat preferences modelling

We evaluated elephant habitat preferences using step selection function (SSF) models (Thurfjell et al., 2014). We first reduced the potential effects of the capture and release of the translocated individuals by removing all the fixes obtained during the first 15 days of tracking for all the individuals. Since the tracked elephants were monitored using different fix acquisition schedules, we resampled the data to constant 4 ± 0.33 h intervals, and then we calculated the distance of each step between consecutive GPS fixes and filtered the data, retaining only steps that measured 50 m or more. This distance threshold was chosen to ensure that steps represent resource use and displacement behaviours of elephants (Zeller et al., 2016). Foraging-related movements in Asian elephants are characterized by short steps and tortuosity, while displacement-related movements are characterized by larger steps and more directionality (Fryxell et al., 2008; Troup et al., 2020; Vogel et al., 2020). We used a step length threshold of 50 m so the model considered crucial areas for foraging or resting, but also areas that are important for displacement. This threshold is long enough to avoid sequential locations within the same 30 m grid cells of our spatial covariates. We simulated 19 'available' steps for each 'used' step to have a proportion of 5% real versus 95% random steps. Given the large number of fixes per individual in our dataset, this ratio is enough for adequate parameter estimation (Thurfjell et al., 2014). Step lengths were drawn from the empirical movement data using a Gamma distribution with rate and shape parameters estimated from the empirical data. Turning angles also were drawn from the empirical data using a von Mises distribution. We used the package Animal Movement Tools 0.05.0 for R to generate the random steps (Signer et al., 2019).

For each used and available step, we calculated the values of the habitat covariates at the end point of the steps. We constructed several SSF models using a conditional logistic regression framework. We built the models using different combinations of habitat covariates, and then used the Akaike information criterion (AIC) to identify the best SSF model (Burnham & Anderson, 2002). We tested all explanatory variables for multicollinearity using the Pearson's correlation matrix, and we excluded variables in the same candidate model that were correlated at $r > 0.5$ (see Appendix S3). We selected the best-fitting models using AIC (Burnham & Anderson, 2002). These analyses were implemented using the MuMIn R package (Bartoń, 2019).

We built separate SSF models at the population level for females and males for Peninsular Malaysia and Sabah. The resulting probability of selection layer characterized each cell with continuous values between 0 and 1. To evaluate the model performance, we retained 10% of the GPS fixes from every elephant tracked before the implementation of any analysis. We performed a 10-fold cross-validation for the best models for female and male elephants, and we classified selection probabilities into 10 bins that ranged from 1 = low to 10 = high, as recommended by Johnson et al. (2006). We counted the number of fixes per bin to evaluate if we would find large number of fixes in the higher preference bins which were normalized by area. We quantified the predictive ability of the models using the concordance correlation coefficient (CCC; Lin, 1989; Zeller et al., 2016). Higher values of the square of the CCC statistic are indicative of a good model.

2.6 | Probability of selection and PAs

Using spatial data describing all PAs located within the area covered by the MERs in Peninsular Malaysia and Sabah, we calculated different buffer areas from the PAs' boundaries defined at different distances: 0–1, 1–3 and 3–5 km. Then, we calculated the mean probability of selection values within the PAs and within the different buffer areas for female and male elephants in Peninsular Malaysia and Sabah. Because the number of grid cells along the buffer areas were always lower than the number of grid cells within the PAs, we randomly sampled 3000 grid cells within these polygons to evaluate an identical number of grid cells for PAs and the buffer areas. To evaluate if the probability of selection was different between PAs and their associated buffers, we contrasted the sampled grid cells using the 95% confidence intervals of their mean probability of selection.

We analysed the differences in probability of selection between type of area, region and sex using a generalized linear model with a binomial distribution. We used probability of selection values (ranging from 0 to 1) randomly sampled as the response variable and the type of area (PA, 0–1, 1–3 and 3–5 km), the region (Peninsular Malaysia, Sabah) and sex as explanatory variables. We used a likelihood ratio test to evaluate the statistical significance of differences between models and constructed several models using a different combination of the predictor variables and used the AIC to select the best model (Burnham & Anderson, 2002).

