Updated range metrics and a global population estimate for the Critically Endangered Philippine Eagle using a spatial ensemble habitat model

Luke J. Sutton[1*], Jayson C. Ibañez[2,3], Dennis I. Salvador[2], Rowell L. Taraya[2], Guiller S. Opiso[2], Tristan P. Senarillos[2] & Christopher J.W. McClure[1]

[1] The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, Idaho 83709 USA

[2] Philippine Eagle Foundation, Philippine Eagle Center, Malagos, Bagulo District, Davao City, 8000, Philippines

[3] University of the Philippines – Mindanao, Bago Oshiro, Mintal District, Davao City, 8000, Philippines

* Corresponding email: lsutton@peregrinefund.org

Short title: Philippine Eagle range metrics and population size

Abstract

Many range-restricted taxa are currently experiencing severe population declines yet lack fundamental biological information regarding distribution and population size. Establishing baseline estimates for both these key biological parameters is however critical for directing long-term monitoring and conservation planning for at-risk range-restricted species. The International Union for the Conservation of Nature (IUCN) Red List uses three spatial range metrics that define species distributions and inform extinction risk assessments: extent of occurrence (EOO), area of occupancy (AOO) and area of habitat (AOH). However, calculating all three metrics using standard IUCN approaches relies on a geographically representative sample of locations,

which for rare species is often spatially biased. Here, we apply model-based interpolation using an ensemble Species Distribution Model (SDM), correlating occurrences with remote-sensing derived environmental covariates, to calculate IUCN range metrics and a global population estimate for the Critically Endangered Philippine Eagle (*Pithecophaga jefferyi*). Our ensemble-averaged SDM had high predictive accuracy and was able to identify key areas of Philippine Eagle habitat across the species global range. We estimated an AOH = 49,426 km^2 and from this metric calculated a maximum EOO = 609,697 km^2 and a minimum EOO = 273,794 km^2, with an AOO = 54,695 occupied cells. Based on inferred habitat from the AOH metric and territorial habitat area from home range estimates, we provide an updated global population estimate of 677 breeding pairs (range: 549-772 pairs), or 1354 mature individuals, across the entire Philippine Eagle range. We demonstrate that even when occurrence sampling is geographically biased, robust habitat models can be built which enable quantification of IUCN range metrics and a baseline population size estimate. In the absence of adequate location data for many rare and threatened taxa, our method is a promising spatial modelling tool with widespread applications, in particular for island endemics facing high extinction risk.

Keywords: area of habitat, area of occupancy, extent of occurrence, population size, range metrics, Species Distribution Models

Introduction

Species that are rare due to either a restricted geographic range, habitat specificity, or small population size are at greater risk of extinction because their populations may not be as resilient to perturbations in the environment (Rabinowitz *et al.* 1986;

Gaston 1994). Therefore, quantifying the two key biological parameters of range extent and population size is fundamental for directing conservation action for threatened rare taxa (Marcer *et al.* 2013; Syfert *et al.* 2014). Habitat loss and fragmentation are the two primary threats to biodiversity globally (Díaz *et al.* 2019), in particular for tropical biodiversity hotspots (Brooks *et al.* 2002). Determining baseline range size metrics and population estimates for threatened species with restricted ranges and low abundance can thus inform long-term conservation monitoring by quantifying the effects of habitat loss and fragmentation on range extent and population size for these at-risk taxa (IUCN 2001; Brooks *et al.* 2019).

The International Union for the Conservation of Nature (IUCN) Red List uses two spatial range metrics that seek to define species distributions and inform extinction risk assessments (IUCN 2019): extent of occurrence (EOO) and area of occupancy (AOO). EOO represents the upper bound of a species distribution, measuring the overall geographic extent of localities and degree of risk spread. Conversely, AOO represents the lower bound of a species distribution. By quantifying where the species actually occurs, AOO is thus linked to population size (Gaston & Fuller 2009). Recently, the IUCN developed a new deductive range metric, area of habitat (AOH, Brooks *et al*. 2019), defined as the extent of habitat factors, such as landcover and elevation, for a species within its range. Estimating AOH is important because it can be used in supporting conservation risk assessments by quantifying habitat loss and fragmentation (Brooks *et al*. 2019; Sutton *et al.* 2021).

Various spatial workflows have been proposed and implemented for calculating AOH, which overlay and clip elevational and landcover preferences within the range

of species presence points (Brooks *et al.* 2019). Deductive methods using clipped environmental layers with expert-drawn maps (Harris & Pimm 2008), or inductive modelling methods using inverse distance weighted interpolation (Palacio *et al.* 2021), and logistic regression (Dahal *et al.* 2021; Lumbierres *et al.* 2021), have been successful in estimating AOH but rely on a spatially homogenous sample of presence points. For many rare species in remote, hard to survey areas presence data is either insufficient, or may be heavily biased towards a well-sampled region but lacking elsewhere (Marcer *et al.* 2013; Syfert *et al.* 2014; Dahal *et al.* 2021). Because of their rarity, occurrence data for these species is limited and thus calculating range metrics based solely on point data is likely to result in unreliable range metrics (Pena *et al.* 2014). To overcome this issue of sampling bias in calculating AOH a new method is required for those rare species with high extinction risk that inhabit remote regions lacking adequate presence data.

The Philippine Eagle (*Pithecophaga jefferyi*) is a large tropical forest raptor and one of the most threatened raptors globally (Bildstein *et al.* 1998), currently classified as 'Critically Endangered' on the IUCN Red List (BirdLife International 2018). The Philippine Eagle is endemic to four islands in the Philippine archipelago (Mindanao, Leyte, Samar, and Luzon), sparsely distributed across lowland and montane dipterocarp forests (Salvador & Ibañez 2006). The population has declined drastically over the past 50 years, mainly due to habitat loss through deforestation (Kennedy 1977; Lewis 1986; Bueser *et al.* 2003; Panopio *et al.* 2021) and persecution (Salvador & Ibañez 2006; Ibañez *et al.* 2016). Thus, the Philippine Eagle fulfils all three components of rarity, and along with its large body size and forest dependency would be associated with a higher risk of extinction (Kittelberger *et al.*

2021). Despite this elevated extinction risk, fundamental aspects of the species biology such as distribution and population size are still uncertain (Collar 1997; BirdLife International 2018) and need updating using a robust methodology.

Most Philippine Eagle research has been conducted on the island of Mindanao (Miranda *et al.* 2000; Bueser *et al.* 2003), and thus occurrence data are biased towards this island. Bueser *et al.* (2003), estimated between 82-233 breeding pairs for Mindanao, and extrapolating this figure across all range islands suggests a global total of between 340 (BirdLife International 2018) and 500 pairs (Salvador & Ibañez 2006). However, pair densities on the other range islands, especially Luzon, are unknown and thus this population size figure should be treated with caution (Miranda *et al.* 2008). Because of these research disparities, there are no current range-wide estimates for the species' global range extent and population size, despite it being a raptor of high priority for research and conservation (Buechley *et al.* 2019). Indeed, the IUCN Red List suggests that further research into distribution, population size, and ecological requirements is urgently required to inform conservation actions (BirdLife International 2018).

Here, we use ensemble-averaged Species Distribution Models (SDMs) calibrated with presence data for the Philippine Eagle on the island of Mindanao, and then predict into the other less-well sampled islands using inductive model-based interpolation (Rodríguez *et al.* 2007; Franklin 2009). SDMs are predictive spatial models that infer species-habitat associations by correlating species presence points with habitat covariates that represent the focal species optimal conditions and resources (Guisan *et al.* 2017; Matthiopoulos *et al.* 2020). Indeed, SDMs are able to

inform IUCN species range metrics and predict habitat in areas that may lack occurrence data for inclusion in Red List assessments (Marcer *et al.* 2013; Pena *et al.* 2014; Syfert *et al.* 2014; Breiner *et al.* 2017). Using interpolated model predictions, range metrics such as AOH, EOO and AOO can then be calculated based on inferred or predicted habitat following IUCN Red List guidelines (IUCN 2019). First, we present a new approach to estimating species range metrics and population size based on predicted habitat for the Philippine Eagle, and second, we outline how our methodology can be incorporated into conservation planning assessments for rare species facing extinction.

Methods

Species locations

We sourced Philippine Eagle occurrences from the Global Raptor Impact Network (GRIN, McClure *et al.* 2021), a data information system for all raptor species. For the Philippine Eagle, GRIN includes nest locations from surveys on Mindanao conducted by the Philippine Eagle Foundation since 1978 to the present (Miranda *et al.* 2000; Ibañez *et al.* 2016), in addition to community science data from eBird (Sullivan *et al.* 2009) and the Global Biodiversity Information Facility (GBIF 2021). Duplicate records and those with no geo-referenced location were removed and all occurrences were merged into a single range-wide database. A total of 151 geo-referenced records were compiled across the Philippine Eagle range after data cleaning. Only occurrences recorded from year 1980 onwards were included to temporally match the approximate timeframe of the habitat covariates, whilst retaining sufficient sample size for robust modelling (van Proosdij *et al.* 2016).

In addition, we included GPS tracking locations from six breeding adult Philippine Eagles on Mindanao and integrated this dataset with the nest and community science data to better represent Philippine Eagle habitat use in territorial nesting areas. The eagles were trapped using either a modified Bal-Chatri (Miranda & Ibanez 2006) or a large bownet baited with domestic rabbit (*Oryctolagus cuniculus*). Two eagles were instrumented with solar-powered GPS/GSM transmitters while four eagles had battery-powered GPS satellite transmitters fitted. All birds were marked with aluminium leg bands – the four females with blue bands on their left leg, and the two males with green bands on their right leg. A total of 80,966 fixes were obtained from the four adult females and two adult males from April 2013 to September 2021. We removed all duplicated records and applied a 1-km spatial filter to this raw dataset (matching the covariate raster resolution) resulting in 325 spatially filtered GPS fixes (Fig. S1).

For the Mindanao calibration models we used the subset of nest and community science occurrences solely located on the island of Mindanao combined with the filtered GPS tracking fixes. We then manually applied a spatial filter between each point, resulting in a single occurrence in each 1-km raster grid cell, resulting in a filtered subset of 435 occurrences for the Mindanao calibration models. We applied a manual filter to ensure we retained as many of the nest locations and GPS fixes as priority data points because of their geolocation accuracy and direct relevance to optimal conditions and resources for Philippine Eagle occurrence. To evaluate the final ensemble range-wide models we used all nest and community science occurrence data and applied a 1-km spatial filter between each occurrence, regardless of the origin of the occurrence point. Applying the 1-km spatial filter

resulted in 101 occurrence records for testing calibration accuracy for the final range-wide ensemble models.

Habitat covariates

We defined the species' accessible area (Barve *et al.* 2011), as the mainland area of all known range islands: Mindanao, Luzon, and Leyte and Samar in the Eastern Visayas (Fig. 1; Salvador & Ibañez 2006; BirdLife International 2018). To predict occurrence, covariates representing climate, landcover, habitat heterogeneity, and human land use were downloaded from the EarthEnv (https://www.earthenv.org), ENVIREM (Title & Bemmels 2018), Socioeconomic Data and Applications Center (SEDAC; https://sedac.ciesin.columbia.edu), and Dynamic Habitat Indices (DHI; https://silvis.forest.wisc.edu/data/dhis/) repositories. Raster covariate layers were cropped to a delimited polygon representing the species accessible area (Fig. 1). We extracted the polygons from the World Wildlife Fund (WWF) terrestrial ecoregions shapefile (Olson *et al.* 2001), which correspond to either lowland or montane moist tropical forest. For Luzon, we masked out the tropical pine forest ecoregion in the north of the island because Philippine Eagles are habitat specialists of tropical moist dipterocarp forests (Kennedy 1977; Bueser *et al.* 2003; Salvador & Ibañez 2006), and thus unlikely to occur in this ecoregion.

