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Factors influencing the habitat suitability of wild Asian elephants and their implications for human–elephant conflict in Myanmar

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A R T I C L E I N F O

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A B S T R A C T

Anthropogenic disturbances are key factors affecting the distribution and ranging behaviour of wild elephants. Such disturbances exaggerate threats to the survival and population decline of wild elephants, and they have negative consequences for the livelihood of local people. We aimed to identify which factors influence the spatial movement, distribution, and suitable habitats of wild Asian elephants, to examine the relationship between elephant habitat use and human–elephant conflict (HEC) incidents, and to explore whether HEC is caused by habitats preferred by elephants or by human predictors. We used presence-only data from 25 GPS-collared elephants from the southern Rakhine State, Ayeyawady, and Yangon-Bago Regions of Myanmar. Maxent modelling was applied to identify suitable habitats for wild elephants and Manly's selection ratio was calculated to find the most utilised habitats by elephants. The generalized linear mixed models (GLMM) were fitted to explore the most liable factors for HEC. The study identified 11,524 km^2 of suitable habitat for wild elephants in southwest Myanmar. Results indicated that elevation, distance to water sources, and mean annual precipitation contribute most to the distribution and suitability of wild elephant habitats. Disturbed and degraded forests were highly utilised by elephants. Elephants in less suitable habitats exhibited more aggressive behaviour leading to intense HEC. This suggests that human encroachment into elephant habitats has intensified HEC. We recommend that areas, where larger croplands exist at the lower altitudes near degraded forests and/or water bodies, should be prioritized to monitor and minimize HEC. Elephant habitats in forested areas should be restored and replenished, with water holes and suitable plants provided for the most severely degraded habitats.

1. Introduction

Habitat loss, fragmentation, and poaching are often cited as the main threats to the survival of wild Asian elephants (*Elephas maximus*), resulting in intense human–elephant conflict (HEC) (Leimgruber et al., 2003; Leimgruber et al., 2011; Sukumar, 2003). HEC refers to any unfavourable interaction between humans and elephants that causes harm to human lives, the economy, property, and

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safety, as well as harming elephant conservation (Dublin and Hoare, 2004; Parker et al., 2007). Increased expansion of agricultural land, mineral mining, infrastructure development, forest resource utilization, logging, and plantation establishment are the main factors responsible for deforestation and degradation of forests (Bhagwat et al., 2017; Leimgruber et al., 2005; Yang et al., 2019). These anthropogenic disturbances cause elephant habitats to be degraded, fragmented, and lost (Leimgruber et al., 2011). If habitats become fragmented, the availability of resources will decline. The increasing presence and activity of humans may be as much a factor explaining increased HEC as the wider-ranging behaviour of elephants in degraded lands (Alfred et al., 2012), where animals in resource-poor habitats will need wider home ranges (Teitelbaum et al., 2015) and longer migrations to meet the forage requirement (Tucker et al., 2018). Such confrontations are causing the mortality of both elephants and humans (Lenin and Sukumar, 2011).

Studies on habitat suitability become widespread in the Asian elephant range countries to better understand the distribution of wild elephants for sustainable conservation and HEC mitigation (for example, Sharma et al., 2020; Taher et al., 2021; Talukdar et al., 2020). Except for the central dry zone area, wild elephants are widely distributed throughout Myanmar, providing a total suitable habitat of 170,000 km^2 in the country (Leimgruber et al., 2003). The average home range size of wild elephants ranges from 184 to 792 km^2 with a mean daily travel distance of 3.9 km in Myanmar (Chan et al., 2022). However, 9.4% of forest cover in Myanmar has been extensively lost or transformed into other land use over the last 20 years (FAO, 2020). Compared to available habitats, the density of wild elephant populations has been relatively low, and the population has declined from 10,000 in 1935 to less than 2000 individuals in 2004 in Myanmar (Leimgruber et al., 2011; Leimgruber et al., 2008). Elephant research in Myanmar has mainly been concentrated on habitat fragmentation (Leimgruber et al., 2003), movement ecology (Chan et al., 2022), HEC (Thant et al., 2021), poaching (Sampson et al., 2018), as well as local attitudes towards elephants and their relation to conservation (Sampson et al., 2019; Thant et al., 2022). However, studies on ecology and habitat suitability for wild elephants have been limited in Myanmar, especially related to habitat factors linked with HEC. It is vital to understand how wild elephants are distributed in the landscape and which habitats are most suitable for elephants in order to prioritize conservation and minimize HEC.

Maximum entropy modelling (Maxent) has been a widely used method for species distribution modelling and predictions of suitable habitats for wildlife (Elith et al., 2011; Merow et al., 2013; Phillips et al., 2006; Phillips et al., 2021). Based on predictions of habitat suitability for wild elephants by Maxent modelling, we aimed to study which factors most influence the spatial distribution and suitable habitats of wild Asian elephants in southwest Myanmar, to explore the association between elephant's habitat preference, and the occurrence of HEC. Finally, we tested whether HEC is largely caused by habitats preferred by elephants or by human predictors.