3 | RESULTS

3.1 | Home ranges

Elephants in Peninsular Malaysia and Sabah had extensive home range areas (Figures S1 and S2). KDE home range sizes in Peninsular Malaysia were 329.1 ± 414.3 km^2 for females and 734.2 ± 702.8 km^2 for males (Table S2), while in Sabah they were 1585.6 ± 1219.2 km^2 for females and 2229.7 ± 2619.6 km^2 for males (Table S2). Home range size varied between regions, with Sabah's elephants using larger areas compared to those of Peninsular Malaysia ($t = 4.84$; $p < 0.01$). Most of the elephants had more than half of their home range and core areas outside PAs (mean = 62.1 and 65.0%, respectively), with only a few individuals having more than 75% of their home range or core areas within PAs (9.7% and 18.7%, respectively; Table S2; Figure S3). Sabah's elephants had a greater proportion of their home range within PAs compared to Peninsular Malaysia's ($t = 3.835$; $p < 0.001$), female elephants had a lesser proportion of their home range within PAs than males ($t = 3.453$; $p < 0.01$) and female elephants had a lesser proportion of their home range within PAs in Peninsular Malaysian than in Sabah ($t = -2.662$; $p < 0.01$).

3.2 | Habitat use

The SSF models revealed important similarities in the habitat use of elephants in Peninsular Malaysia and Sabah (Table S3; Figure 2). Overall, both females and males in Peninsular Malaysia and Sabah preferred secondary forest, forest gaps, and areas of regrowth and new plantations. This was revealed by the strong effect of the quadratic term of wetness (wetness^2), which indicates that elephants preferred intermediate values of forest openness, and the positive effect of percentage of regrowth and new plantations. Furthermore,