Six continuous covariates were used at a spatial resolution of 30 arc-seconds (~1-km): Climatic Moisture Index (CMI), Evergreen Forest, Habitat Homogeneity, Human Footprint Index (HFI), Leaf Area Index (LAI) and Mosaic Forest. CMI is a scaled measure ($-1 \leq CMI \leq 1$) of the ratio of annual precipitation and annual

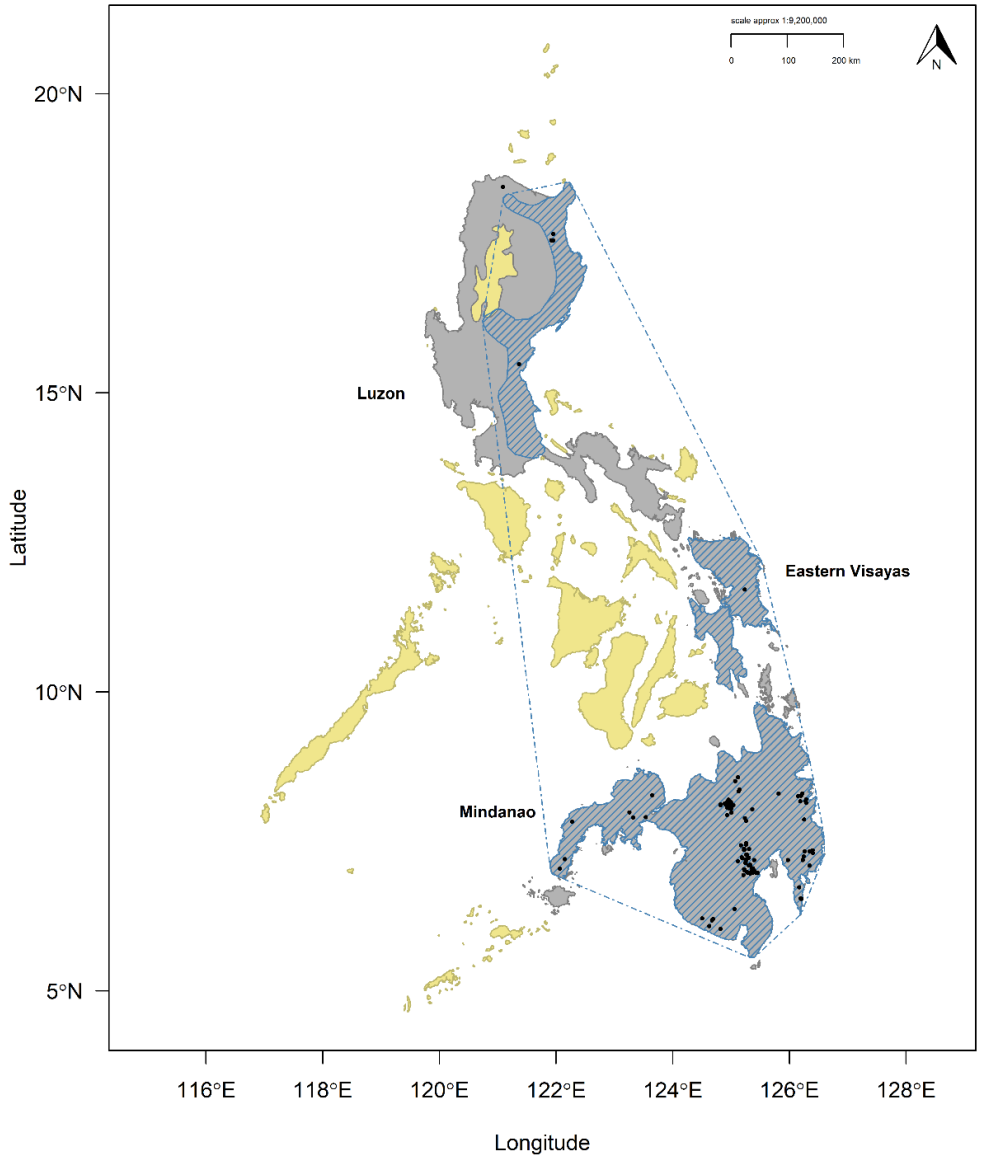

Figure 1. Range map for the Philippine Eagle with our model accessible area (dark grey) and IUCN range map (hashed blue areas) and IUCN EOO polygon (hashed blue line). Yellow polygons define the national boundary of the Philippines outside of the species accessible area. Black points define unfiltered Philippine Eagle occurrences from nests and community science data. For clarity, GPS locations from the six tagged adults in Mindanao are shown in Fig. S1.

vegetation structure, composition and diversity) derived from textural features for Enhanced Vegetation Index (EVI) between adjacent pixels representing habitat heterogeneity; sourced from the Moderate Resolution Imaging Spectroradiometer (MODIS, https://modis.gsfc.nasa.gov/). Homogeneity varies between zero (zero similarity = maximum heterogeneity) and one (complete similarity) to represent the spatial variability and arrangement of vegetation species richness on a continuous scale. Evergreen and Mosaic Forest are consensus products of percentage landcover integrating GlobCover (v2.2), MODIS land-cover product (v051), GLC2000 (v1.1) and DISCover (v2) (Tuanmu & Jetz 2014), used here to represent both closed and open dipterocarp forest.

Human Footprint Index (HFI) represents human population density, land use, and infrastructure, including built-up areas and access routes such as roads and rivers (WCS, CIESIN 2005). We included HFI because we expect Philippine Eagles to avoid areas of high human impact. Leaf Area Index (LAI) is a measure of the amount of foliage within the plant canopy based on MODIS vegetation products and is used here as a composite Dynamic Habitat Index (DHI) product spanning the years 2003-2014 (Radeloff 2019). LAI values range from 0 (bare ground) to > 10 (needleleaf coniferous forest) and is a key driver of primary productivity (Asner *et al.* 2003). The DHI product summarises three measures of vegetation productivity: annual cumulative, minimum throughout the year, and seasonality as the annual coefficient of variation. Combined, we used the LAI Dynamic Habitat Index as a proxy for food availability, assuming that higher LAI values would be associated with higher species richness (Hobi *et al.* 2017).

Covariates were selected *a prioiri* to those related empirically to resources and conditions influencing Philippine Eagle distribution from previous studies (Kennedy 1977; Bueser *et al.* 2003; Ibañez *et al.* 2003; Salvador & Ibañez 2006). We aimed to include both landcover and topographic factors from the AOH model criteria (Brooks *et al.* 2019) but added covariates for climate, human impact and proxies of food because these are important variables for determining species distributions (Franklin 2009). We excluded elevation and terrain roughness because including both covariates in initial calibration models resulted in restricting predictions to unrealistic areas of high elevation and topographic complexity, without capturing the full range of environmental conditions and resources available to the Philippine Eagle. All selected covariates showed low collinearity (Variance Inflation Factor < 2; Table S2).

Ensemble Spatial Logistic Regression model

Most Philippine Eagle occurrences and nest locations deposited in GRIN are from the island of Mindanao, with sparse occurrences across the eastern Visayas and Luzon (Fig. 1). Due to this geographical sampling bias, which would likely bias any model predictions (Syfert *et al.* 2014), we developed a novel Ensemble Spatial Logistic Regression (ESLR) model workflow (Fig. 2) to first predict habitat suitability for Mindanao (Fig. 2, box 3a). Next, we then projected each Mindanao model into the islands of the Eastern Visayas and Luzon (Fig. 2, boxes 3b,c), before finally merging each island model into a single range-wide prediction from each algorithm (Fig. 2, box 3c). We fitted four logistic regression-based algorithms via maximum likelihood estimation: penalized generalized linear model (GLM); generalised additive model (GAM); and Multivariate Adaptive Regression Splines (MARS), fitted with no interactions between covariates, and with interactions fitted between covariates

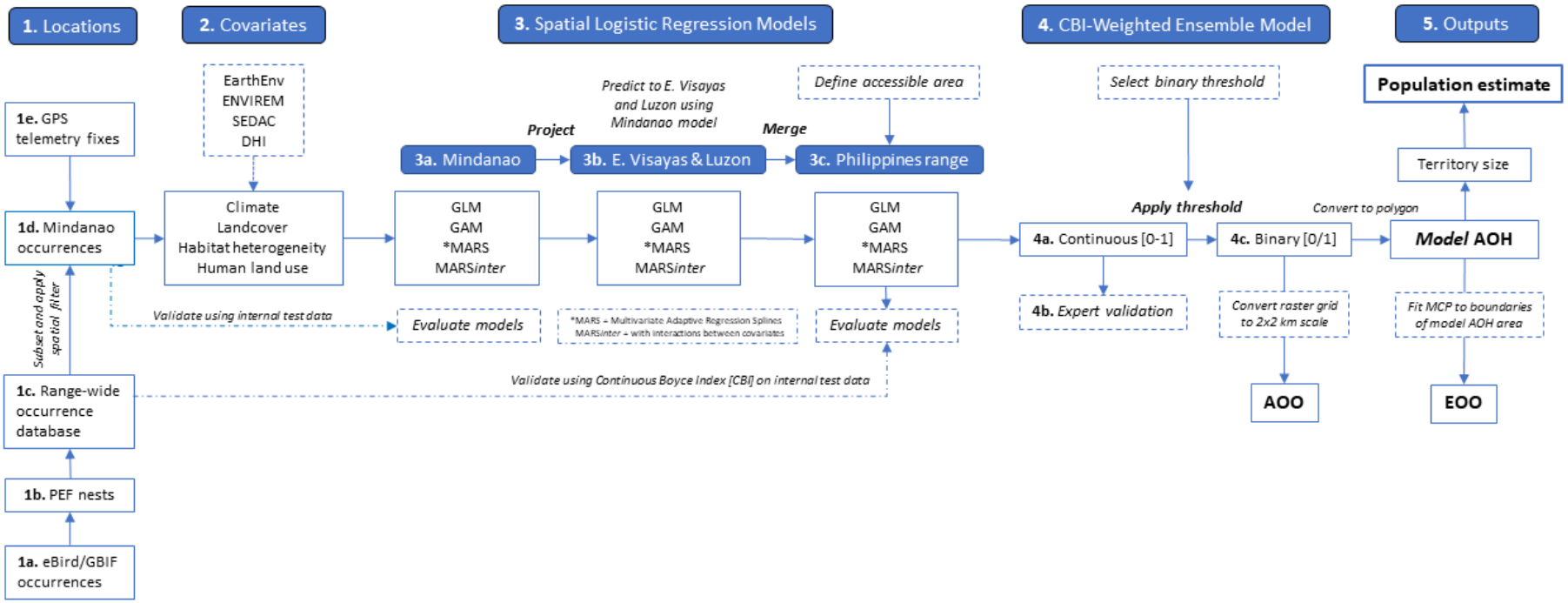

Figure 2. Ensemble Spatial Logistic Regression workflow for the Philippine Eagle Species Distribution Models.

(MARS*inter*). Full details on the parameter settings for each algorithm are outlined in the Supplementary Material. We limited model complexity in all four algorithms because this is necessary when the primary goal is to use SDMs for predictive transferability in space (Helmstetter *et al.* 2020).

We parametrized the spatial logistic regression models using a fine pixel grid (~1-km), equivalent to fitting a Poisson point process model (PPM) with loglinear intensity (Baddeley *et al.* 2010), because the PPM framework is the most effective method to model presence-background data as used here (Warton & Shepherd 2010). Using the ensemble workflow generates robust predictions compared to single-algorithm models (Araújo & New 2007; Valavi *et al.* 2021), accounting for any model uncertainty between each algorithm prediction (Marmion *et al.* 2008). We used an ensemble of tuned individual model algorithms because this methodology outperforms other ensemble modelling methods (Valavi *et al.* 2021). We only used regression-based algorithms with semi-parametric functions because these types of models predict better with a lower number of presences, as used here, compared to complex non-parametric data-driven machine learning methods (James *et al.* 2013; Valavi *et al.* 2021).

We evaluated calibration accuracy for both the Mindanao and range-wide models using a random sample of 10,000 background points as pseudo-absences recommended for regression-based modelling (Barbet-Massin *et al.* 2012) and to sufficiently sample the background calibration environment (Guevara *et al.* 2018). Presence points and pseudo-absences were weighted equally for all models, allowing consistent sampling across the model calibration area. We did this to avoid

saturating the model with excessive absence weighting, which makes presence trends difficult to detect (Elith & Leathwick 2007). We used Continuous Boyce index (CBI; Hirzel *et al.* 2006) as a threshold-independent metric of how predictions differ from a random distribution of observed presences (Boyce *et al.* 2002). CBI is consistent with a Spearman correlation (r_s) and ranges from -1 to +1. Positive values indicate predictions consistent with observed presences, values close to zero suggest no difference with a random model, and negative values indicate areas with frequent presences having low environmental suitability. Mean CBI was calculated using five-fold cross-validation on 20 % test data with a moving window for threshold-independence and 101 defined bins in the R package enmSdm (Smith 2019).

For the Mindanao models, we tested the optimal predictions against random expectations using partial Receiver Operating Characteristic ratios (pROC), which estimate model performance by giving precedence to omission errors over commission errors (Peterson *et al.* 2008). Partial ROC ratios range from 0 to 2 with 1 indicating a random model. Function parameters were set with a 10% omission error rate, and 1000 bootstrap replicates on 50% test data to determine significant ($\alpha = 0.05$) pROC values >1.0 in the R package ENMGadgets (Barve & Barve, 2013). Each range-wide model was then weighted by its CBI evaluation score and a weighted ensemble generated as a final continuous range-wide prediction (Fig. 2, box 4). We used Schoener's *D* niche overlap as a measure of spatial agreement between each of the Mindanao and range-wide models, where 0 = no overlap and 1 = total overlap.

Finally, calibration accuracy for the final range-wide continuous ensemble prediction was tested using CBI and then converted into a binary threshold prediction based on expert validation from J.C.I., which we term *model* AOH (Fig. 2, box 5), so as to be distinct from the standard IUCN AOH methodology (Brooks *et al.* 2019). We validated our models in conjunction with expert judgement because this approach gives most benefit to conservation risk assessments (Marcer *et al.* 2013; Syfert *et al.* 2014). Following modelling protocols established by Velásquez-Tibatá *et al.* (2019), we assessed a range of four binary thresholds for biological realism (median, 75 % upper quantile, maximizing the sum of sensitivity and specificity (maxTSS) and Cohen's Kappa), using expert critical feedback to assess the predictive ability of our models (Fig. 2, boxes 4b,c). Both maxTSS and upper quantile binary models were evaluated as plausible range extents. We opted for upper quantile because this threshold is not reliant on measuring predictive ability based on unknown pseudo-absences as used here (Merow *et al.* 2013), unlike measures that use specificity such as maxTSS (Liu *et al.* 2013). We followed a participatory modelling process methodology to ensure a robust expert validation of our models, concurring with current knowledge of species biology and its application to conservation planning (Ferraz *et al.* 2020).

Range sizes

To calculate *model* AOH in suitable pixels we reclassified the continuous prediction to a binary threshold prediction (Fig. 2, boxes 4a,b), using all pixel values equal to or greater than the upper quantile threshold from the continuous model. We calculated two further IUCN range metrics from our *model* AOH binary prediction. First, Area of Occupancy (AOO) was calculated as the number of raster pixels predicted to be

occupied, scaled to a 2x2 km grid following IUCN guidelines (IUCN 2018) in the R package redlistr (Lee *et al.* 2019). Second, we converted the *model* AOH raster to a polygon using an 8-neighbour patch rule and applied a smoothing function using the Chaikin algorithm (Chaikin 1974) in the R package smoothr (Strimas-Mackey 2021). From this we calculated Extent of Occurrence (EOO), fitting a minimum convex polygon (MCP) around the furthest boundaries of the smoothed *model* AOH polygon following IUCN guidelines (IUCN 2018). We calculated both a maximum EOO, including all the area with the MCP, and a minimum EOO, masking out the areas that could never be occupied within the MCP, in our case over the ocean (Mercer *et al.* 2013). All range metric calculations were performed using a Transverse cylindrical equal area projection following IUCN guidelines (IUCN 2018). General model development and geospatial analysis were performed in R (v3.5.1; R Core Team, 2018) using the dismo (Hijmans *et al.* 2017), raster (Hijmans 2017), rgdal (Bivand *et al.* 2019), rgeos (Bivand & Rundle 2019), and sp (Bivand *et al.* 2013) packages.