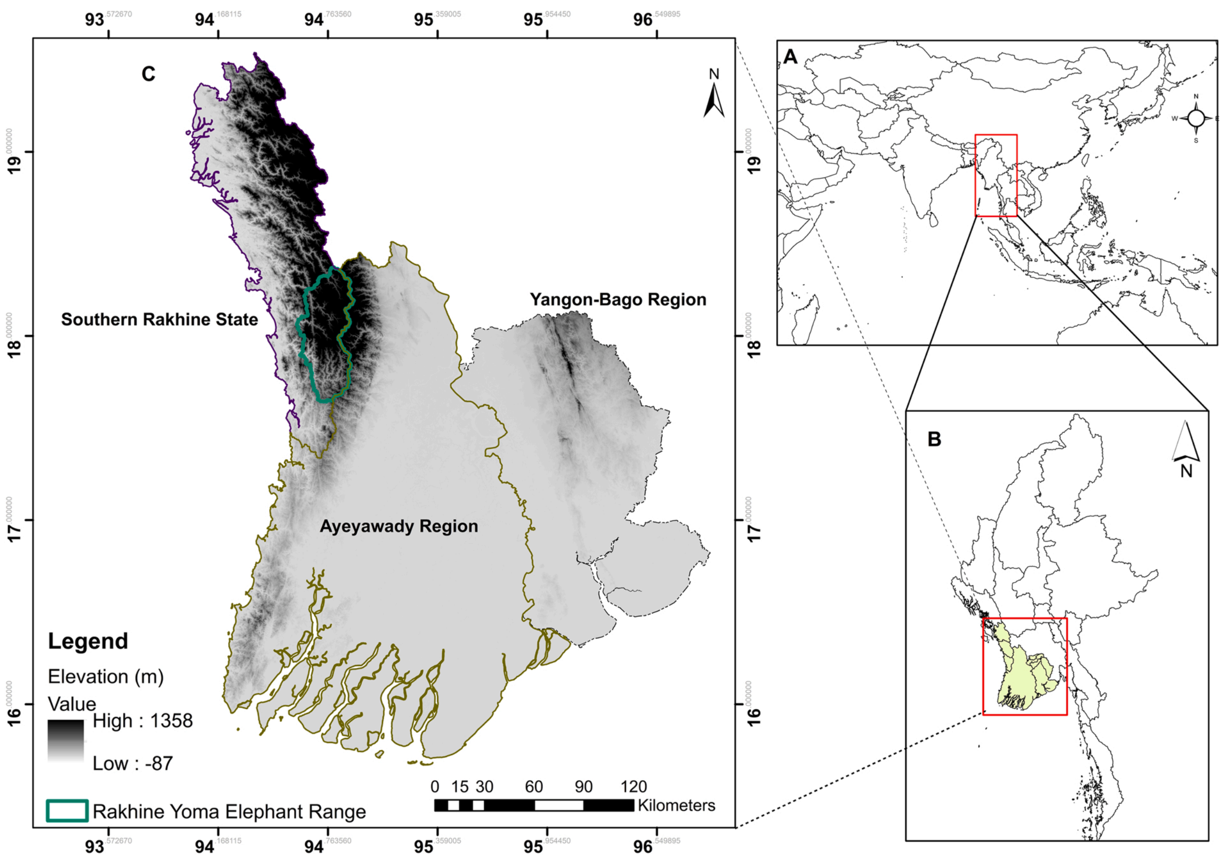

Fig. 1. A map showing the location of Myanmar in the continent of Asia (**1-A**), location of the study area in Myanmar (**1-B**), and the extent of the study area showing different altitudes (**1-C**).

2. Methodology

2.1. Description of the study area

This study was carried out in the south-western part of Myanmar, extending over an area of 60,000 km^2 encompassing southern Rakhine State, Ayeyawady Region and Yangon-Bago Region (Fig. 1). The average annual precipitation in this region (2009–2018) is 3573 mm (SE ± 485), and the average minimum and maximum temperatures (2009–2018) are 21.6°C and 33°C (MOPF, 2019). Within this study area, the western coast and mid-eastern part are covered by semi- and evergreen forests, fragmented mixed deciduous forests, and bamboo. These areas are home for wildlife including wild Asian elephants and are also heavily used by local people for their livelihoods. The extent of forest reserve areas includes about 12,244 km^2 in the study area. The central lowland area is almost completely dominated by agricultural crops and few wildlife species persist there (Fig. 1).

2.2. Presence-only data of GPS collared elephants and environmental predictors

We used GPS collaring data of 25 wild elephants fitted between 2015 and 2020. Iridium satellite GPS collars were fitted on 13 elephants in Yangon and Bago, eight elephants in Ayeyawady (Chan et al., 2022) whereas Inmarsat satellite collars were used on four elephants in the southern Rakhine region. The initial collaring dataset included a total of 117,319 GPS location points of elephant movements.

We included ten different environmental predictors with their explanation and sources presented in Table 1. These environmental predictors fell within four categories: 1) topographic variables including elevation, terrain ruggedness index (TRI), and distance to

Table 1
Explanation and sources of the environmental predictors used in the Maxent model.

Variables	Resolution	Explanation	Sources
Topographic variables			
Elevation	30 m	Digital Elevation Model (DEM) derived from SRTM (Shuttle Radar Topography Mission) was used.	https://portal.opentopography.org/ (SRTM, 2013)
Terrain ruggedness Index (TRI)	30 m	Terrain ruggedness index (TRI) was calculated from DEM 30 m (SRTM) using Arc Hydro Tools in ArcGIS 10.8.1. TRI is used to measure the topographic heterogeneity of the landscapes.	https://portal.opentopography.org/ (SRTM, 2013)
Distance to river/ stream (River)	Vector	The river/stream shape file was extracted from the OpenStreetMap and calculated the distance in kilometer using Euclidean Distance tool in ArcGIS 10.8.1.	http://download.geofabrik.de/asia.html (Planet OpenStreetMap)
Climatic variables			
Mean Annual Precipitation (MAP)	~1 km	Mean annual precipitation (MAP) was downloaded from the WorldClim. website.	https://www.worldclim.org/data/worldclim21.html (Fick and Hijmans, 2017)
Mean Annual Temperature (MAT)	~1 km	Mean annual temperature (MAT) was downloaded from the WorldClim. website.	https://www.worldclim.org/data/worldclim21.html (Fick and Hijmans, 2017)
Vegetation variables			
Land-use/land-cover (LULC)	30 m	LULC stands for land use and land cover, where the former is used to identify how land is used, such as for human settlements, cultivation, etc., whereas the latter is used to quantify what covers the surface of the land, such as forests, water bodies, grasslands, etc. It was derived from the land use land cover dataset from Myanmar National Land Portal. Twelve different categories of LULC were identified in the dataset.	https://www.landcovermapping.org/en/myanmar-national-portal/ (Saah et al., 2020)
Normalized Difference Vegetation Index (NDVI)	250 m	NDVI is measured to indicate the greenness of the vegetation displaying vegetation dynamics. The MODIS (Moderate Resolution Imaging Spectroradiometer) 10-days composited dataset for NDVI was derived from the Earth Resources Observation and Science (EROS) Center. We only used five monthly NDVI images for 2019 because of cloud free available images. Then, we calculated the average NDVI for the study area.	https://earthexplorer.usgs.gov/ Data available from the U.S. Geological Survey
Anthropogenic variables			
Human footprint (HFP)	~1 km	The human footprint map measures the cumulative impact of anthropogenic activities. This dataset used the 2009 global dataset and released in 2018. It includes eight inputs: 1) the extent of man-made land features, 2) crop cultivation area, 3) grazing land, 4) density of human population, 5) nightlights, 6) railroads, 7) roads, and 8) waterways.	https://urs.earthdata.nasa.gov/ (Venter et al., 2016)
Distance to road (Road)	Vector	Distance to road was calculated in kilometer from the road shape file of OpenStreetMap using the Euclidean Distance tool in ArcGIS 10.8.1.	http://download.geofabrik.de/asia.html (Planet OpenStreetMap)
Distance to water sources (Water)	Vector	Distance to water or dam/reservoir was calculated in kilometer from water points' shape file of OpenStreetMap using the Euclidean Distance tool in ArcGIS 10.8.1.	http://download.geofabrik.de/asia.html (Planet OpenStreetMap)

river (River); 2) climatic variables including mean annual precipitation (MAP), and mean annual temperature (MAT); 3) vegetation variables including land-use/land-cover (LULC) and normalized different vegetation index (NDVI); and 4) anthropogenic variables including human footprint (HFP), distance to road (Road), and distance to water source (Water). All environmental variables were resampled and resized into the same geographic coordinate system (World Geodetic System 1984 - WGS 1984), spatial resolution (30 m), and extent. All GIS data preparation was performed using ArcGIS 10.8.1.

2.3. HEC data

We used HEC data from Thant et al. (2021, 2022) to compare elephant use of habitats relative to different levels of conflicts. They collected data for HEC and local attitudes towards elephant conservation. We extracted four conflict types (crop damage, property damage, elephant attacks, and overall HEC), human predictors ((education; no formal education, primary school, and secondary education and above), (size of farmland; no farmland, <2 ha, 2–4 ha, >4 ha), (distance to the forest; <1 km, 1–4 km, 4–10 km, >10 km), (residency; non-native, native)) and elephant predictors (elephant behaviour; do not know, no problem at all, clam, aggressive) from the above sources (Thant et al., 2021, 2022). These four types of conflict data were aggregated by village into the proportion of respondents who encountered conflicts. All individual responses in a village were converted into a village level (sampling unit level), allowing us to compare habitat suitability level with HEC for each sampled village. The same method was thereafter applied on human predictors, viz. the proportion (between 0 and 1) of the respondents who had no formal education, the proportion with farmland size (>4 ha), the proportion living 1–4 km from the forest reserves, and the proportion who were non-native respondents. Finally, the proportion of elephant aggressiveness predictors was calculated from the respondents' answers that elephants they encountered were aggressive (Thant et al., 2021, 2022).