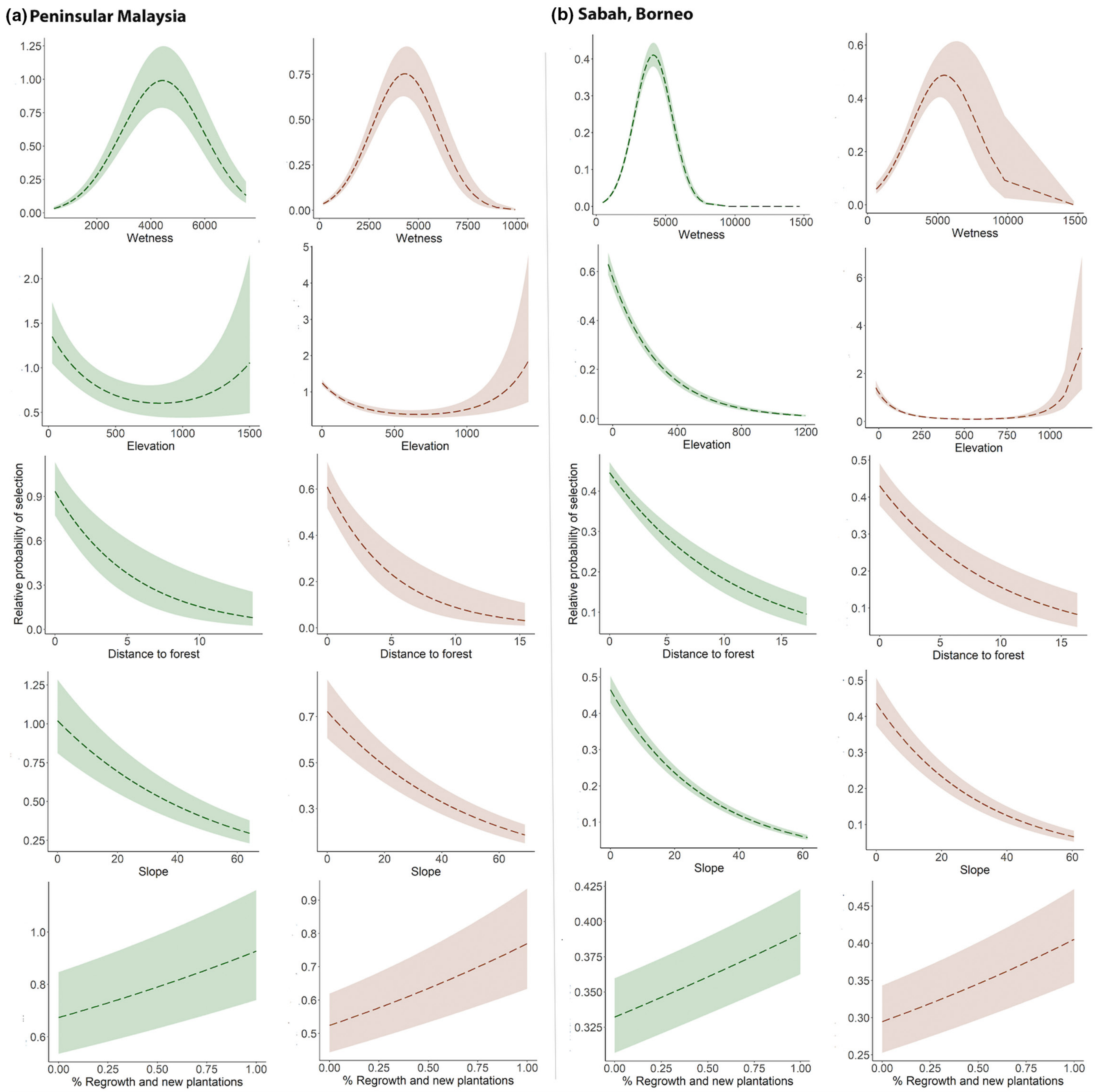

FIGURE 2 Marginal plots with the relationship between the predicted relative probability of selection and the covariates that best explained the habitat preferences of female (green) and male (brown) elephants of (a) Peninsular Malaysia and (b) Sabah

elephants in both areas preferred open vegetation but always close to forest, as indicated by the negative effect of distance to forest. In both areas, elephants also preferred lowland areas (elevation) and avoided areas with steep and rugged terrain (slope). The quadratic term of elevation (elevation^2), however, indicates that elephants also preferred higher areas in the mountain ranges, such as ridges, and this relationship was stronger for males both in Peninsular Malaysia and Sabah. Elephants had a complex response to plantations, being attracted to the proximity of plantations (distance to plantations) but also avoiding areas with high plantation coverage (proportion of large-scale oil palm plantations). An exception to this were elephant males in Sabah, who seemed to be more tolerant to high plantation coverage (Table S3).

3.3 | Probability of selection models

The probability of selection models performed generally well. The CCC of females' and males' probability of selection models was 0.98 and 0.99 in Peninsular Malaysia, and 0.99 and 0.91 in Sabah, respectively, indicating that our models have high potential for predicting the habitat use of elephants in both areas (Figure 3).