Population size estimation

Based on the premise that territorial, central-place foragers, such as the Philippine Eagle, require a semi-fixed area of habitat to survive and reproduce, we calculated the number of Philippine Eagle pairs our *model* AOH could support as directly proportional to the available habitat within a given home range required by a breeding pair of Philippine Eagles (Kennedy 1977; Rabor 1989). We based the habitat area required for each pair on home range estimates from six breeding adult Philippine Eagles fitted with satellite telemetry tags (Table S1). Because of varied telemetry sampling rates between the six adults, we subsampled the raw location

fixes using a minimum 3-hour interval between fixes to achieve consistency across individual estimators. We calculated home range sizes using three different estimators to provide a range of habitat area estimates for calculating population size because of variation in outputs between different home range estimation methods (Signer & Fieberg 2021). All home range estimates were calculated in the R package adehabitatHR (Calenge 2006), using code adapted from Tétreault & Franke (2017).

For calculating the median habitat area and population size estimates we fitted Kernel Density Estimators (KDE) using a 95 % bivariate normal kernel with an ad-hoc reference smoothing parameter (h_{ref}). We then fitted 99 % Minimum Convex Polygons (MCP) to calculate the maximum habitat area, and thus minimum population size, and Local Convex Hulls (LoCoH) using the sphere of influence radius method (r-LoCoH, maximizing all nearest neighbour distances (Getz *et al.* 2007)), for calculating the minimum habitat area and thus maximum population size. We summed all individual home range estimates from each adult and calculated a median value for each estimator method. We then used the three median values from each estimator method to apply an overall median, and minimum to maximum range for the area of territorial habitat. Using the territorial habitat area from the three estimates, we then calculated the median, and a range of minimum to maximum population sizes of potential breeding pairs that our *model* AOH prediction could support using the formulation of Kennedy (1977),

$$\hat{\mathrm{T}} = (\mathrm{N}/\mathrm{n})\ \mathrm{t}$$

where T_{hat} = total population size; N = area of habitat; n = territorial habitat area and t = sample total multiplied by 2. We used the IUCN Red List definitions for population size as the total number of mature individuals across the species range (IUCN 2019), then divided that figure by 2 to give the number of potential breeding pairs.

Results

Ensemble Spatial Logistic Regression models

All four Mindanao models had high calibration accuracy, were robust against random expectations (Table 1), and had high spatial agreement (Table S3). The largest continuous areas of Philippine Eagle habitat were predicted across the eastern and central mountain ranges of Kitanglad, Pantaron, Diwata, and the Bukidnon plateau (Fig. 3). Patchy areas of habitat were identified throughout western Mindanao, largely confined to areas of steep, forested terrain, and extending further south into the Tiruray Highlands and Mount Latian complex. Little habitat was predicted across the now largely deforested lowland plains.

Table 1. Model accuracy and null model metrics for all four model algorithms using Continuous Boyce Index (CBI) and partial ROC (pROC) for both the Mindanao and range-wide Species Distribution Models.

	Mindanao		Range-wide
Model	CBI	pROC	CBI
Penalized GLM	0.906	1.645	0.891
GAM	0.930	1.602	0.934
MARS	0.938	1.627	0.827
MARS*inter*	0.930	1.644	0.852

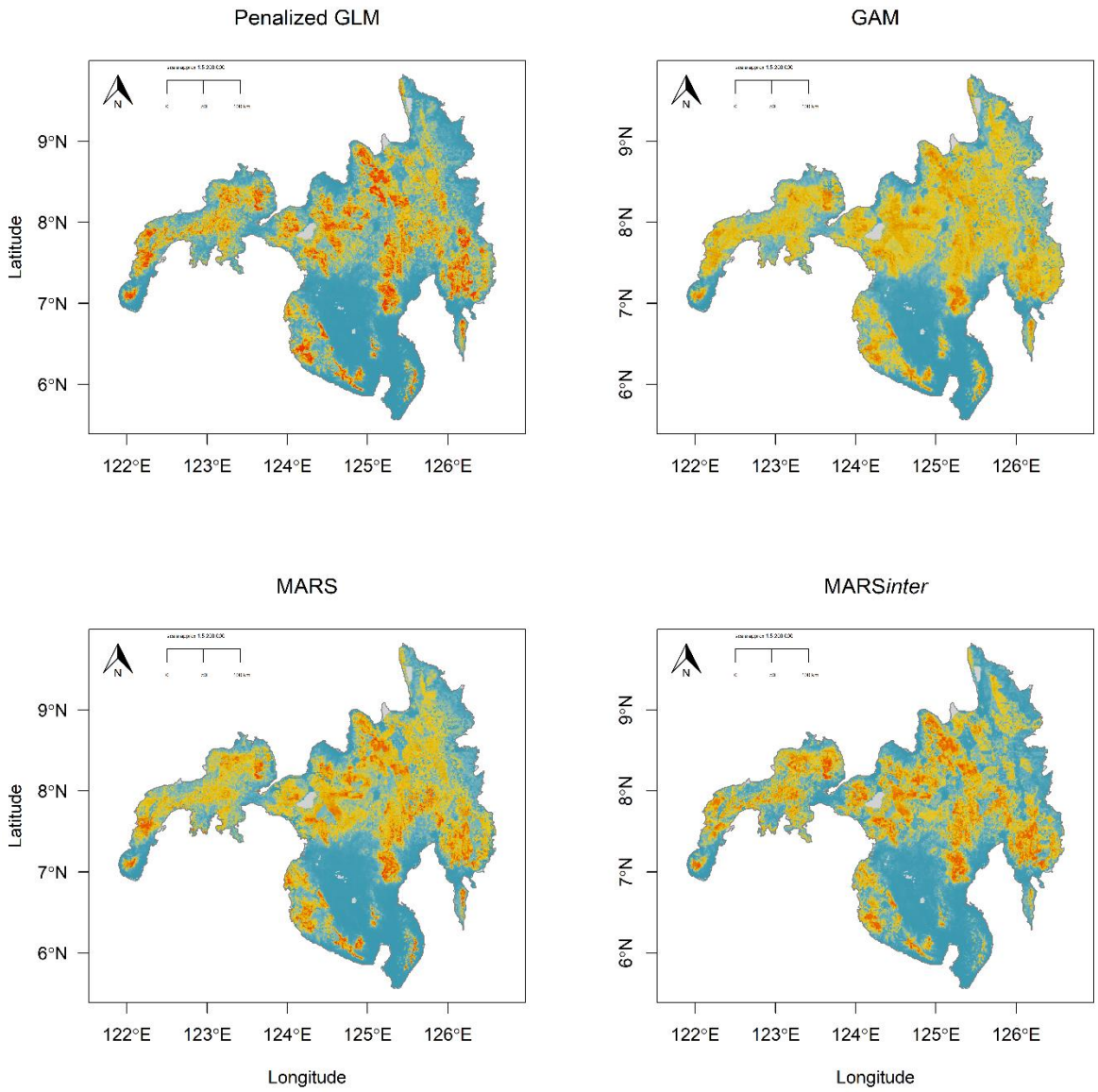

Figure 3. Continuous Species Distribution Models for the Philippine Eagle on the island of Mindanao using four logistic regression-based model algorithms. Maps denote habitat suitability predictions with red areas (values closer to 1) having highest habitat suitability, yellow moderate suitability and blue low suitability (values closer to zero).

Using the GAM response curves, Philippine Eagles on Mindanao had a strong, positive association with high percentage of evergreen forest (Fig. 4), with a peak for CMI = 0.3, and a steadily increasing response to habitat homogeneity from 0.2-0.8, indicating a preference for moist, densely forested areas with medium to high vegetation species richness. Conversely, Philippine Eagles were negatively associated with mosaic forest cover and more likely to be associated with lower values of HFI, peaking at 25, indicating low tolerance to human land use. Philippine Eagles had a negative response to increasing Leaf Area Index, suggesting habitat use of open canopy areas with an LAI of 0.5, decreasing steadily to denser canopies with an LAI of 3.

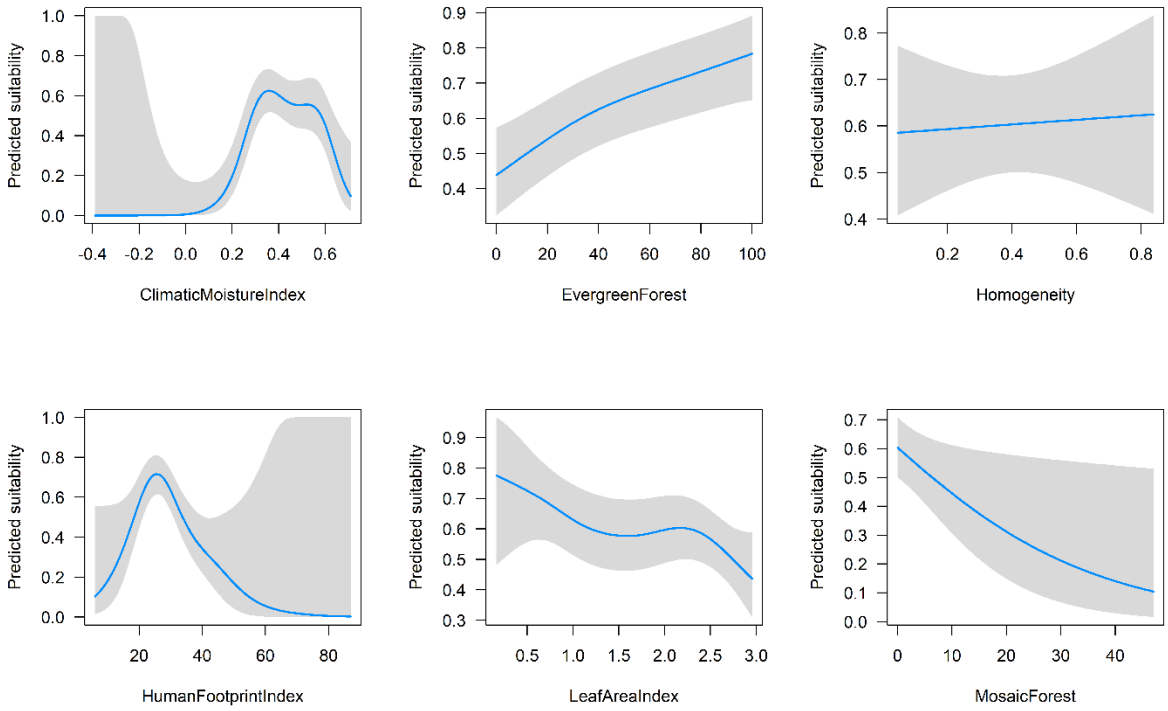

Figure 4. GAM response curves with 95 % Confidence Intervals (grey shading) derived from maximum likelihood estimates obtained from the continuous GAM prediction for Mindanao.

All four range-wide predictions were in general spatial agreement (Table S4) and had high calibration accuracy (Table 1; Fig. S2). The final range-wide continuous ensemble model had higher predictive performance than all the individual range-wide models (CBI = 0.977; Fig. 5). For the Eastern Visayas, most Philippine Eagle habitat was predicted in the central mountainous areas of both Leyte and Samar. In Luzon the largest continuous areas of Philippine Eagle habitat extended along the east of the island in the Sierra Madres mountain range and in the west of Luzon in the northern Cordillera mountain range. A further smaller area of habitat was predicted for the Zambales mountain range in the far west of Luzon, with patchy habitat predicted across the Bicol peninsula in the south-east of the island.