2.4. Modelling of habitat suitability and other statistical analyses

We used Maxent software for Species Distribution Modelling Version 3.4.4, to analyse habitat suitability, allowing us to utilise "presence-only data" recorded by elephant GPS collars (Phillips et al., 2021). Data processing and preparation for the Maxent model were implemented in R Version 4.1.0 (R Core Team, 2021) and ArcGIS. To minimize spatial autocorrelation we applied spatial filtering, selecting one GPS location per 4 km^2 grid cell using the raster function in the raster package (Hijmans, 2021) and the elimCellDups function in the enmSdm package (Smith, 2021). Geographical thinning of relocation data render better predictions of the species distribution and reduce the effects of sampling bias in the modelling (Boria et al., 2014; Varela et al., 2014). After the initial data were trimmed, 924 remaining locations were included in the final Maxent modelling.

Before running the Maxent model, we examined correlations among the environmental predictors. Merow et al. (2013) suggested to minimize the correlation among the predictors for Maxent modelling. Because of the non-normal distribution of these predictors, Spearman rank correlations were calculated using the rstatix package (0.7.0) (Kassambara, 2021). In addition, we calculated the Variance Inflation Factor (VIF) to check multicollinearity among the environmental predictors with the usdm package (Naimi et al., 2014). The model with the highest correlated variables and collinearity, statistically affected its performance and variables more than 0.7 (Spearman's rho) were assumed as the highest correlated variables. The variables with a VIF threshold more than 10 were collinear (Belsley, 1991; Dormann et al., 2013; Hair et al., 1995; Montgomery and Peck, 1992). Mean annual temperature (MAT) had the highest correlation (Table 2) and collinearity with other predictors. After MAT was excluded, there was no collinearity identified (Table S1). The description of the remaining nine environmental predictors analysed can be seen in Figure S1.

In the Maxent modelling, the output format was set up as a logistic type as it can generate an estimate of probability of species presence (Elith et al., 2011). The selection of features included linear, quadratic and hinge (Kitratporn and Takeuchi, 2020). Regularization multiplier and background points were set up with default setting 1, and we randomly selected 10,000 points. We fitted 10-fold cross validation to generate a more robust estimate of the Maxent model (Glover-Kapfer, 2015). Although the default number in Maxent was 500 iterations, we used 5000 for maximum iterations to avoid over/under prediction of the model. The evaluation of the habitat suitability model was assessed by two approaches: 1) the threshold-independent evaluation, and 2) the threshold-dependent evaluation. In the threshold-independent evaluation, the area under the receiver-operator characteristic curve (AUC) was used (Boria

Table 2
Spearman rank correlation matrix between the environmental predictors in relation to one point per 4 km^2 grid cell (geographically thinned) (Spearman Rho (ρ) > 0.7 is assumed as the highest correlation and will be excluded in the Maxent model.).

Elevation									
0.57 * **	TRI								
0.11 * **	-0.05	River							
-0.01	0.36 * **	-0.21 * **	MAP						
-0.76 * **	-0.69 * **	0.03	-0.46 * **	MAT					
0.09 * *	0.08*	0.03	0.05	-0.08*	LULC				
0.40 * **	0.44 * **	-0.06	0.58 * **	-0.53 * **	0.26 * **	NDVI			
-0.50 * **	-0.50 * **	-0.08*	-0.44 * **	0.66 * **	-0.18 * **	-0.59 * **	HFP		
0.45 * **	0.22 * **	0.32 * **	-0.19 * **	-0.39 * **	0.08*	0.07*	-0.31 * **	Road	
0.21 * **	0.18 * **	0.11 * **	0.34 * **	-0.40 * **	-0.12 * **	0.19 * **	-0.19 * **	0.11*	Water

* $p \leq 0.05$ * * $p \leq 0.01$ * ** $p \leq 0.001$

et al., 2014; Phillips et al., 2006).

The model which has AUC less than 0.7 indicates poor performance, between 0.7 and 0.9 indicates relatively good performance, whereas more than 0.9 indicates very good performance of the model (Araújo et al., 2005; Pearce and Ferrier, 2000; Swets, 1988). For the threshold-dependent evaluation, we used the True Scale Statistic (TSS) (Allouche et al., 2006; Sharma et al., 2020). We also used a 10-percentile training presence logistic threshold to identify the binary suitable habitat (suitable versus unsuitable) (Huang et al., 2018; Hughes, 2017). The TSS was calculated in R with a formula of TSS = Sensitivity + Specificity – 1. Its value ranges from − 1 to + 1 where + 1 indicates the best fit model (Allouche et al., 2006; Sharma et al., 2020). A Jackknife test was used to find the most important variables for the prediction of suitable habitat for elephants. The response curves were generated to examine the relationship between the individual environmental predictor and the prediction of suitability (Phillips et al., 2021).

After a binary suitable habitat was produced in ArcGIS from the Maxent ASCII, mean habitat suitability was calculated within a 10 km buffer of HEC villages. In addition, we calculated the areas of land-use/land-cover (LULC) and forest reserves inside the study area in ArcGIS. Then, Manly's selection ratios (w_i) were calculated using the widesI function in the adehabitatHS package (Calenge, 2006). This ratio was used to compare selection ratios of the used and available forest reserves with LULC, forest reserves with suitable habitat, and suitable habitat with LULC, to explore which habitats were mostly preferred by wild elephants (Manly et al., 2002). The w_i values > 1 indicate preference of that habitat (Desbiez and Medri, 2010; Osborn, 2005).

The HEC variables were fitted as response variables in generalized linear mixed models (GLMM). The human and elephant predictors with mean habitat suitability value for each village were used as fixed factors whereas HEC region was used as a random effect in the mixed model. The GLMMs were fitted with the glmer function using the lme4 package (Bates et al., 2015) with a binomial distribution.

3. Results

3.1. Evaluation of the Maxent model

The Maxent prediction for habitat suitability was 0.871 (mean AUC) which indicates that the model performance is relatively good (Fig. 2). The average threshold for the 10-percentile training presence logistic threshold was 0.329 ± 0.006 SD (Table 3). In addition, the model evaluation of TSS indicated a mean of 0.684 ± 0.0261 SD (Table 3), indicating that the Maxent model accurately predicted the suitable habitat for wild elephants.