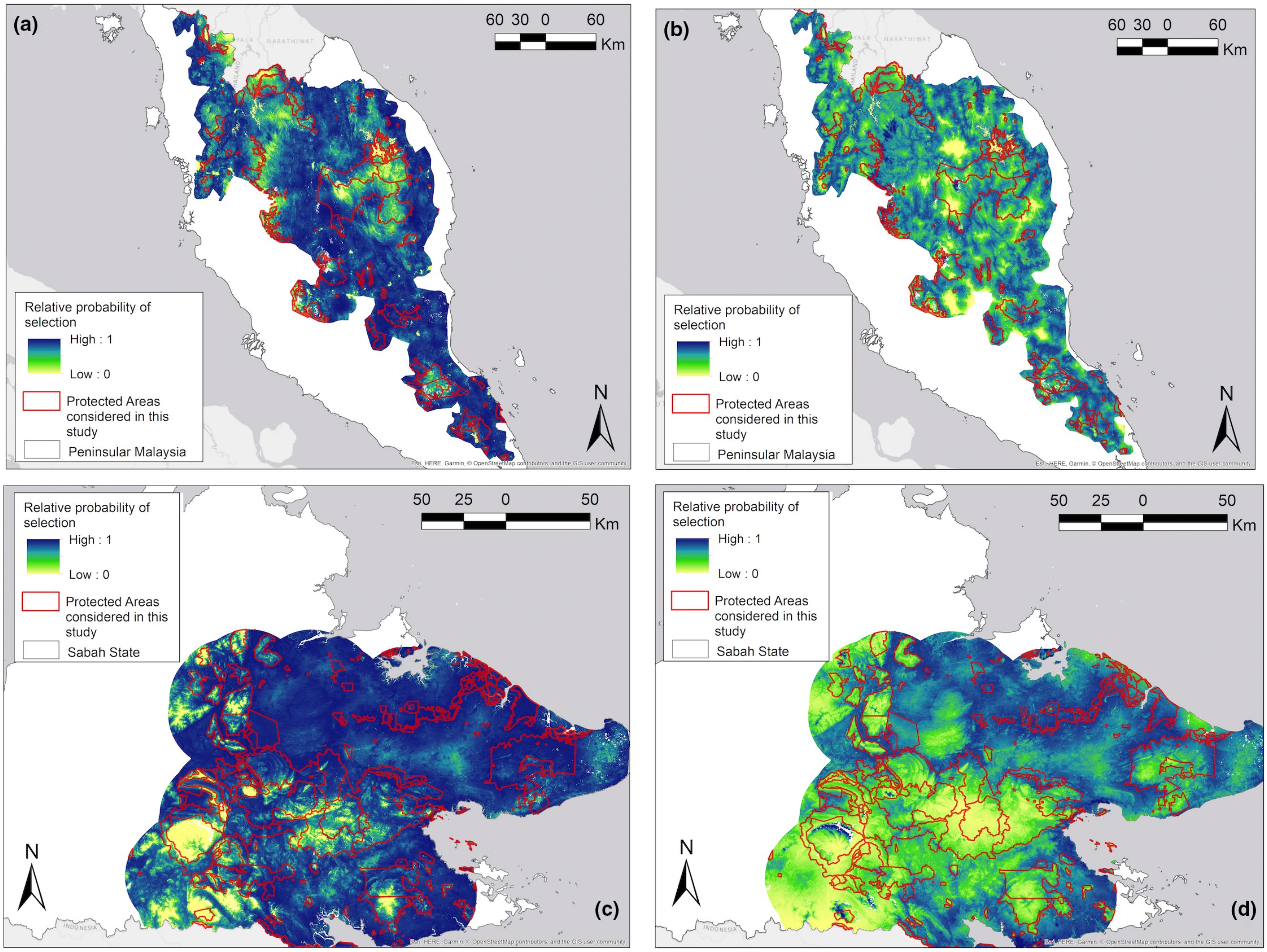

FIGURE 3 Habitat preference maps of Asian elephants and protected areas (PAs): (a) females and (b) males in Peninsular Malaysia and (c) females and (d) males in Sabah

TABLE 1 Results of the generalized linear models used to analyse the differences in probability of selection between regions (Peninsular Malaysia, Sabah), type of area (protected area [PA], 0–1, 1–3 and 3–5 km) and sexes

Models	df	Log-likelihood	AICc	Delta AIC	Weight
PA Buffer + Region + Sex + Region:Sex	7	−74,794.9	149,603.7	0	1
PA Buffer + Region + Sex + PA Buffer:Sex	9	−75,604.9	151,227.7	1624.0	0
PA Buffer + Region + Sex	6	−75,652.7	151,317.5	1713.8	0
PA Buffer + Region	5	−78,161.3	156,332.5	6728.8	0
Region	2	−81,390.6	162,785.3	13,181.5	0
Null Model	1	−82,281.2	164,564.4	14,960.6	0

3.4 | Probability of selection in relation to PAs

There were differences in probability of selection between the different conservation land types, and these differences varied by region and sex (Table 1, Table S4). AIC values of our cumulative generalized linear model indicated significant differences in probability of selection between land types, sexes and regions. The best model included the interaction of region and sex (Table 1). However, in both Peninsular Malaysia and Sabah, probability of selection for females and males showed the lowest values within PAs, and it improved as the distance from PA boundaries increased (Figure 4; Table S4). According to the probability of selection maps, the areas most preferred by elephants were within 1–3 km away from the PA boundaries (Figure S4). In almost all cases, female elephants showed higher mean probability of selection than males for the PAs and the different buffer areas.