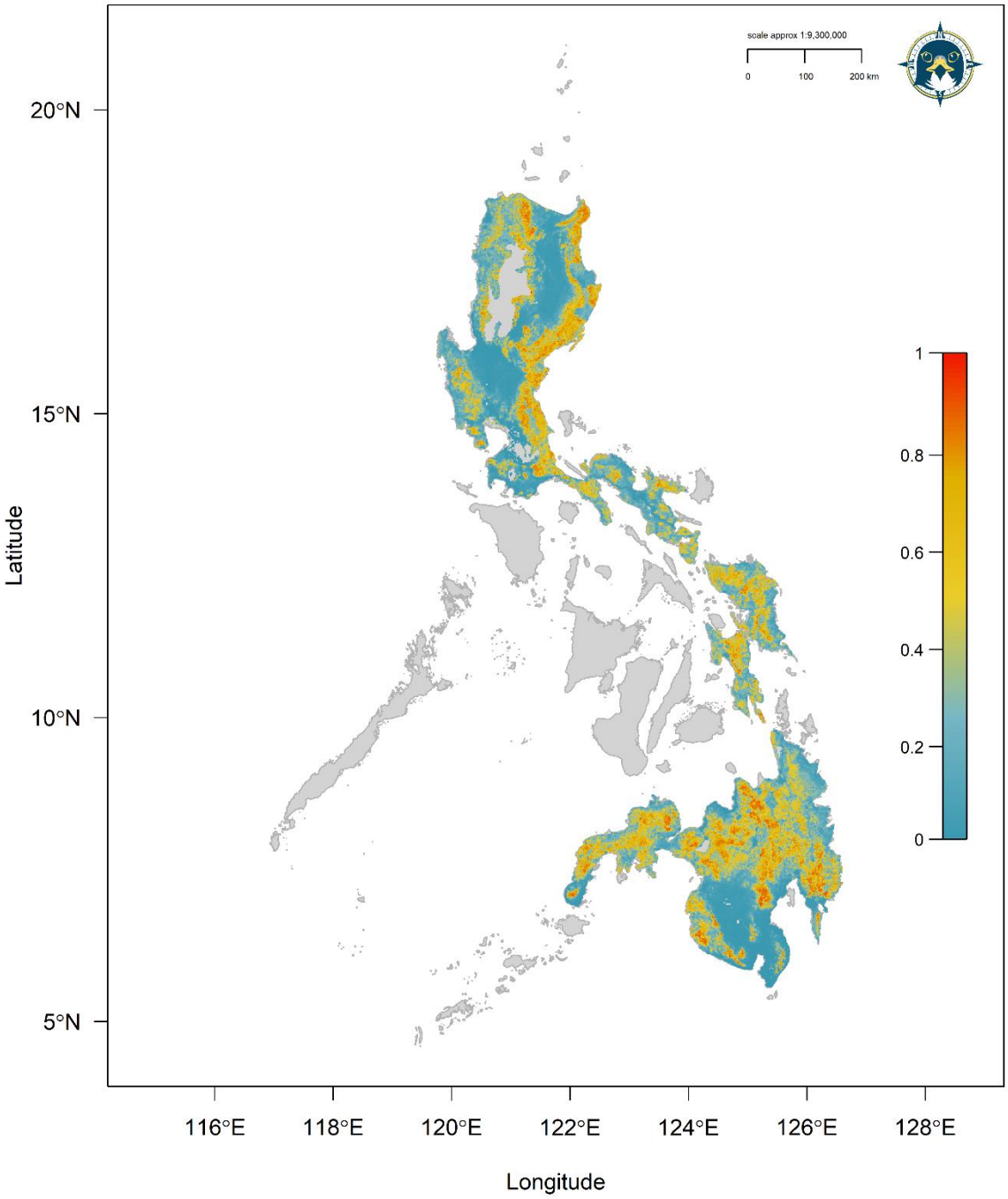

Figure 5. Range-wide Ensemble Spatial Logistic Regression model for the Philippine Eagle using four CBI-weighted logistic regression-based model algorithms. Map denotes continuous prediction with red areas (values closer to 1) having highest habitat suitability, yellow moderate suitability and blue low suitability .

Range metrics and population size

The reclassified binary model (upper quantile threshold = 0.498) calculated a *model* AOH totalling 49,426 km^2 (Fig. 6). From the *model* AOH, maximum EOO was 609,697 km^2 and minimum EOO 273,794 km^2 (Fig. 6), with an AOO of 54,695 occupied cells. **T**he median territorial habitat area based on the home range estimates from the six adults was 73 km^2 using the KDE estimator (Table 2; Fig. S3), with a minimum and maximum range of 64 and 90 km^2 of territorial habitat area using the median home range estimates from the r-LoCoH and 99 % MCP estimators respectively (Table 2; Fig. S4). Using our formulation we calculated the *model* AOH could support 677 breeding pairs (range: 549-772), or 1354 mature individuals, across the entire Philippine Eagle range based on the *model* AOH area of 49,426 km^2. The area of habitat in Mindanao could potentially support 305 breeding pairs (range: 248-348; Fig. S5), in Luzon 310 pairs (range: 252-354; Fig. S6) and in the Eastern Visayas 61 pairs (range: 49-69; Fig. S7).

Table 2. Home range estimates for six breeding adult Philippine Eagles using three home range estimators. r-LoCoH = radius Local Convex Hull; KDE = Kernel Density Estimate, MCP = Minimum Convex Polygon.

Adult ID	r-LoCoH	95% KDE	99% MCP
001F	61	70	88
002F	85	75	105
003F	37	43	36
004M	66	107	91
005M	53	41	57
006F	120	147	173
Median	64	73	90

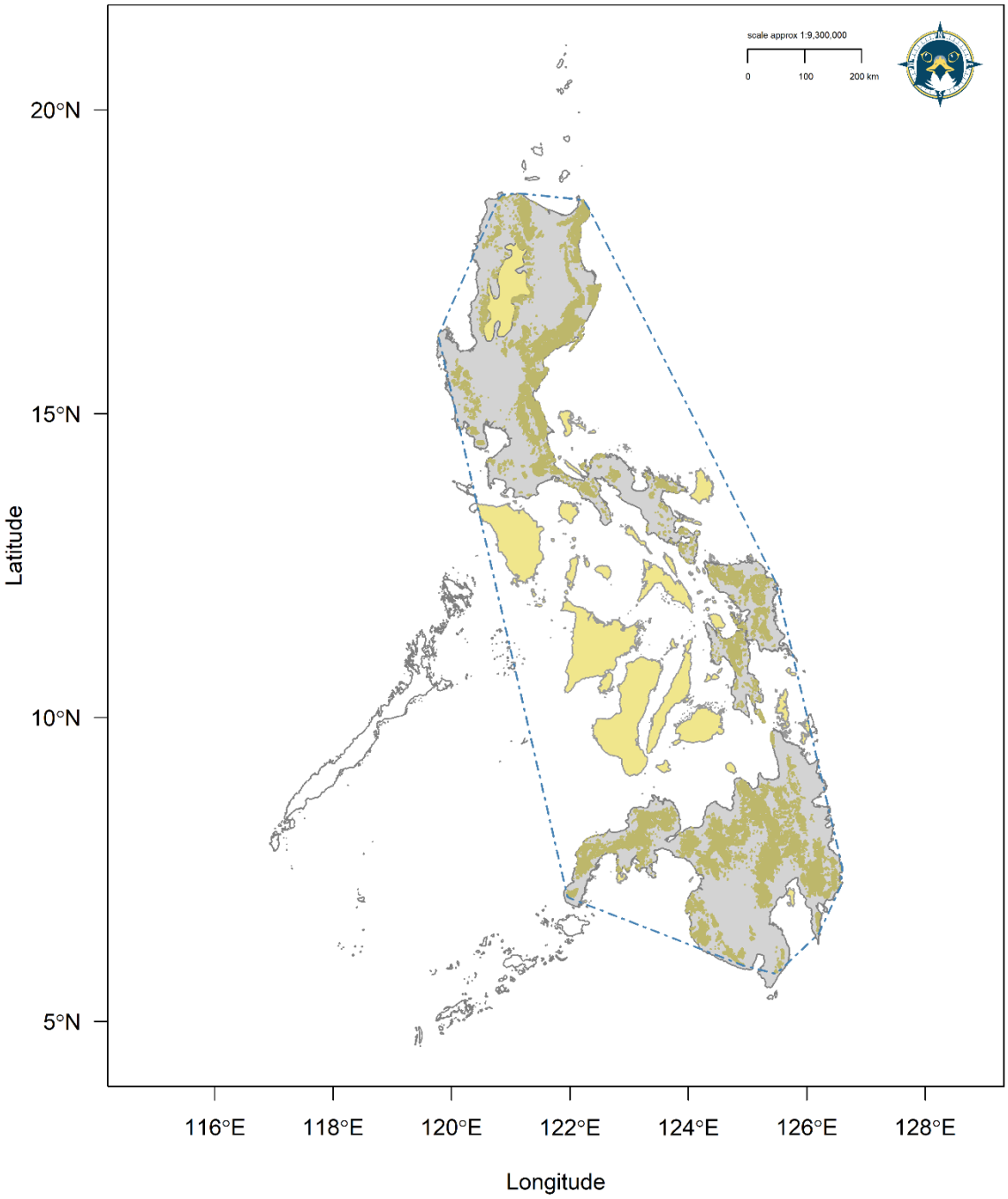

Figure 6. Range metrics for the Philippine Eagle showing the reclassified binary *model* AOH area (brown) and EOO (hashed blue polygon). Grey island polygons represent the species accessible area. Yellow polygons define the national boundary of the Philippines not within the species accessible area.

Discussion

Range-restricted tropical raptors are particularly threatened by human-induced land use activities (Bildstein *et al.* 1998; Cruz *et al.* 2021), with many experiencing severe population declines and in need of immediate research and conservation (McClure *et al.* 2018; Buechley *et al.* 2019). Correlating occurrence data from multiple sources with remote-sensing environmental data, we provide a first estimate of Area of Habitat for the Philippine Eagle, update the species' IUCN range metrics, and provide the first empirically derived global population estimate. By establishing baselines for these key biological parameters, our model outputs are useful for directing long-term monitoring and conservation planning for this Critically Endangered raptor. Despite issues of geographic sampling bias in our occurrence dataset, we were able to overcome any analytical setbacks by implementing a robust and straightforward modelling framework. We view our methodology as a widely applicable tool for quantifying species-habitat associations for many taxa of conservation concern, not just raptors. However, we recognise that our model framework would be most effective for use in habitat models for rare species that lack sufficient occurrence data across their geographic range.

Our ensemble-averaged habitat model had high predictive accuracy and was able to identify key areas of Philippine Eagle habitat across all range islands (Figs. 5-6 & S5-7). Indeed, the final ensemble model had higher predictive accuracy than all the individual range-wide models, consistent with previous broad-scale ensemble comparison analyses using a range of taxa (Valavi *et al.* 2021). However, we recognise that our model was unable to predict into certain areas known to have Philippine Eagles present, even though our covariates covered a broad range of

conditions and resources assumed to be optimal for Philippine Eagles. On Mindanao, our models failed to predict habitat in low-lying areas where several nest sites are located, and on Luzon where immature eagles have dispersed. Because evergreen forest cover in Mindanao is largely confined to rugged mountainous terrain, the correlation with mid to high elevation and rough terrain may not have been able to predict into lower elevation areas elsewhere. Thus these inaccuracies may be related to the environmental covariates used rather than the model algorithms because the erroneous predictions were consistent across all four algorithms. Perhaps incorporating covariates such as those from remotely sensed satellite images of current vegetation with sufficient ground truthing may improve model predictions (Shirley *et al.* 2013; Busetto & Ranghetti 2016). Despite these minor drawbacks, we view our ESLR method as a promising spatial tool for modelling species-habitat associations with limited numbers of geographically biased occurrence data.

Our *model* AOH map updates previous estimates of potential habitat for the Philippine Eagle, and we note the similarity of our *model* AOH to the habitat map from Rabor (1989)**.** We were able to use our binary model prediction to calculate a first estimate for AOO (54,695 occupied cells) and an updated EOO bounded from the *model* AOH polygon (see Fig. 6). Our maximum EOO (609,697 km^2), was almost 10 % larger than the current IUCN estimate (551,000 km^2; BirdLife International 2018). However, when considering the area of EOO not covering the unoccupiable area of the ocean, our minimum EOO (273,794 km^2) was nearly 50 % less. We posit that using a minimum EOO is more relevant for species that range across island archipelagos because including areas that cannot be occupied within the entire area

of the MCP in the EOO range metric calculation is potentially misleading. We recognise the need to have a consistent global methodology for species range metrics but not at the cost of inflating the spread of risk in the EOO range metric for threatened island ranging species. Thus, we recommend that both a minimum and maximum EOO be reported in future IUCN range assessments where relevant.

Area of Habitat maps are useful in many conservation applications such as protected area assessments, targeting surveys and monitoring habitat loss (Brooks *et al.* 2019). Here, we applied our *model* AOH to calculating a key biological parameter used in IUCN conservation risk assessments, that of a global population estimate (IUCN 2019). However, we stress that our global estimate of 677 pairs (1354 mature individuals) is the *potential* breeding population size based on inferred habitat with a small sample size of home range estimates. Our global population size was higher than both the current suggested estimates of 340 pairs (BirdLife International 2018) and 500 pairs (Salvador & Ibañez 2006) and from an earlier estimate of 88-221 pairs (Rabor 1989). However, the key difference here is that we used an empirical estimate of habitat area needed for each pair based on home range estimates. Assuming our baseline population estimate is accurate we urge more investment and research, such as ground truthing surveys, into conserving these remaining populations and their forest habitat.

Our population estimate for Mindanao (n = 305 pairs) was higher than the current estimate for the island (82-233 pairs; Bueser *et al.* 2003), and higher than other previous population estimates which used assumed estimates of habitat area (Kennedy 1977; Krupa 1989; but see Collar 1997). The potential population estimate

for Luzon (*n* = 310 pairs) was slightly higher than for Mindanao and from a previous estimate of 33-83 pairs (Krupa 1989), suggesting that more research and exploratory, ground truthing surveys are required across Luzon to establish how accurate our baseline population estimate is. Historically, Philippine Eagles were recorded throughout Luzon (Kennedy 1977) and are known to currently nest in the eastern Sierra Madre range (Panopio *et al.* 2021), albeit at assumed low densities (Krupa 1989). Indeed, recent surveys in the north of Luzon discovered the first nest in the northern Cordillera range (Abaño *et al.* 2016), with our model predicting extensive Philippine Eagle habitat across both the Sierra Madre and Cordillera ranges. Interestingly, our estimate of 61 pairs for the Eastern Visayan islands of Leyte and Samar was far higher than previous estimates (Kennedy 1977; Krupa 1989). Previous pair numbers for Samar estimated between 8-19 pairs (Krupa 1989), with numbers on Leyte estimated to be between 8-10 pairs (Kennedy 1977), or as low as 1-4 pairs (Krupa 1989). Similar to the situation on Luzon, we urge more research and surveys are carried out on both Eastern Visayan islands to ground truth the estimates given here.