3.2. Environmental factors influencing the elephant habitat suitability

In the Jackknife test, elevation had the highest gain when it was used as the only independent predictor in the Maxent model. In contrast, the Maxent model had the lowest gain when elevation was excluded from the modelling. This indicated that elevation was the most important factor in the elephant's suitability modelling (Fig. 3). This Jackknife test for elevation was consistent with the analysis of variable contribution, indicating that elevation contributed 64.6% in the Maxent model for the estimates of relative contribution of the different environmental predictors (Table S2). Further, when mean annual precipitation and distance to water were omitted from the Maxent model, the training gain would be the second and third lowest gains. Likewise, distance to water and mean annual

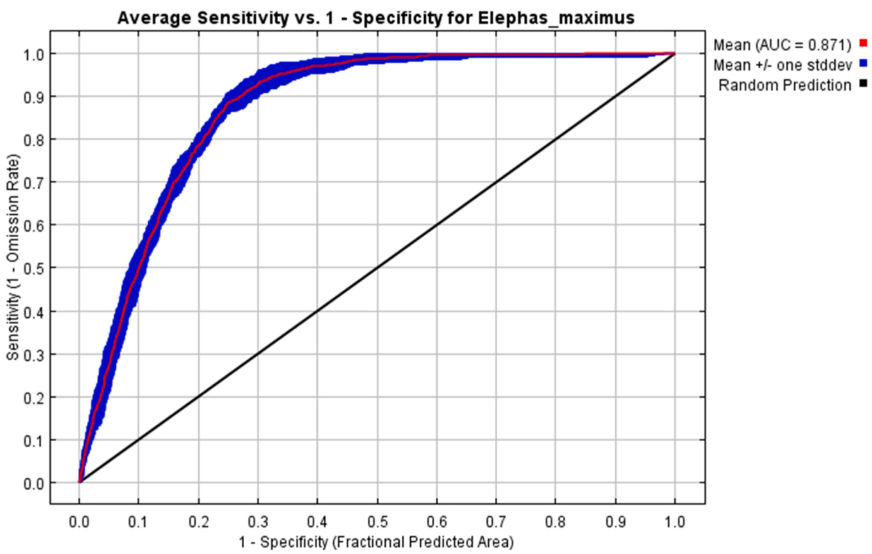

Fig. 2. The receiver operating characteristic (ROC) curve or area under the curve (AUC) for 10-fold replications. The averaged test AUC is 0.871 and the standard deviation is 0.008.

Table 3
Model evaluation of habitat suitability by the 10-fold cross-validation results (AUC), True Skill Statistics (TSS) and 10-percentile training presence logistic threshold.

	1	2	3	4	5	6	7	8	9	10	Mean	SD
Test AUC	0.872	0.885	0.876	0.876	0.861	0.860	0.871	0.873	0.860	0.879	**0.871**	0.0085
TSS	0.690	0.686	0.734	0.652	0.637	0.692	0.698	0.688	0.689	0.677	**0.684**	0.0261
Threshold	0.318	0.333	0.324	0.336	0.322	0.325	0.329	0.334	0.331	0.335	**0.329**	0.0060

precipitation contributed 13.3% and 9.2%, respectively, in the Maxent model (Table S2). When land-use/land-cover (LULC) and terrain ruggedness were used individually as independent predictors, they were the second and third highest gain variables (Fig. 3). However, if these two variables were excluded, the training gain performed better and had the highest gain. Other environmental predictors such as human footprint, normalized difference vegetation index, distance to river and LULC were the least important variables in explaining elephant habitat suitability (Fig. 3).

3.3. Response curves for environmental variables

In the Maxent modelling, the response curves showed how the individual environmental predictor affected the prediction of the model. Landscape topography played an important role in the suitability of elephant habitats in the study area. We found that elephant habitat suitability steadily declined at higher altitudes (Fig. 4-A). We also found that the highest frequency of elevation used by wild elephants was 0–200 m while it gradually declined up to 800 m altitude (Figure S2). Elephant habitat suitability declined with distance to water sources (river, stream, dam, or reservoir) above 8 km (Fig. 4-B & 4-G). In relation to the mean annual precipitation, habitat suitability was high up to 5000 mm rainfall, but declined above that precipitation level (Fig. 4-C). There was a similar trend in terrain ruggedness, indicating that Asian elephants preferred to use the lower terrain ruggedness (Fig. 4-D). Of the LULC categories, wild Asian elephants are highly likely to be distributed in grasslands and degraded forests, such as woody areas and open forests (Fig. 4-E). These factors revealed that wild Asian elephants preferred to use lower altitudes close to relatively wet areas.

3.4. Prediction of habitat suitability and habitat selection by elephants

The area of suitable habitats for wild elephants covered 11,524 km^2 (19.2%) of the total study area of 60,000 km^2; 61.6% of which was located within forest reserve areas (Fig. 5). Most (80.7%) of the elephant habitat was found in degraded forests such as woody and open forests (Table 4). The analyses of selection ratios showed that the distribution of LULC inside the forest reserve areas was significantly different from LULC availability within the entire study area (Log-likelihood $\chi^2 = 7102.8$, $df = 10$, $p < 0.001$). Elephant habitat selection within the forest reserves encompassed more grassland, open forests, closed forests, woody habitats, and mangroves, compared to the entire study area (Table 5). Elephants showed non-random use within their suitable habitats relative to LULC availability, both within forest reserve areas (Log-likelihood $\chi^2 = 3584.2$, $df = 10$, $p < 0.001$) and within the entire study area (Log-likelihood $\chi^2 = 13149.6$, $df = 10$, $p < 0.001$). Relative to availability within forest reserves, wild elephants selected for human-dominated areas (urban and built-up) and woody forests (Table 5). Within the entire study area, wild elephants preferred to use grasslands, woody, and open forests (Table 5). However, woody forests were significantly overused compared to its availability (Figure S3).

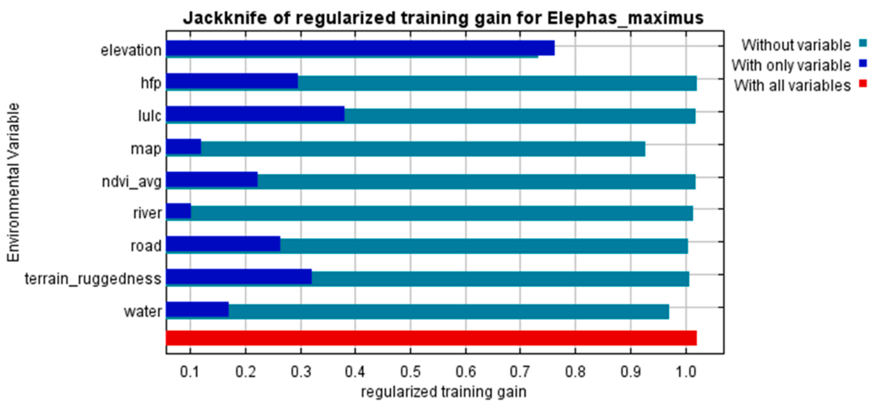

Fig. 3. Jackknife test indicates the importance of each environmental predictor to the Maxent model prediction for habitat suitability. Azure blue color represents if the individual covariate was used as an independent predictor in the Maxent model, the probability of its training gain would have the value as shown at the respective line. Aqua blue represents if the respective covariates were excluded from the Maxent model, the overall output would have its value at each scale. The red bar shows the overall output of training gain if all environmental predictors were used in the Maxent model.