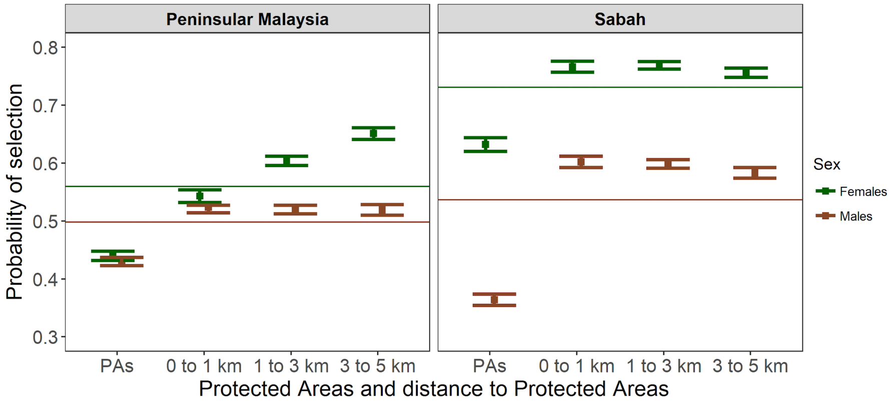

FIGURE 4 Probability of selection of Asian elephants in different land use areas in Peninsular Malaysia and Sabah. Error bars represent 95% confidence intervals

4 | DISCUSSION

We conducted the most comprehensive analysis of Asian elephant movements and habitat use to date, using over 600,000 GPS locations from 102 different elephants belonging to two different subspecies (*E. m. indicus* and *E. m. borneensis*) in two distinct biogeographical units of Southeast Asia's Sundaic region. We analysed Asian elephant space use and habitat preference in PAs and near their boundaries and found that most of the elephants tracked had more than half of their home range and core areas outside PAs and that elephants generally favoured habitats outside PAs, rather than inside.

Elephants in both regions exhibited extensive home ranges, frequently moving outside PAs. Female elephants, especially in Peninsular Malaysia, showed a smaller proportion of their home ranges within PAs, indicating the importance of PA buffers to maintain the spatial requirements of female groups in the region. Furthermore, Asian elephants in our sample showed clear and consistent habitat preferences. They preferred secondary forest, forest gaps and areas of regrowth and new plantations, never far from forest, as well as lowland terrains, and avoiding steep and rugged areas (Figure 2). These results are consistent with previous studies in Southeast Asia, which found that Asian elephants prefer habitats with somewhat disturbed vegetation, including human-dominated landscapes (Evans et al., 2018, 2020 for *E. m. borneensis*; Wadey et al., 2018, de la Torre et al., 2019, 2021 for *E. m. indicus*; and Wilson et al., 2020 for *E. m. sumatranus*). Asian elephants' preference for disturbed environments and human-dominated landscapes is related to their food habits, with a clear preference for monocots (e.g. palms, grasses, bamboo, gingers) and fast-growing early succession trees (English et al., 2014) that are common in disturbed environments, but relatively scarce under the canopy of old-growth Sundaic forests (Terborgh et al., 2018). Our results also showed that elephants prefer forest edges, since the probability of selection decreased as distance to forest increased. Forested areas could provide refuge to elephants while they are close to regrowth or plantations.