Whilst we envision the possibility of broad applications for our methodology, we recognise that the spatial workflow we have set out is likely most useful for island endemic species with low numbers of occurrences, or with pronounced geographic sampling bias in species locations. There is no one overriding ‘best’ method for modelling species-habitat associations but multiple approaches dependent on the purpose of the study (Qiao *et al.* 2015). Our approach was useful because of its ability to predict beyond the known range limits of the Philippine Eagle, providing a *potential* area of habitat. This was appropriate in this context when our goal was to

provide baseline estimates for global range extent and population size, with geographically biased species locations, rendering standard habitat modelling approaches unsuitable. Further, the standard IUCN approach to estimating AOH uses solely landcover and elevation as covariates (Brooks *et al.* 2019). Here, along with landcover we also incorporated important predictors for determining species' habitat associations such as climate and human land use (Guisan *et al.* 2017). We recommend that analysts consider these key variables in future area of habitat assessments to fully capture the environmental range limits for a given taxa.

Globally, more than half of all raptor species are threatened, largely due to increasing human land use activities, driving habitat loss and degradation (McClure *et al.* 2018). Quantifying baseline biological parameters, such as range extent and population size is key to establishing a solid foundation from which to build effective conservation action (Watson 2018). With the fundamentals of where a given species is and how many individuals there are, conservation planning can be more effectively directed to areas of high conservation priority (IUCN 2001; Rodríguez *et al.* 2007). Our results demonstrate that even with geographically biased occurrence datasets, useful and accurate habitat models can be produced which can then be translated into globally recognised range metrics and baseline population estimates. In the absence of widespread occurrence data for many rare species, our method is a promising spatial tool with widespread applications for many taxa, in particular for those island endemic species facing high extinction risk.

Acknowledgements

We thank all staff and volunteers from the Philippine Eagle Foundation who conducted fieldwork over the past four decades, including our local forest guards, nest wardens and Indigenous co-researchers. We are grateful to Cornell University for supplying the restricted eBird location data and thank all individuals and organisations who contributed data to the GRIN information system. LJS thanks The Peregrine Fund for providing a post-doctoral research grant and we thank the M.J. Murdoch Charitable Trust for funding. The PEF would like to thank our local government partners across the Philippines, and the following institutions that funded and supported the field surveys and nest monitoring that led to this paper across the years: Mohammed Bin Zayed Conservation Fund, Local Government of Apayao and Calanasan, Disney Conservation, Whitley Fund for Nature, Microwave Telemetry, Inc, KoEko, Forest Foundation Philippines, The Peregrine Fund, Direct Aid Program - AusAID, USAID/Phil-Am Fund, USAID/Protect Wildlife, Insular Life Foundation, GIZ-Coseram, Pacific Paints (Boysen) Philippines, Energy Development Corporation, UNDP Global Environment Fund, Italy Debt Swamp/Department of Finance, US Forest Service, San Roque Power Corporation, Cornell Lab of Ornithology, Raptor Resource Project, and the Department of Environment and Natural Resources through the Biodiversity Management Bureau and its regional and local offices (DENR Regions 2, 4, 8, 9, 10, 11, 12, and 13). We are required by the national government of the Philippines to acquire a Gratuitous Permit to trap and tag the birds. Part of the permit requirement is the presence of the veterinarian during each trapping attempt. All trappings were done with a GP and in the presence of a veterinarian

Data Accessibility Statement

Upon acceptance the data that support the findings of this study will be made openly available on the data repository *figshare*

Conflict of Interest

The authors have no conflict of interest to declare.

References

Abaño, T.R.C., Salvador, D J. & Ibañez, J.C. (2016). First nesting record of Philippine eagle *Pithecophaga jefferyi* from Luzon, Philippines, with notes on diet and breeding biology. *Forktail*. 32: 86-88.

Araújo, M.B. & New, M. (2007). Ensemble forecasting of species distributions. *Trends in Ecology & Evolution*. 22: 42-47.

Asner, G.P., Scurlock, J.M. & A. Hicke, J. (2003). Global synthesis of leaf area index observations: implications for ecological and remote sensing studies. *Global Ecology and Biogeography*. 12: 191-205.

Baddeley, A., Berman, M., Fisher, N.I., Hardegen, A., Milne, R.K., Schuhmacher, D., Shah, R. & Turner, R. (2010). Spatial logistic regression and change-of-support in Poisson point processes. *Electronic Journal of Statistics*. 4: 1151-1201.

Barve, N., Barve, V., Jiménez-Valverde, A., Lira-Noriega, A., Maher, S.P., Peterson, A.T., Soberón, J. & Villalobos, F. (2011). The crucial role of the accessible area in ecological niche modeling and species distribution modeling. *Ecological Modelling*. 222: 1810-1819.

Becker, J.J., Sandwell, D.T., Smith, W.H.F., Braud, J., Binder, B., Depner, J.L., Fabre, D., Factor, J., Ingalls, S., Kim, S.H. & Ladner, R. (2009). Global bathymetry

and elevation data at 30 arc seconds resolution: SRTM30_PLUS. *Marine Geodesy*. 32: 355-371.

Bildstein, K.L., Schelsky, W., Zalles, J. & Ellis, S. (1998). Conservation status of tropical raptors. *Journal of Raptor Research*. 32: 3-18.

Buechley, E.R., Santangeli, A., Girardello, M., Neate-Clegg, M.H., Oleyar, D., McClure, C.J., & Şekercioğlu, Ç.H. (2019). Global raptor research and conservation priorities: Tropical raptors fall prey to knowledge gaps. *Diversity and Distributions*. 25: 856-869.

Bueser, G.L.L., Bueser, K.G., Afan, D.S., Salvador, D.I., Grier, J.W., Kennedy, R.S., & Miranda, H.C. (2003). Distribution and nesting density of the Philippine Eagle *Pithecophaga jefferyi* on Mindanao Island, Philippines: what do we know after 100 years? *Ibis*. 145: 130-135.

Busetto, L. & Ranghetti, L. (2016). MODIStsp: An R package for automatic preprocessing of MODIS Land Products time series. *Computers & Geosciences*. 97: 40-48.

BirdLife International (2018). *Pithecophaga jefferyi* (amended version of 2017 assessment). The IUCN Red List of Threatened Species 2018: e.T22696012A129595746. http://dx.doi.org/10.2305/IUCN.UK.2017-3.RLTS.T22696012A129595746.en

Bivand, R., Keitt, T. & Rowlingson, B. (2019). rgdal: Bindings for the 'Geospatial' Data Abstraction Library. R package version 1.4-3. https://CRAN.R-project.org/package=rgdal.

Bivand, R., Pebesma, E. & Gomez-Rubio, V. (2013). *Applied spatial data analysis with R.* 2nd Ed. Springer, NY, USA.

Bivand, R. & Rundel, C. (2019). rgeos: Interface to Geometry Engine - Open Source ('GEOS'). R package version 0.4-3. https://CRAN.R-project.org/package=rgeos.

Breiner, F.T., Guisan, A., Nobis, M.P., & Bergamini, A. (2017). Including environmental niche information to improve IUCN Red List assessments. *Diversity and Distributions*. 23: 484-495.

Brooks, T.M., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A., Rylands, A.B., Konstant, W.R., Flick, P., Pilgrim, J., Oldfield, S., Magin, G. & Hilton-Taylor, C. (2002). Habitat loss and extinction in the hotspots of biodiversity. *Conservation Biology*. 16: 909-923.

Brooks, T.M., Pimm, S.L., Akçakaya, H.R., Buchanan, G.M., Butchart, S.H., Foden, W., Hilton-Taylor, C., Hoffmann, M., Jenkins, C.N., Joppa, L. & Li, B.V. (2019). Measuring terrestrial area of habitat (AOH) and its utility for the IUCN Red List. *Trends in Ecology & Evolution*. 34: 977-986.

Calenge, C. (2006). The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modelling*. 197: 516-519.

Chaikin, G. (1974). An algorithm for high speed curve generation. *Computer Graphics and Image Processing.* 3: 346–349.

Collar, N.J. (1997). Species survival versus perpetuation of myth - The case of the Philippine eagle. *Oryx.* 31: 4-7.

Cruz, C., Santulli-Sanzo, G. & Ceballos, G. (2021). Global patterns of raptor distribution and protected areas optimal selection to reduce the extinction crises. *Proceedings of the National Academy of Sciences*. 118: e2018203118

Dahal, P.R., Lumbierres, M., Butchart, S.H., Donald, P.F. & Rondinini, C. (2021). A validation standard for Area of Habitat maps for terrestrial birds and

mammals. *Geoscientific Model Development Discussions*. 1-25. DOI: gmd-2021-245.pdf (copernicus.org)

Díaz, S., Settele, J., Brondízio, E.S., Ngo, H.T., Agard, J., Arneth, A., Balvanera, P., Brauman, K.A., Butchart, S.H., Chan, K.M., Garibaldi, L.A. *et al.* (2019). Pervasive human-driven decline of life on Earth points to the need for transformative change. *Science*. 366: eaax3100. DOI: 10.1126/science.aaw3100

Elith, J. & Leathwick, J. (2007). Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. *Diversity and Distributions*. 13: 265-275.

Ferraz, K.M.P.M.D.B., Morato, R.G., Bovo, A.A.A., da Costa, C.O.R., Ribeiro, Y.G.G., de Paula, R.C., Desbiez, A.L.J., Angelieri, C.S.C. & Traylor-Holzer, K. (2020). Bridging the gap between researchers, conservation planners, and decision makers to improve species conservation decision-making. *Conservation Science and Practice*. e330.

Franklin, J. (2009). *Mapping Species Distributions.* Cambridge University Press, UK.

Gaston K.J. (1994). *Rarity*. Population and Community Biology Series, vol 13. Springer, Dordrecht.

Gaston, K.J. & Fuller, R.A. (2009). The sizes of species' geographic ranges. *Journal of Applied Ecology*. 46: 1-9.

GBIF (2021) GBIF Occurrence Download https://doi.org/10.15468/dl.7vpddn

Getz, W.M., Fortmann-Roe, S., Cross, P.C., Lyons, A.J., Ryan, S.J. & Wilmers, C. C. (2007). LoCoH: nonparameteric kernel methods for constructing home ranges and utilization distributions. *PloS one*. 2: e207.

Guisan, A., Thuiller, W. & Zimmermann, N. E. (2017). *Habitat suitability and distribution models: with applications in R*. Cambridge University Press.

Harris, G. & Pimm, S. L. (2008). Range size and extinction risk in forest birds. *Conservation Biology*. 22: 163-171.

Helmstetter, N.A., Conway, C.J., Stevens, B.S. & Goldberg, A.R. (2021). Balancing transferability and complexity of species distribution models for rare species conservation. *Diversity and Distributions*. 27: 95-108.

Hijmans, R.J. (2017). raster: Geographic Data Analysis and Modeling. R package version 2.6-7. https://CRAN.R-project.org/package=raster.

Hijmans, R.J., Phillips, S., Leathwick, J. & Elith, J. (2017). dismo: Species Distribution Modeling. R package version 1.1-4. https://CRAN.R-project.org/package=dismo.

Hobi, M.L., Dubinin, M., Graham, C.H., Coops, N.C., Clayton, M.K., Pidgeon, A.M. & Radeloff, V.C. (2017). A comparison of Dynamic Habitat Indices derived from different MODIS products as predictors of avian species richness. *Remote Sensing of Environment*. 195: 142-152.

Ibañez, J.C., Miranda, H.C., Balaquit-Ibañez, G., Afan, D.S. & Kennedy, R.S. (2003). Notes on the breeding behavior of a Philippine eagle pair at Mount Sinaka, Central Mindanao. *The Wilson Journal of Ornithology*. 115: 333-336.

Ibañez, J., Sumaya, A. M., Tampos, G., & Salvador, D. (2016). Preventing Philippine Eagle hunting: what are we missing? *Journal of Threatened Taxa*. 8: 9505-9511.

IUCN. (2001). *IUCN Red List categories and criteria: version 3.1*. IUCN Species Survival Commission. Gland, Switzerland & Cambridge, UK.

IUCN Red List Technical working group. (2018). Mapping standards and data quality for the IUCN Red List Categories and Criteria. Version 1.16.

IUCN Standards and Petitions Committee. (2019). *Guidelines for Using the IUCN Red List Categories and Criteria.* Version 14. Prepared by the Standards and Petitions Committee. http://www.iucnredlist.org/documents/RedListGuidelines.pdf.

James, G., Witten, D., Hastie, T. & Tibshirani, R. (2013). *An introduction to statistical learning.* Springer, New York.

Kennedy, R.S. (1977). Notes on the biology and population status of the monkey-eating eagle of the Philippines. *The Wilson Bulletin*. 89: 1-20.

Kittelberger, K.D., Neate-Clegg, M.H., Blount, J.D., Posa, M.R.C., McLaughlin, J. & Şekercioğlu, Ç.H. (2021). Biological correlates of extinction risk in resident Philippine avifauna. *Frontiers in Ecology and Evolution*. 9: 664764.

Krupa, R.E. (1989). Social and biological implications for endangered species management: the Philippine Eagle *Pithecophaga jefferyi*. *Raptors in the modem world.* World Working Group on Birds of Prey and Owls. Pp. 301-313.

Lee, C.K., Keith, D.A., Nicholson, E. & Murray, N.J. (2019). Redlistr: tools for the IUCN Red Lists of ecosystems and threatened species in R. *Ecography*. 42: 1050-1055.

Lewis, R.E. (1986). A rain-forest raptor in danger. *Oryx*. 20: 170-175.

Liu, C., White, M. & Newell, G. (2013). Selecting thresholds for the prediction of species occurrence with presence-only data. *Journal of Biogeography*. 40: 778-789.

Lumbierres, M., Dahal, P.R., Di Marco, M., Butchart, S.H., Donald, P.F. & Rondinini, C. (2021). A habitat class to land cover translation model for mapping Area of Habitat of terrestrial vertebrates. *bioRxiv*. DOI: https://doi.org/10.1101/2021.06.08.447053

Marcer, A., Sáez, L., Molowny-Horas, R., Pons, X. & Pino, J. (2013). Using species distribution modelling to disentangle realised versus potential distributions for rare species conservation. *Biological Conservation*. 166: 221-230.