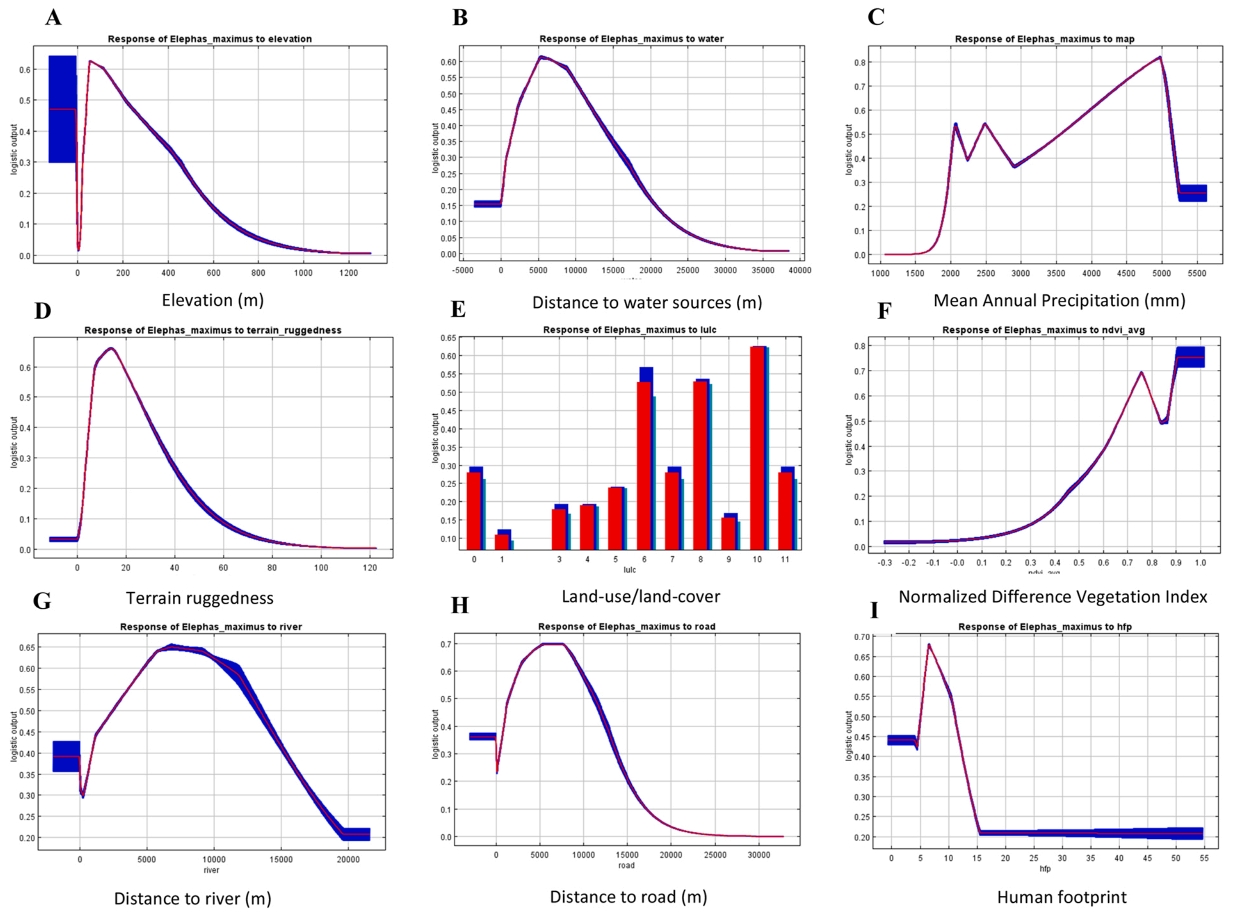

Fig. 4. The response curves in relation to habitat suitability for wild Asian elephants of elevation (**4-A**); distance to water sources (dam/reservoir) (**4-B**); mean annual precipitation (**4-C**); terrain ruggedness (**4-D**); land-use/land-cover types (0. Unknown, 1. Surface water, 3. Mangrove Forest, 4. Cropland, 5. Urban and built-up, 6. Grassland, 7. Closed Forest, 8. Open Forest, 9. Wetland, 10. Woody, and 11. Other land) (**4-E**); normalized difference vegetation index (**4-F**); distance to the river (stream/river) (**6-G**); distance to road (**4-H**); human footprint (**4-I**).

3.5. Relationship between HEC and habitat suitability

The GLMM analysis showed that larger farmlands (>4 ha) and elephants' aggressive behaviour were the strongest predictors enhancing the proportion of respondents who encountered crop damage (Fig. 6; Table 6). Elephants' aggressive behaviour and suitable habitats significantly affected both the proportion of respondents who encountered property damage, as well as the proportion of respondents who encountered elephant attacks (Table 6). However, while aggressive behaviour tended to enhance property damage and elephant attacks, suitable habitat decreased such human–elephant conflicts (Fig. 7 and 8). We further assessed whether the presence (or lack) of suitable habitats affected elephants' aggressive behaviour and thereby enhancing HEC for property damage and human attacks. While inclusion of an interaction term of suitable habitat with elephant behaviour did not significantly improve our model for property damage ($\chi^2 = 1.2$, $df = 1$, $p = 0.282$), it did significantly affect the probability of human attack ($\chi^2 = 7.5$, $df = 1$, $p < 0.006$). The probability for human attacks was highest when elephants displayed aggressive behaviour in less suitable habitats (Fig. 9). The analysis of GLMM for overall HEC showed that elephants' aggressive behaviour and larger farmlands (>4 ha) were the most influential factors, whereas suitable habitats was not significant (Fig. 10; Table 6).

4. Discussion

Our results revealed that the evaluation of the Maxent model was relatively good, indicating that the prediction of habitat suitability for wild elephants was reliable. The application of GPS telemetry data from wildlife movements has become a widespread use in the species distribution modelling, especially for Maxent models, e.g., for African elephants (*Loxodonta africana)* by Chibeya et al. (2021), Ndaimani et al. (2017a), Ndaimani et al. (2017b), Xu et al. (2016) and Xu et al. (2017); banteng (*Bos javanicus*) by Chaiyarat et al. (2019); black bears (*Ursus americanus*) by Boudreau et al. (2021) and Poor et al. (2020); feral cats (*Felis catus*) by Williamson et al. (2021); Persian leopard (*Panthera pardus ciscaucasica*) by Rozhnov et al. (2020); and wildebeest (*Connochaetes taurinus*) by Bond et al.