Our results supported the prediction that PAs do not represent Asian elephants' preferred habitats in the Sundaic region. We should note, however, that in our dataset we only used the Forest Reserves included in the Word Database of PAs, which are Forest Reserves of restricted use or for protection, excluding all the Forest Reserves that are exploited for logging or other kind of production. In both Peninsular Malaysia and Central Sabah, exploited Forest Reserves are generally located on the periphery of the restricted use PAs, and our results indicate that elephants are selecting and benefiting from those areas. PAs in Peninsular Malaysia (e.g. Royal Belum State Park and Taman Negara National Park) are dominated by mature dipterocarp forests and often surrounded by selectively logged Forest Reserves and mixed-use landscapes (PMDWNP, 2013). On the other hand, the Central Sabah MER, where the largest subpopulation of Bornean elephants occurs, consists of a mosaic of commercial Forest Reserves exploited for timber under sustainable practices (Class II according to the Sabah Forestry Department classification), fully protected Class I Forest Reserves, and Conservation Areas (Danum Valley, Imbak Canyon and Maliau Basin; Sabah Wildlife Department, 2020).

Nevertheless, we found some differences between Peninsular Malaysia and Sabah, and this indicates that habitat preferences for elephants are complex and mediated by the local context (i.e. landscape configuration, history and forest structure). The two other main PAs in our dataset in Sabah present a different picture from Central Sabah and Peninsular Malaysia. Tabin Wildlife Reserve is a relatively disturbed forest that was logged from the mid-1960s until 1989, and only the core area was spared from logging (Sale, 1994). The Lower Kinabatangan Wildlife Sanctuary is a very narrow band of old-growth forest along the Kinabatangan River, where alluvial disturbances and grasslands are common (Sabah Wildlife Department, 2020). Both Tabin and Kinabatangan showed higher probability of selection values than other PAs in Central Sabah and Peninsular Malaysia probably because they are at lower altitude, are highly fragmented and isolated and have harder borders (sometimes protected by electric fences) with the extensive oil palm plantations surrounding them. Our results underscore the importance of history and local context on PAs' functionality.

Probability of selection values were generally higher for females than males in all land types, especially in Sabah (Figure 4). This result is probably due to the more extreme values of probability of selection for male elephants in the higher altitude forests or in sites near crop areas with more human activities, compared with the more homogeneous values for females throughout the landscape. Such consistent differences in probability of selection are counterintuitive and can be attributed to sexual differences in social behaviour and anatomy, that make male Asian elephants more tolerant of both food-poor and high-risk habitats (Figure S5). Female Asian elephants form matrilineal social groups (Vidya & Sukumar, 2005), which constrains their choice of habitats to those with sufficient food resources to feed the whole group, while making them avoid areas that present high risks to infants (Vidya & Sukumar, 2005). Males, on the other hand, tend to be solitary or move in loosely associated bachelor groups (Srinivasaiah et al., 2019) and these solitary habits, together with the Jarman–Bell principle (Bell, 1971; Jarman, 1968)—that states that larger mammal herbivores can survive with lower quality food—means that males can persist in marginal (food poor) habitats where female groups would not find enough food to subsist. In addition, males are more willing to risk getting close to people in exchange of high-quality food (crops), as this gives them a competitive advantage over other males (Srinivasaiah et al., 2019; Sukumar & Gadgil, 1988). Additionally, in our dataset, translocation was more prevalent among males than among females. Translocated elephants often leave the release site and use larger home ranges than resident individuals (Fernando et al., 2012), and this means that they use a wider range of values for the different habitat covariates evaluated than females, hence, skewing the models towards lower values of probability of selection. For these reasons, male elephants can use a much broader range of habitats than females, including much less optimal habitats.

We acknowledge that combining data of resident and translocated individuals could bias our habitat selection analyses. However, in both regions, a large number of elephants have been translocated in recent decades; only in Peninsular Malaysia more than 600 elephants have been translocated out of a population of approximately 1500 (~40% of the entire estimated population; Saaban et al., 2011). Hence, our dataset would represent a sample of the current status of the study populations. Another caveat is that some landscape covariates did not match the exact timing when the movement data were collected, despite our best efforts to match the time of both datasets (Table S1). Furthermore, our habitat selection did not show strong effects of covariates related to human disturbance, perhaps because these factors do not affect elephant habitat selection of elephants at the scale we used. In future analysis, it is crucial to understand how landscape transformation affects elephant range at coarser scale (Wall et al., 2021).