Marmion, M., Parviainen, M., Luoto, M., Heikkinen, R.K. & Thuiller, W. (2009). etEvaluation of consensus methods in predictive species distribution modelling. *Diversity and Distributions*. 15: 59-69.

Matthiopoulos, J., Fieberg, J. & Aarts, G. (2020). *Species-Habitat Associations: Spatial data, predictive models, and ecological insights.* University of Minnesota Libraries Publishing. Retrieved from the University of Minnesota Digital Conservancy. http://hdl.handle.net/11299/217469.

McClure, C.J.W., Anderson, D.L., Buij, R., Dunn, L., Henderson, M.T., McCabe, J., ... & Tavares, J. (2021). Commentary: The past, present, and future of the Global Raptor Impact Network. *Journal of Raptor Research.* DOI: 10.3356/JRR-21-13.

McClure C.J.W., Westrip J.R.S., Johnson J.A., Schulwitz S.E., Virani M.Z., Davies R., Symes A., Wheatley H., Thorstrom R., Amar A., Buij R., Jones V.R., Williams N.P., Buechley E.R. & Butchart S.H.M. (2018). State of the world's raptors: Distributions, threats, and conservation recommendations. *Biological Conservation*. 227: 390–402.

Merow, C., Smith, M.J. & Silander Jr, J.A. (2013). A practical guide to MaxEnt for modeling species' distributions: what it does, and why inputs and settings matter. *Ecography*. 36: 1058-1069.

Miranda H.C., Salvador, D.I., & Bueser, G. L. (2008). Updates on the nesting biology and population status of the Philippine Eagle *Pithecophaga jefferyi.*

Miranda, H.C., Salvador, D.I., Ibañez, J.C., & Balaquit-Ibañez, G.A. (2000). Summary of Philippine Eagle reproductive success, 1978-98. *Journal of Raptor Research.* 34: 37-41.

Miranda, H.C. & Ibañez, J.C. 2006. A modified Bal-Chatri to capture Great Philippine eagles for radio-telemetry. *Journal of Raptor Research.* 40:235-237.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V., Underwood, E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C. & Loucks, C.J. (2001). Terrestrial Ecoregions of the World: A New Map of Life on Earth. A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience*. 51: 933-938.

Palacio, R. D., Negret, P. J., Velásquez-Tibatá, J., & Jacobson, A. P. (2021). A data-driven geospatial workflow to improve mapping species distributions and assessing extinction risk under the IUCN Red List. *Diversity & Distributions.* 00: 1-12. DOI: https://doi.org/10.1111/ddi.13424

Panopio, J.K., Pajaro, M., Grande, J.M., Dela Torre, M., Raquino, M. & Watts, P. (2021). Conservation Letter: Deforestation—The Philippine Eagle as a Case Study in Developing Local Management Partnerships with Indigenous Peoples. *Journal of Raptor Research*. 55: 460-467.

Qiao, H., Soberón, J. & Peterson, A.T. (2015). No silver bullets in correlative ecological niche modelling: insights from testing among many potential algorithms for niche estimation. *Methods in Ecology and Evolution*. 6: 1126-1136.

R Core Team. (2018). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.

Rabinowitz, D., Cairns, S. & Dillon, T. (1986). Seven forms of rarity and their frequency in the flora of the British Isles. In: Soulé, M.E. (Ed.). *Conservation Biology. The Science of Scarcity and Diversity.* Sinauer, Mass. USA.

Radeloff, V.C., Dubinin, M., Coops, N.C., Allen, A.M., Brooks, T.M., Clayton, M.K., Costa, G.C., Graham, C.H., Helmers, D.P., Ives, A.R. & Kolesov, D. (2019). The dynamic habitat indices (DHIs) from MODIS and global biodiversity. *Remote Sensing of Environment*. 222: 204-214.

Rodríguez, J.P., Brotons, L., Bustamante, J. & Seoane, J. (2007). The application of predictive modelling of species distribution to biodiversity conservation. *Diversity and Distributions*. 13: 243-251.

Salvador, D.J. & Ibanez, J.C. (2006). Ecology and conservation of Philippine Eagles. *Ornithological Science.* 5*:* 171-176.

Signer, J. & Fieberg, J.R. (2021). A fresh look at an old concept: Home-range estimation in a tidy world. *PeerJ*. 9: e11031.

Strimas-Mackey, M. (2021). smoothr: Smooth and Tidy Spatial Features. R package version 0.2.1. https://CRAN.R-project.org/package=smoothr

Sullivan, B.L., Wood, C.L., Iliff, M.J., Bonney, R.E., Fink, D. & Kelling, S. (2009). eBird: A citizen-based bird observation network in the biological sciences. *Biological Conservation*. 142: 2282-2292.

Sutton, L.J., Anderson, D.L., Franco, M., McClure, C.J.W., Miranda, E.B., Vargas, F.H., Vargas González, J. de J. & Puschendorf, R. (2021). Range-wide habitat use and Key Biodiversity Area coverage for a lowland tropical forest raptor across an increasingly deforested landscape. *bioRxiv.* DOI: https://doi.org/10.1101/2021.08.18.456651

Syfert, M.M., Joppa, L., Smith, M.J., Coomes, D.A., Bachman, S.P. & Brummitt, N.A. (2014). Using species distribution models to inform IUCN Red List assessments. *Biological Conservation*. 177: 174-184.

Tétreault, M., & Franke, A. (2017). Home range estimation: examples of estimator effects. *Applied Raptor Ecology: essentials from Gyrfalcon research.* pp 207-242. The Peregrine Fund, Boise, Idaho, USA,

Title, P.O. & Bemmels, J.B. (2018). ENVIREM: An expanded set of bioclimatic and topographic variables increases flexibility and improves performance of ecological niche modeling. *Ecography*. 41: 291-307.

Tuanmu, M.N. & Jetz, W. (2014). A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*. 23: 1031-1045.

Velásquez-Tibatá, J., Olaya-Rodríguez, M.H., López-Lozano, D., Gutiérrez, C., González, I. & Londoño-Murcia, M.C. (2019). BioModelos: A collaborative online system to map species distributions. *PloS one*. 14: e0214522.

Warton, D.I. & Shepherd, L.C. (2010). Poisson point process models solve the "pseudo-absence problem" for presence-only data in ecology. *The Annals of Applied Statistics*. 4: 1383-1402.

Watson, R. T. (2018). Raptor conservation in practice. In: *Birds of Prey: Biology and Conservation in the XXI Century* (J.H. Sarasola, J.M. Grande & J.J. Negro, Eds). Springer, Switzerland. pp. 373–498.

WCS, CIESIN (2005). Last of the Wild Project, v2, 2005 (LPW-2): Global Human Footprint Dataset (Geographic). Palisades, NY: NASA Socioeconomic Data and Application Center (SEDAC). http://sedac.ciesin.columbia.edu/data/set/wildareas-v2-human-footprint-geographic.

Willmott, C.J. & Feddema, J.J. (1992). A more rational climatic moisture index. *The Professional Geographer*. 44: 84-88.

Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J J. & Elith, J. (2021). Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. *Ecological Monographs*. e1486.

van Proosdij, A.S., Sosef, M.S., Wieringa, J.J. & Raes, N. (2016). Minimum required number of specimen records to develop accurate species distribution models. *Ecography*. 39: 542-552.

Supplementary Material

Ensemble Spatial Logistic Regression model

Penalized GLM

We fitted a penalized generalized linear model (GLM) using elastic net logistic regression (Zou & Hastie 2005; Fithian & Hastie 2013), in the R packages glmnet (Friedman *et al.* 2010) and maxnet (Phillips *et al.* 2017). Elastic net logistic regression imposes a regularization penalty on the model coefficients, shrinking towards zero the coefficients of covariates that contribute the least to the model, reducing model complexity (Zou & Hastie 2005; Gastón & García-Viñas 2011; Helmstetter *et al.* 2020). The maxnet package uses an elastic net (via the glmnet package, Friedman et al. 2010) to perform automatic covariate selection (lasso) and continuous shrinkage (ridge regression) simultaneously (Zou and Hastie 2005; Phillips et al. 2017), evaluating the contribution of all covariates and shrinking low-contribution coefficients towards zero. Overall, penalizing model coefficients reduces model variance, resulting in a regression model that generalizes better (Valavi *et al.*

2021). We selected the complementary log-log (cloglog) link function within the maxnet package as a continuous index of habitat suitability, with 0 = low suitability and 1 = high suitability.

Optimal-model selection was based on Akaike's Information Criterion (Akaike 1974) corrected for small sample sizes (AIC_c; Hurvich & Tsai 1989), to determine the most parsimonious model from two maxnet parameters: regularization multiplier (β) and feature classes (Warren & Seifert 2011). Twenty-eight candidate models of varying complexity were built by conducting a grid search with a range of regularization multipliers from 1 to 5 in 0.5 increments, and three feature classes (response functions: Linear, Quadratic, Hinge) in all possible combinations using the 'k-fold' method of cross-validation (k = 5) in the ENMeval package in R (Muscarella *et al.* 2014). We considered all models with a $\Delta AIC_c < 2$ as having strong support (Burnham & Anderson 2004) and based on the model with the lowest ΔAIC_c selected a regularization multiplier of 1 and feature classes, Linear, Quadratic and Hinge.

Thin-plate spline GAM

We fitted a generalized additive model (GAM) using logistic regression with a cloglog link function using a binomial error term in the R package mgcv (Wood 2011, 2017). GAMs are a semi-parametric extension of a GLM able to fit flexible responses to non-linear data, and thus well-suited to complex species-environment relationships (Leathwick *et al.* 2006). We included thin-plate regression spline smoothers on all covariates via restricted maximum likelihood to estimate coefficients and control complexity of the smoother terms (Pederson *et al.* 2019; Saeedi *et al.* 2019). We set the maximum number of effective degrees of freedom (via the k parameter) for each

smoother term at 10 and gamma = 1.4 to avoid over-fitting the data whilst still allowing some complexity in the functions (Pearce & Ferrier 2000; Granadeiro *et al.* 2004; Kim & Gu 2004). We did not include interaction terms as they often reveal complex terms in GAMs, ecologically difficult to interpret (Suárez-Seoane *et al.* 2002; Granadeiro *et al.* 2004).

Multivariate Adaptive Regression Splines

We fitted Multivariate Adaptive Regression Splines (MARS; Friedman 1991) as a semi-parametric extension of a GLM, fitting piecewise linear basis functions with recursive partitioning splines using a binomial error distribution. MARS is a flexible method able to fit complex relationships between response variables and predictors, in particular for species-habitat associations (Leathwick *et al.* 2006; Elith & Leathwick 2007). MARS assesses non-linear relationships at every data cut point with a knot for each predictor, similar to a step function. Knots are chosen automatically in a forward stepwise procedure fitting a linear regression model with the covariate features. Candidate knots are placed within the range of each predictor, defining a pair of basis functions. Once a full set of knots has been created, those knots that contribute the least are removed sequentially by backwards pruning using generalized cross-validation (GCV) to find the optimal model. We fitted both MARS models in the R package earth (Milborrow 2018). First, we used the default additive MARS model (*degree*=1) with a cloglog link function, and second including local interactions between covariates confined to the non-zero parts of the basis functions of each predictor (*degree*=2, MARS*inter*) with a logit link function to achieve model convergence.

References

Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control.* AC-19: 716–723.

Burnham, K. & Anderson, D. (2004). *Model selection and multi-model inference.* Second Edition. Springer-Verlag, NY, USA.

Elith, J. & Leathwick, J. (2007). Predicting species distributions from museum and herbarium records using multiresponse models fitted with multivariate adaptive regression splines. *Diversity and Distributions*. 13: 265-275.

Fithian, W. & Hastie, T. (2013). Finite-sample equivalence in statistical models for presence-only data. *The Annals of Applied Statistics*. *7*: 1917-1939.

Friedman, J. (1991). Multivariate Adaptive Regression Splines. *The Annals of Statistics.* 19: 1-141.

Friedman, J., Hastie, T. & Tibshirani, R. (2010). Regularization Paths for Generalized Linear Models via Coordinate Descent. *Journal of Statistical Software*. 33: 1-22.

Gastón, A. & García-Viñas, J.I. (2011). Modelling species distributions with penalised logistic regressions: A comparison with maximum entropy models. *Ecological Modelling*. 222: 2037-2041.

Granadeiro, J.P., Andrade, J. & Palmeirim, J.M. (2004). Modelling the distribution of shorebirds in estuarine areas using generalised additive models. *Journal of Sea Research*. 52: 227-240.

Helmstetter, N.A., Conway, C.J., Stevens, B.S. & Goldberg, A.R. (2020). Balancing transferability and complexity of species distribution models for rare species conservation. *Diversity and Distributions*. 1-14. DOI: 10.1111/ddi.13174.

Hurvich, C.M. & Tsai C.L. (1989). Regression and time-series model selection in small sample sizes. *Biometrika.* 76: 297–307.

Kim, Y.J. & Gu, C. (2004). Smoothing spline Gaussian regression: more scalable computation via efficient approximation. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)*. 66: 337-356.

Leathwick, J.R., Elith, J. & Hastie, T. (2006). Comparative performance of generalized additive models and multivariate adaptive regression splines for statistical modelling of species distributions. *Ecological Modelling*. 199: 188-196.

Milborrow, S. Derived from mda:mars by T. Hastie and R. Tibshirani. (2018). earth: Multivariate Adaptive Regression Splines. R package version 4.6.3. https://CRAN.R-project.org/package=earth

Muscarella, R., Galante, P.J., Soley-Guardia, M., Boria, R.A., Kass, J.M., Uriarte, M. & Anderson, R.P. (2014). ENMeval: an R package for conducting spatially independent evaluations and estimating optimal model complexity for Maxent ecological niche models. *Methods in Ecology and Evolution.* 5: 1198-1205.