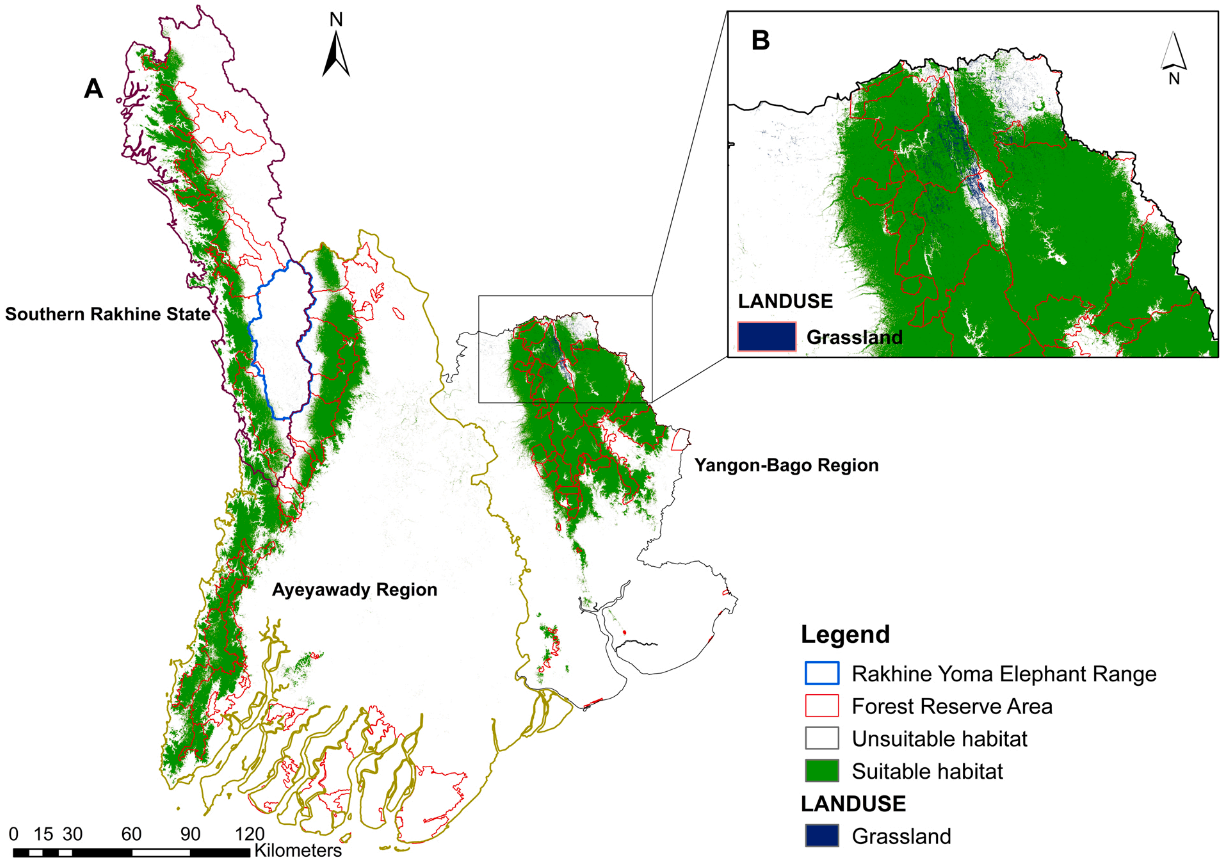

Fig. 5. Habitat suitability map for wild Asian elephants in southwest Myanmar. The figure was generated in ArcGIS from the Maxent output (ASCII format) to identify the habitat suitability (suitable versus unsuitable) using the 10-percentile training presence logistic threshold (**5-A**). A habitat suitability map showing the higher density of grassland in the study area (Letpadan, Thayarwady, and Bago townships) (**5-B**).

Table 4
Area of land-use/land-cover (LULC), forest reserves and suitable habitat across the study area.

Category	LULC		Forest reserve		Suitable habitat	
	Extent (km^2)	%	Extent (km^2)	%	Extent (km^2)	%
Unknown	93.4	0.16	20.6	0.17	7.1	0.06
Surface Water	1282.0	2.14	162.1	1.32	36.7	0.32
Mangroves	2239.9	3.73	875.1	7.15	132.0	1.15
Cropland	32523.8	54.21	2552.8	20.84	1544.9	13.41
Urban and Built-up	350.3	0.59	3.8	0.03	14.1	0.12
Grassland	78.0	0.13	68.2	0.56	50.8	0.44
Closed Forest	2568.9	4.28	968.0	7.91	297.2	2.58
Open Forest	6111.5	10.19	2819.5	23.03	2307.6	20.02
Wetland	2531.2	4.22	268.4	2.19	133.7	1.16
Woody	12135.0	20.23	4504.6	36.79	6997.7	60.72
Other land	85.6	0.14	0.9	0.01	2.0	0.02
Total	60000.0	100.00	12244.0	100.00	11524.0	100.00

(2017). Ndaimani et al. (2017b) demonstrated that presence-only data obtained from GPS collars outperform aerial survey data for the prediction of elephant distribution modelling.

Our findings indicate that elevation, distance to water sources, and mean annual precipitation were the most important predictors of elephant distribution. Other studies have also found that elevation was one of the most important variables for predicting elephant habitat suitability (Chibeya et al., 2021; Sharma et al., 2020; Taher et al., 2021; Talukdar et al., 2020; Xu et al., 2016). Choudhury (1999) and Williams et al. (2020) highlighted that elephants can be found up to 3000 m altitude. However, elevational differences depend on the local topographical conditions, for example < 133 m altitude in Taher et al. (2021) and < 400 m in Alfred et al. (2007)

Table 5
Manly's selection ratios of habitat by wild Asian elephants regarding land-use/land-cover, forest reserve and suitable habitat. The wi value > 1 is assumed as preference and < 1 is assumed as avoidance by elephant habitat use (Desbiez and Medri, 2010). The bold values indicate that elephants significantly preferred or used those habitats.

Category	Selection ratio (forest reserve/LULC) ($w_i \pm$ S.E.)	Selection ratio (Suitable habitat /forest reserve) ($w_i \pm$ S.E.)	Selection ratio (Suitable habitat/LULC) ($w_i \pm$ S.E.)
Unknown	1.082 ± 0.238	0.368 ± 0.138 * **	0.398 ± 0.149 * **
Surface Water	0.620 ± 0.048 * **	0.240 ± 0.040 * **	0.149 ± 0.025 * **
Mangroves	**1.915** ± 0.062 * **	0.160 ± 0.014 * **	0.307 ± 0.027 * **
Cropland	0.385 ± 0.007 * **	0.643 ± 0.015 * **	0.247 ± 0.006 * **
Urban and Built-up	0.053 ± 0.027 * **	**3.938** ± 1.047 * *	0.210 ± 0.056 * **
Grassland	**4.282** ± 0.517 * **	0.791 ± 0.111	**3.388** ± 0.474 * **
Closed Forest	**1.846** ± 0.057 * **	0.326 ± 0.019 * **	0.602 ± 0.034 * **
Open Forest	**2.261** ± 0.037 * **	0.870 ± 0.016 * **	**1.966** ± 0.037 * **
Wetland	0.520 ± 0.031 * **	0.529 ± 0.046 * **	0.275 ± 0.024 * **
Woody	**1.819** ± 0.022 * **	**1.651** ± 0.012 * **	**3.002** ± 0.022 * **
Other land	0.053 ± 0.055 * **	2.344 ± 1.645	0.123 ± 0.087 * **

*p ≤ 0.05 * *p ≤ 0.01 * **p ≤ 0.001

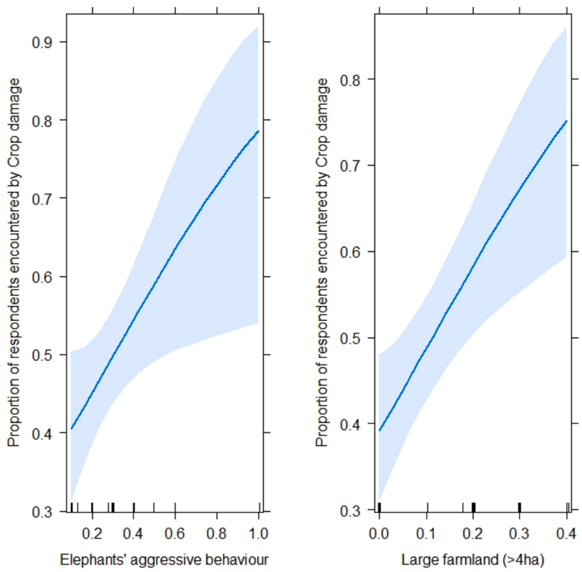

Fig. 6. Effect plots of GLMM displaying the relationship between crop damage relative to elephant behaviour and large farmland.

Table 6
Effects of simple random models (GLMM) on different HEC levels with habitat suitability and human predictors. The value was shown in z-value with the significant level. The bold values indicate the statistical significance between the respective variables and individual conflict type.