Our findings on elephant habitat preferences in different land types (inside vs. outside the PAs) have important implications for conservation planners and practitioners. Sharing landscapes with elephants can be very costly for local communities (Gulati et al., 2021) and many people do not want to have elephants 'in their backyards' (e.g. Tan et al., 2020). In this context, conservation planners and practitioners will often be inclined to rely on conservation within restricted use PAs as the main Asian elephant conservation strategy. As shown here, however, elephants are likely to prefer habitats outside PAs, including exploited Forests Reserves, compromising the effectiveness of conservation strategies based on PAs alone. These strategies need to acknowledge that Asian elephants will tend to move outside PA boundaries and towards more disturbed landscapes (Fernando et al., 2008; Leimgruber et al., 2003) and avoid PA cores, especially when these are primary rainforests.

Does it mean that PAs are not important for Asian elephant conservation in Southeast Asia? No, by any means. We do advocate for PAs as the core basis for Asian elephant conservation, since the safety they provide (even if food resources are not as abundant as in surrounding landscapes) is key. We advocate for Asian elephant conservation strategies that are based around three key points. First, large PAs and commercial forest reserves are necessary as core areas where elephants can find safety and potentially survive in the long term. Second, since many PAs in tropical Asia are small, it is important to promote connectivity among them by systems of ecological corridors, where connectivity is protected (e.g. de la Torre et al., 2019; Evans et al., 2020). And third, since elephants prefer habitats outside PAs, they will either temporarily exit or permanently live outside PAs. In many circumstances, the highest elephant densities will be found in human-dominated landscapes, often in the surroundings of PAs and corridors, sometimes even around plantations, where elephants can access high-quality food from early succession vegetation and crops (de la Torre et al., 2021). Effective HEC management and fostering coexistence outside PAs, especially in human-dominated landscapes such as plantations and village areas, is therefore the third pillar of these conservation strategies. Habitat restoration and enrichment, for example, planting native grass species in degraded areas or promoting forest gaps and small-scale disturbances, can increase habitat quality for elephants and other large herbivores within PAs and other areas where their presence is considered desirable.

Much progress has been made in recent years to understand the spatial ecology of Sundaic elephants due to the use of GPS telemetry, remote sensing and GIS tools (e.g. de la Torre et al., 2019, 2021; Evans et al., 2018, 2020; Wadey et al., 2018; Wilson et al., 2020). These studies provide consistent results, providing an opportunity for evidence-based conservation strategies, in a way that was not possible just one decade ago. Overall, this body of work is showing that elephants are ecological generalists with preference for somewhat disturbed forests, whose long-term survival in the region relies on our capacity to promote human–elephant coexistence in human-dominated landscapes, particularly around the boundaries of PAs, as this study has shown.

AUTHOR CONTRIBUTIONS

J. Antonio de la Torre, Alex M. Lechner, Benoit Goossens and Ahimsa Campos-Arceiz conceptualized and designed the study. J. Antonio de la Torre analysed the data and wrote the first draft. Benoit Goossens and Ahimsa Campos-Arceiz made major edits and directed the revisions. J. Antonio de la Torre, Cheryl Cheah, Alex M. Lechner, Ee Phin Wong, Augustine Tuuga, Salman Saaban, Benoit Goossens and Ahimsa Campos-Arceiz contributed to the data collection and reviewed the manuscript critically.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Elephant movement data are not publicly available due to concerns related to animal poaching but will be available upon request to the corresponding authors and upon agreement from Peninsular Malaysia's Department of Wildlife and National Parks, Sabah Wildlife Department and WWF Malaysia. Other data (shapefiles of environmental covariates, protected areas, and elephant home ranges and probabilities of habitat selection) are available via the Dryad Digital Repository http://doi.org/10.5061/dryad.sj3tx967x (de la Torre et al., 2022).

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