Pearce, J.L. & Ferrier, S. (2000). An evaluation of alternative algorithms for fitting species distribution models using logistic regression. *Ecological Modelling.* 128: 127–147.

Pedersen, E.J., Miller, D.L., Simpson, G.L. & Ross, N. (2019). Hierarchical generalized additive models in ecology: an introduction with mgcv. *PeerJ*. 7: e6876.

Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., & Blair, M.E. (2017). Opening the black box: an open-source release of Maxent. *Ecography*. 40: 887-893.

Saeedi, H., Costello, M.J., Warren, D. & Brandt, A. (2019). Latitudinal and bathymetrical species richness patterns in the NW Pacific and adjacent Arctic Ocean. *Scientific Reports*. 9: 9303.

Suárez-Seoane, S., Osborne, P.E. & Alonso, J.C. (2002). Large-scale habitat selection by agricultural steppe birds in Spain: identifying species–habitat responses using generalized additive models. *Journal of Applied Ecology*. 39: 755-771.

Valavi, R., Guillera-Arroita, G., Lahoz-Monfort, J J. & Elith, J. (2021). Predictive performance of presence-only species distribution models: a benchmark study with reproducible code. *Ecological Monographs*. e1486.

Warren, D.L. & Seifert, S.N. (2011). Ecological niche modeling in Maxent: the importance of model complexity and the performance of model selection criteria. *Ecological Applications.* 21: 335-342.

Wood, S.N. (2011). Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B).* 73: 3-36.

Wood, S.N. (2017). *Generalized Additive Models: An Introduction with R* (2nd Ed). Chapman and Hall/CRC.

Zou, H. & Hastie, T. (2005). Regularization and variable selection via the elastic net. *Journal of the Royal Statistical Society: series B (statistical methodology)*. 67: 301-320.

Supplementary Tables

Table S1. GPS metadata for the six tagged adult Philippine Eagles from the island of Mindanao, used for home range estimation. Fixes are subsampled from the raw data locations using a 3-hr sampling rate interval.

ID	From	To	Fixes
001F	16/02/2014	10/05/2015	1,186
002F	22/12/2014	20/01/2016	1,063
003F	11/04/2013	19/02/2014	263
004M	19/04/2014	05/08/2014	190
005M	17/11/2019	12/09/2021	5,252
006F	15/10/2019	05/06/2021	2,344
Total			10,298

Table S2. Variance Inflation Factor (VIF) scores for six habitat covariates used in Species Distribution for the Philippine Eagle.

Covariate	R^2	Tolerance	VIF
Evergreen Forest	0.420	0.580	1.725
Climatic Moisture Index	0.408	0.592	1.689
Human Footprint Index	0.333	0.667	1.499
Leaf Area Index	0.146	0.854	1.170
Homogeneity	0.118	0.882	1.133
Mosaic Forest	0.028	0.972	1.029

Table S3. Niche overlaps using Schoener's *D* metric calculated from four Species Distribution Models for the Philippine Eagle on the island of Mindanao.

Model	GLM	GAM	MARS
GAM	0.849		
MARS	0.880	0.893	
MARS*inter*	0.839	0.809	0.835

Table S4. Niche overlaps using Schoener's *D* metric calculated from four Species Distribution Models for the Philippine Eagle across the species range.

Model	GLM	GAM	MARS
GAM	0.837		
MARS	0.863	0.888	
MARS*inter*	0.817	0.802	0.811

Supplementary Figures

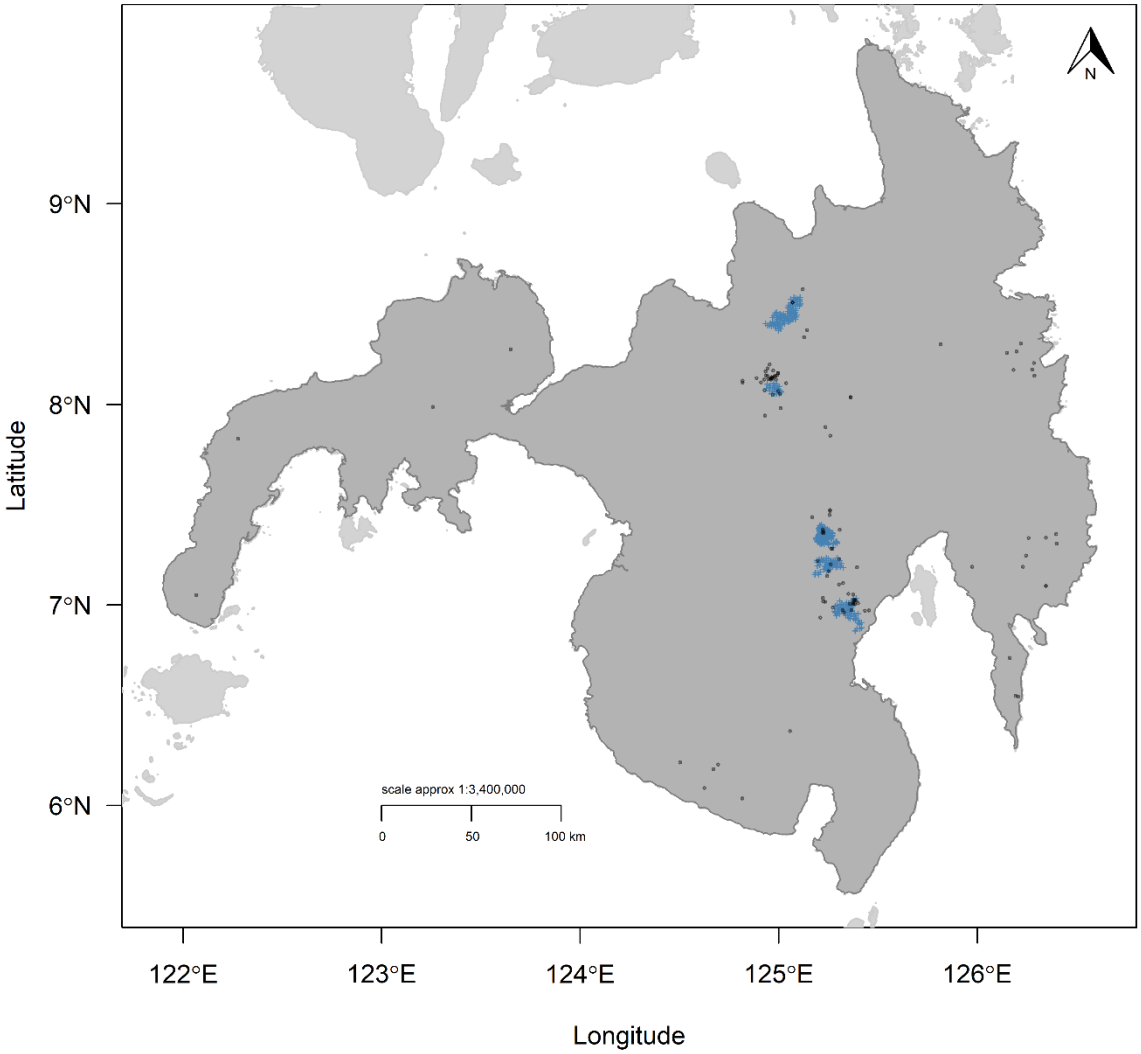

Figure S1. Filtered GPS fixes using a 1-km filter (blue points) for the six tagged adult Philippine Eagles from the island of Mindanao, used in the Species Distribution Models. Black points denote the Philippine Eagle occurrences from nests and community science data.

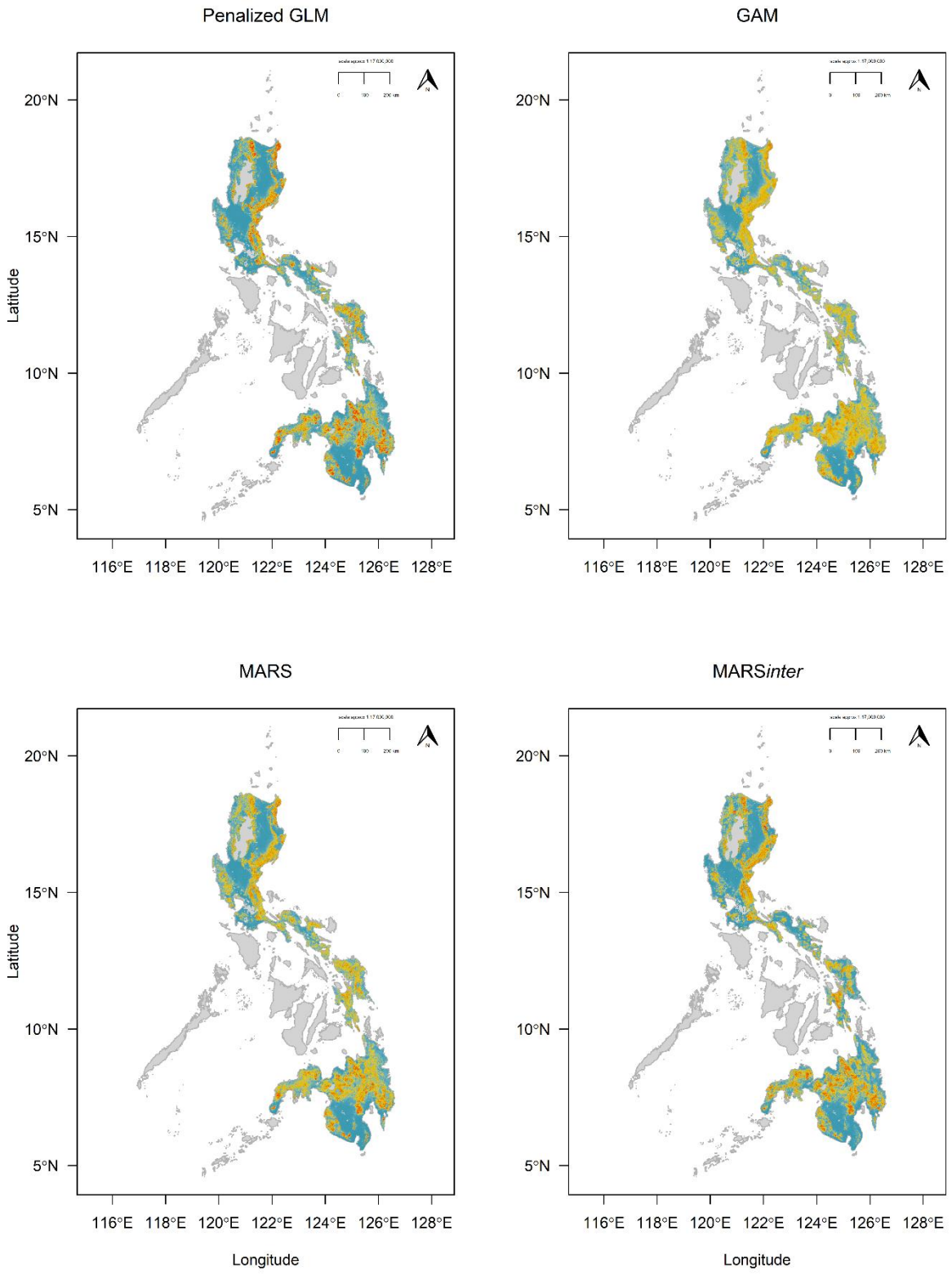

Figure S2. Species Distribution Models for the Philippine Eagle using four logistic regression-based model algorithms. Maps denotes continuous predictions with red areas (values closer to 1) having highest habitat suitability, yellow moderate suitability and blue low suitability (values closer to zero).

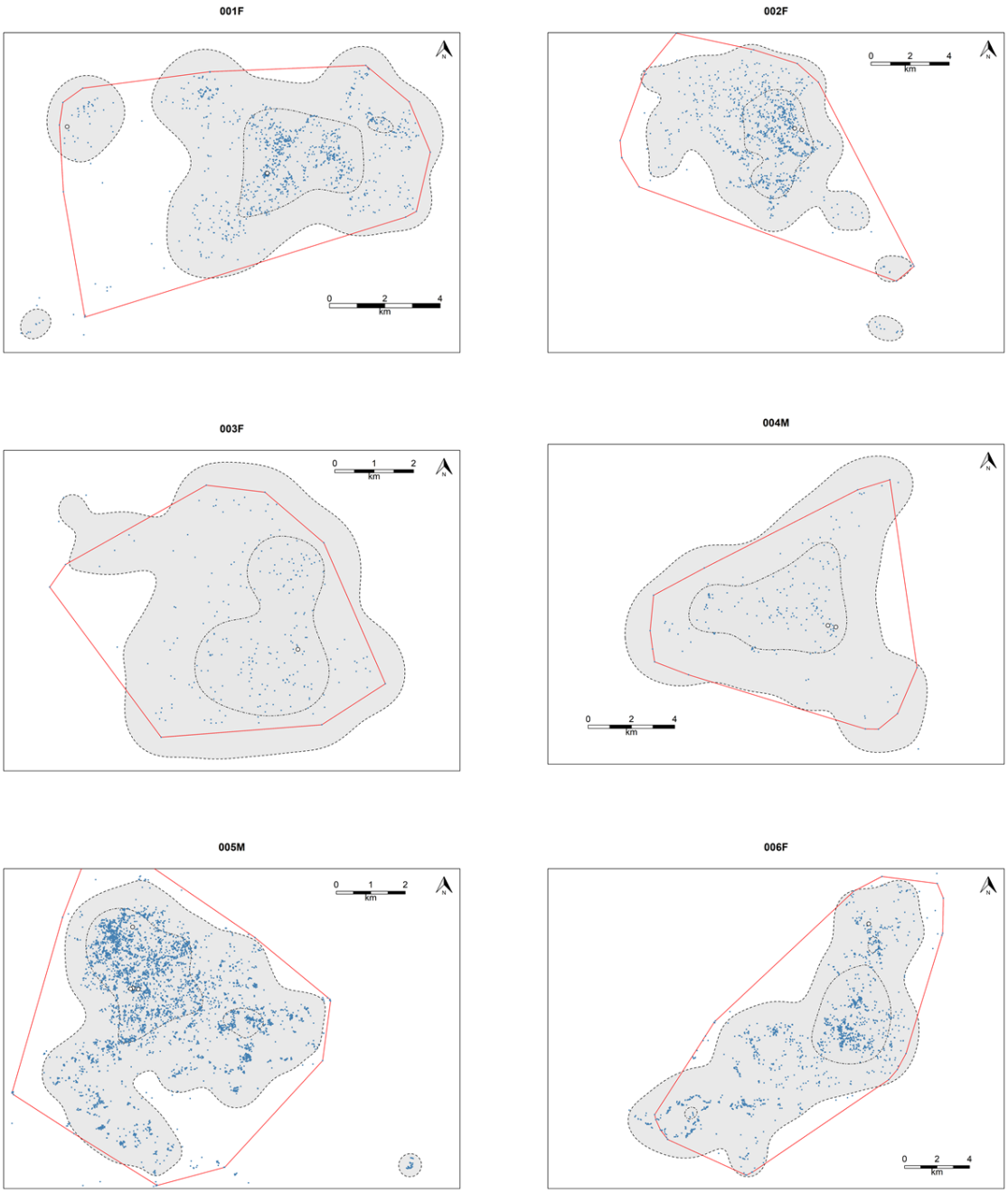

Figure S3. Home range estimates for six adult Philippine Eagles using a bivariate 95% Kernel Density Estimate (KDE, light grey with black dashed line) and 99% Minimum Convex Polygon (MCP, red line). Blue points are GPS fixes, white points known nests, with 50% KDE estimate shown in black dot-dash line.