Conflict type	Mean Habitat Suitability	Elephant behaviour	Large farmland	Distance to the forest	Education	Residency
Crop damage	-1.414	**2.305***	**3.196*** **	0.198	0.258	0.595
Property damage	**-2.459***	**3.040*** *	0.242	0.380	0.780	0.072
Human attack	**-2.506***	**3.235*** *	0.462	0.918	-0.477	1.034
HEC	-1.091	**2.715*** *	**2.661*** *	0.654	0.624	0.249

* $p \leq 0.05$ * * $p \leq 0.01$ * ** $p \leq 0.001$

in Malaysia; > 153 m in Talukdar et al. (2020) in India; < 200 m in Wilson et al. (2021) in Indonesia; < 200 m in Sharma et al. (2020) in Nepal; 900–1200 m in Lin et al. (2008) in China; and 990–1020 m in Chibeya et al. (2021) in Zambia. Wall et al. (2006) demonstrated that behavioural decisions by elephants favours low elevation and gentle slopes to avoid overheating, insufficient water and forage, and potential risk of injury. Also, climbing 100 m altitude by African savannah elephants would cost 10,000 calories and ranging in the lowland might be an energy saving behavioural strategy (Wall et al., 2006). Elephants migrated from a lower to higher elevation when green vegetation became scarce in the lowlands (Bohrer et al., 2014).

Water sources are also a strong predictor on movement and distribution of elephants (Alfred et al., 2007; Ndaimani et al., 2017a; Wato et al., 2018), as elephants are well known as water-dependent animals (Western, 1975). Elephants need to hydrate and to reduce

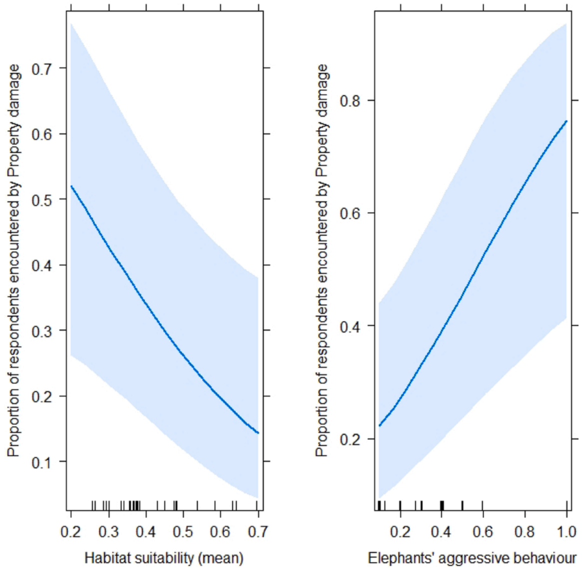

Fig. 7. Effect plots of GLMM displaying the relationship between property damage relative to habitat suitability and elephant behaviour.

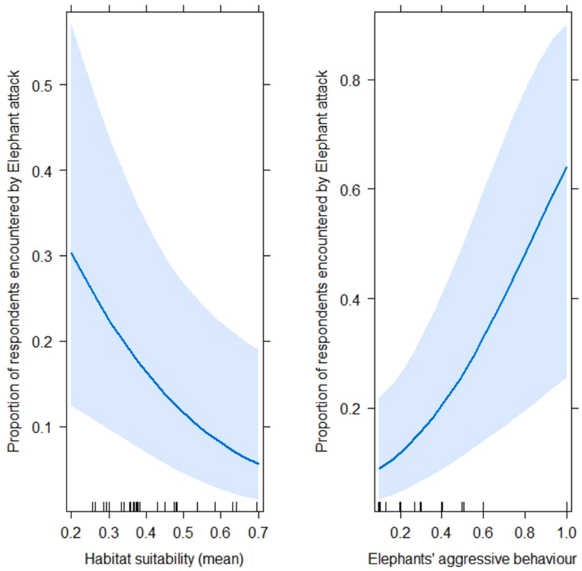

Fig. 8. Effect plots of GLMM displaying the relationship between human attack by elephants relative to habitat suitability and elephant behaviour.

the evaporative water loss (Dunkin et al., 2013) and thermal stress (Thaker et al., 2019). Sukumar (1992) stated that elephants need a daily water intake of 225 liters. These factors explain the elephant preference to range close to water sources. Our findings support studies of Sharma et al. (2020), Taher et al. (2021), Talukdar et al. (2020) and Xu et al. (2016). Annual rainfall pattern influences the availability of water. These two factors highly correlate with each other and determine the distribution and ranging behaviour of elephants. The study area receives a good (average) rainfall compared to other parts of Myanmar. In addition, numerous artificial water sources such as reservoirs were constructed especially in the Yangon-Bago region. They created an increased rate of human–elephant encounters as elephants frequently visited near the villages after construction of Nga-moe-yeik Reservoir (U Aung Min, personal communication).

We found that woody areas were more used by wild elephants than what would be expected based on their availability. Woody areas are also known as other wooded areas which are degraded forests consisting mainly of short trees, bushes, and shrubs. In addition, open forests are frequently utilised by elephants. Our results are similar to those of Alfred et al. (2007) who showed that elephants utilised mixed secondary forests more than intact primary forests, as the available forage was abundant in the mixed secondary forests (English et al., 2014; Suba et al., 2017). The open areas in secondary forests stimulate the growth of successional plants

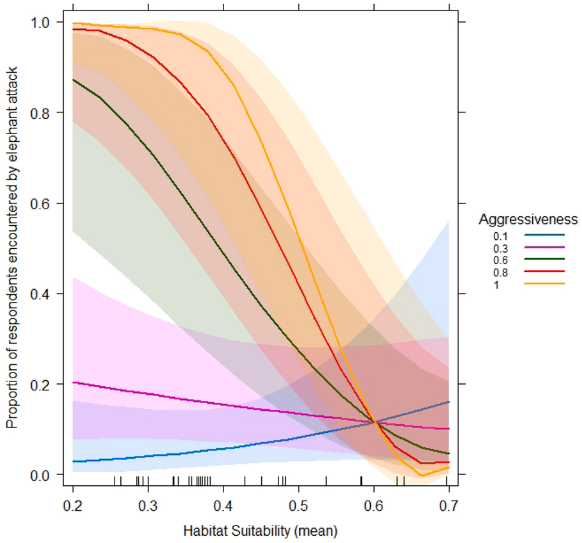

Fig. 9. Effect plot of GLMM displaying the probability of elephant attacks on human in relation to the significant interaction between elephants' aggressive behaviour and habitat suitability.

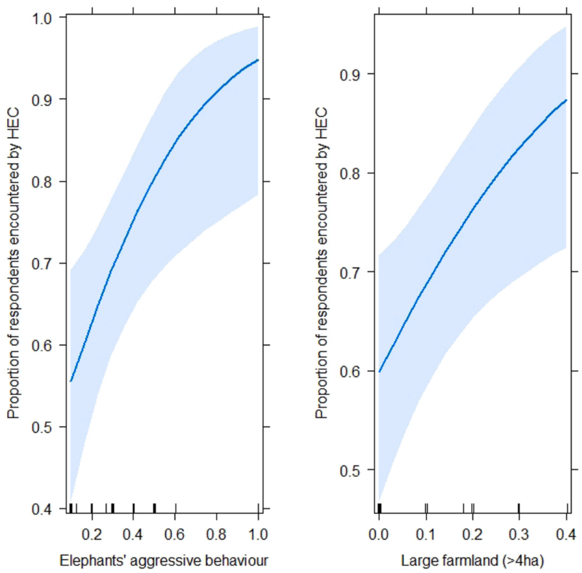

Fig. 10. Effect plots of GLMM displaying the relationship between HEC relative to elephant behaviour and large farmland.

which are preferred by elephants (English et al., 2014). In addition, after primary forests are degraded into other land-uses due to anthropogenic activities, such as excessive logging, land clearing for crop cultivation, etc., bamboo has become dominant in some parts of secondary forests in Myanmar. Bamboo is one of the elephant's preferred diets (Campos-Arceiz et al., 2008; Chen et al., 2006; Himmelsbach et al., 2006). Elephants prefer grassland, though grass contribution to their diet is lower than that of browse due to the scarcity of grass in habitats where browse vegetation is predominant (Sukumar, 1992). For example, 6–7 grass species out of 103–124 plant species were found in the study of Asian elephant's food plants in Myanmar (Campos-Arceiz et al., 2008; Himmelsbach et al., 2006) and in China (Chen et al., 2006). The secondary vegetation with bamboo, grasses and other herbaceous plants may attract the elephants' appetite more than the primary dense habitats (Sukumar, 2003). The grassland in this study area was not a true grassland as it mixes with disturbed herbs, shrubs, and grasses. It was mostly found in the southern Bago region, especially in Letpadan, Thayarwady, and Bago townships. However, broad grassland was rare in other parts of the study area.

Our results indicate that the majority of suitable habitats for elephants were found inside the forest reserves. A forest resource assessment in 2020 has indicated that forest cover in Myanmar has declined from 57.96% in 1990 to 42.19% in 2020 (FAO, 2020). The main factors attributing to deforestation and forest degradation are excessive logging, conversion of forests to large-scale commercial plantations, mineral mining, firewood collection, land encroachment for shifting cultivation, small scale plantations, and human settlements (Bhagwat et al., 2017; Leimgruber et al., 2005). Agricultural expansion into the forests was the major cause of deforestation between 1988 and 2017 in Myanmar (Yang et al., 2019). Mon et al. (2012) observed that low elevation and vicinity to human settlement areas are most vulnerable to deforestation and forest degradation. These anthropogenic factors driving deforestation and forest degradation would consequently lead to loss and fragmentation of elephant habitats. Habitat fragmentation causes wild elephants to become restricted largely to small patches within an isolated landscape (Leimgruber et al., 2003), ultimately resulting in a decline of genetic diversity (Goossens et al., 2016). Loss and fragmentation of elephant habitats will, therefore, have a negative effect on the survival and decline of elephant populations (Leimgruber et al., 2003; Sukumar, 1992). Habitat fragmentation influences the movements and home ranges of elephants indicating that movements of elephants are wider-ranging in fragmented areas (Alfred et al., 2012). Likewise, degradation of habitat encourages the resource competition between humans and elephants. These factors increase encounters with humans, leading to intense HEC (Fernando and Leimgruber, 2011; Leimgruber et al., 2003). Our study implies the important role of forest reserves and forest management for wild elephant conservation. If human encroachment into forest areas is ongoing, fragmentation and degradation of elephant habitats will then increase resulting in an increased HEC and habitat loss.

We found higher property damage and elephant attacks on humans in less suitable habitats. This may occur due to higher resource competition between elephants and humans. Resource competition causes decrease in forage for elephants and results in an increase in human mortality (Lenin and Sukumar, 2011; Sukumar, 1992). Our results also indicate that elephants within less suitable habitats are more aggressive, leading to more conflict with humans. Kumar and Singh (2010) stated that elephants are more alert and vigilant in open habitats than when they are in higher forest cover areas, probably leading to higher level of aggressiveness. Additionally, poaching is probably higher in the disturbed or degraded open forests (Ling et al., 2016). Sampson et al. (2018) reported that elephant poaching (for their skin) has been intensified in Myanmar. Elephants become aggressive when they are sick, injured, harassed, in musth, or with young calves (Leggat et al., 2001; Lenin and Sukumar, 2011). Blocking the elephants' traditional migration routes by settlements or agriculture will arouse aggressiveness and lead to HEC (Lenin and Sukumar, 2011). It is also shown that elephants are more stressed when they are in less protected areas (Hunninck et al., 2017; Tingvold et al., 2013). Elephant behaviour in our study refers to the perceived behaviour of elephants by local people to understand how they will respond to HEC. It is not an assessment on factual behaviour by local people. Therefore, the potential misidentification of elephant behaviour was assumed not a problem.

5. Conclusion

We identified 11,524 km^2 of suitable habitats for wild Asian elephants in southwest Myanmar. Elephants prefer to live at lower elevations, near water sources, and in areas with adequate rainfall. Furthermore, they are highly likely to be distributed in grasslands and degraded forests, resulting in increased HEC because of the higher probability of human land use in these habitats. This will also impact the behaviour of wild elephants. Our findings indicate that reported elephant aggressiveness increased in less suitable habitats, resulting in more damage to human property and loss of lives due to the increased likelihood of challenging elephants to find forage and increased self-defence.

Implications for conservation

Effective forest management is vital for the sustainability of wild elephants. Although elephants use disturbed and degraded forests extensively, these habitats seem not optimal for elephants due to the increased risk of forest fragmentation and resource depletion caused by anthropogenic pressures and disturbances. The habitat quality in these habitats, with a buffer from croplands, should be improved by providing elephant food plants and water sources. Also, overcoming sectorial approaches will be important for elephant conservation and overcoming HEC. This can be exemplified by the Myanmar Reforestation and Rehabilitation Programme (MRRP, 2017–2026) only emphasizing the forestry sector and, a habitat restoration programme for protected areas initiated in Myanmar in 2019. The conservation potential would have been greatly enhanced if this habitat programme had been extended to potential elephant habitats in forest reserves, while wildlife habitat restoration in the MRRP was strengthened. Areas where larger croplands exist at the lower altitudes near degraded forests and water sources are most vulnerable to encounter conflicts. Those areas should, therefore, be prioritized to minimize the HEC. In addition, corridors play a vital role in habitat connectivity encouraging species fitness and genetic diversity. Potential elephant corridors should be identified and protected to secure elephant migration, to improve the safety of local people and to reduce the elephant-induced damages. Physical or psychological trauma from elephant poaching will intensify elephants' aggressiveness, indicating that reducing poaching will enhance the coexistence between humans and elephants. The recommendation by Kumar and Singh (2010) that people should stay more than 50 m away from wild elephants should be followed for those who live in the proximity of elephants, to avoid potential attacks. Behavioural studies of wild elephants should be carried out in the future, e.g., stress physiology and hormone changes of wild elephants within human-dominated and natural landscapes to examine elephants' behaviours.

Ethical statement

Elephant collaring was approved by the Ministry of Natural Resources and Environmental Conservation (MONREC) and collaring process was executed and supervised by the veterinarians from Myanma Timber Enterprise under MONREC. We followed all ethical requirements for the safety of the animals concerned.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability

Data will be made available on request.

Acknowledgement

We would like to thank the Norwegian Environment Agency for a financial support to four elephants to fit the GPS collars around the Rakhine Yoma Elephant Range. We are also grateful to the Smithsonian Institution and WWF Myanmar for sharing the elephant movement data. It is highly appreciated to the Ministry of Natural Resources and Environmental Conservation (MONREC) for the approval of the elephant collaring work. Special thanks to Dr. San Lin, the veterinarians, and the elephant keepers from the Myanma Timber Enterprise for the collar fitting processes. We would also like to express our sincere thanks to the park staff from the Rakhine Yoma Elephant Range. We are thankful to three anonymous reviewers for their suggestions and insightful comments to improve our paper.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2023.e02468.

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