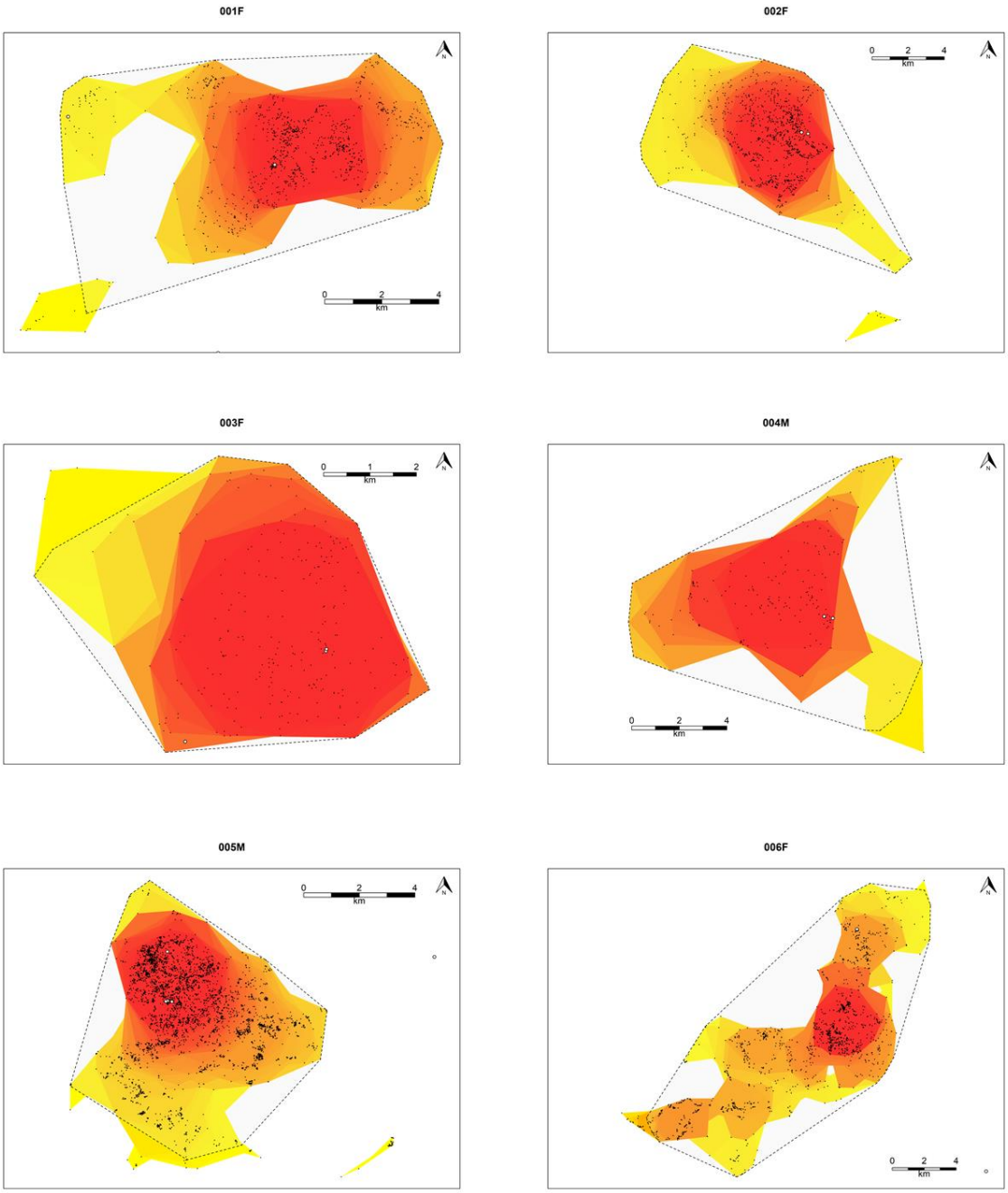

Figure S4. Home range estimates for six adult female Philippine Eagles using a radius Local Convex Hull estimator (r-LoCoH) and 99% Minimum Convex Polygon (MCP, black hashed line). Black points are GPS fixes, white points known nests. The gradient for utilization distribution is represented from high use (red) to low use (yellow).

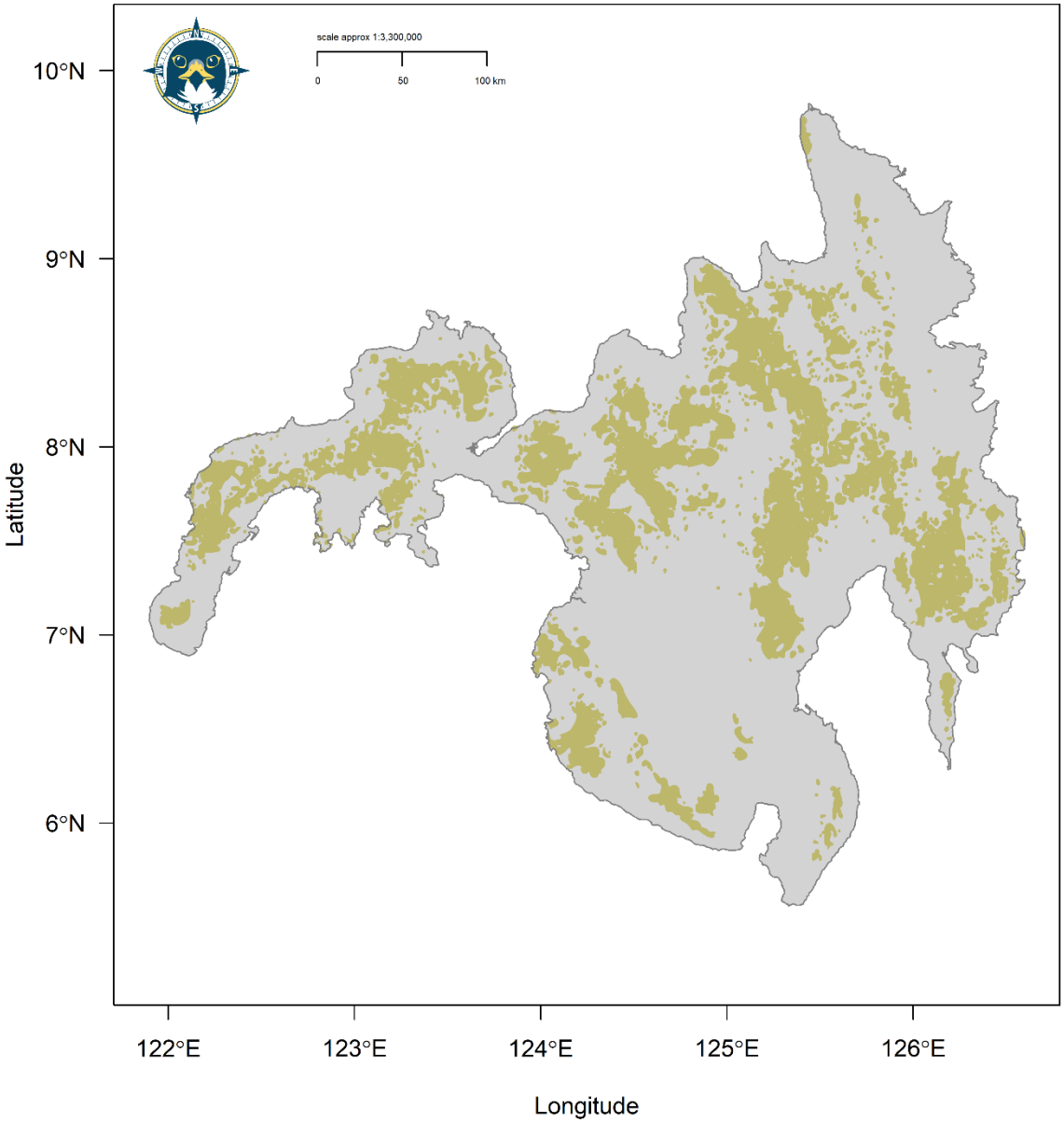

Figure S5. Reclassified binary *model* AOH area (dark khaki) for the Philippine Eagle on the island of Mindanao.

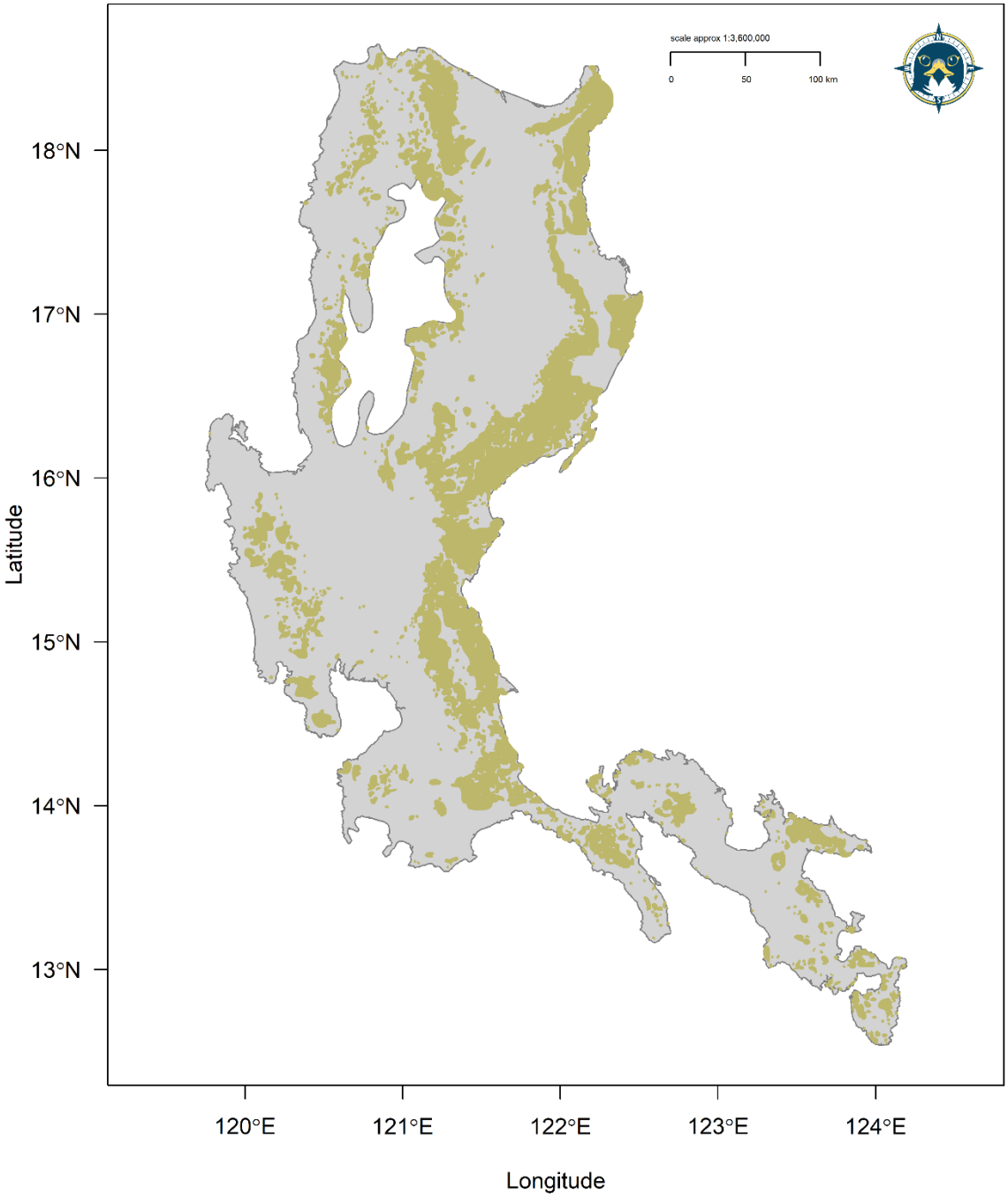

Figure S6. Reclassified binary *model* AOH area (dark khaki) for the Philippine Eagle on the island of Luzon.

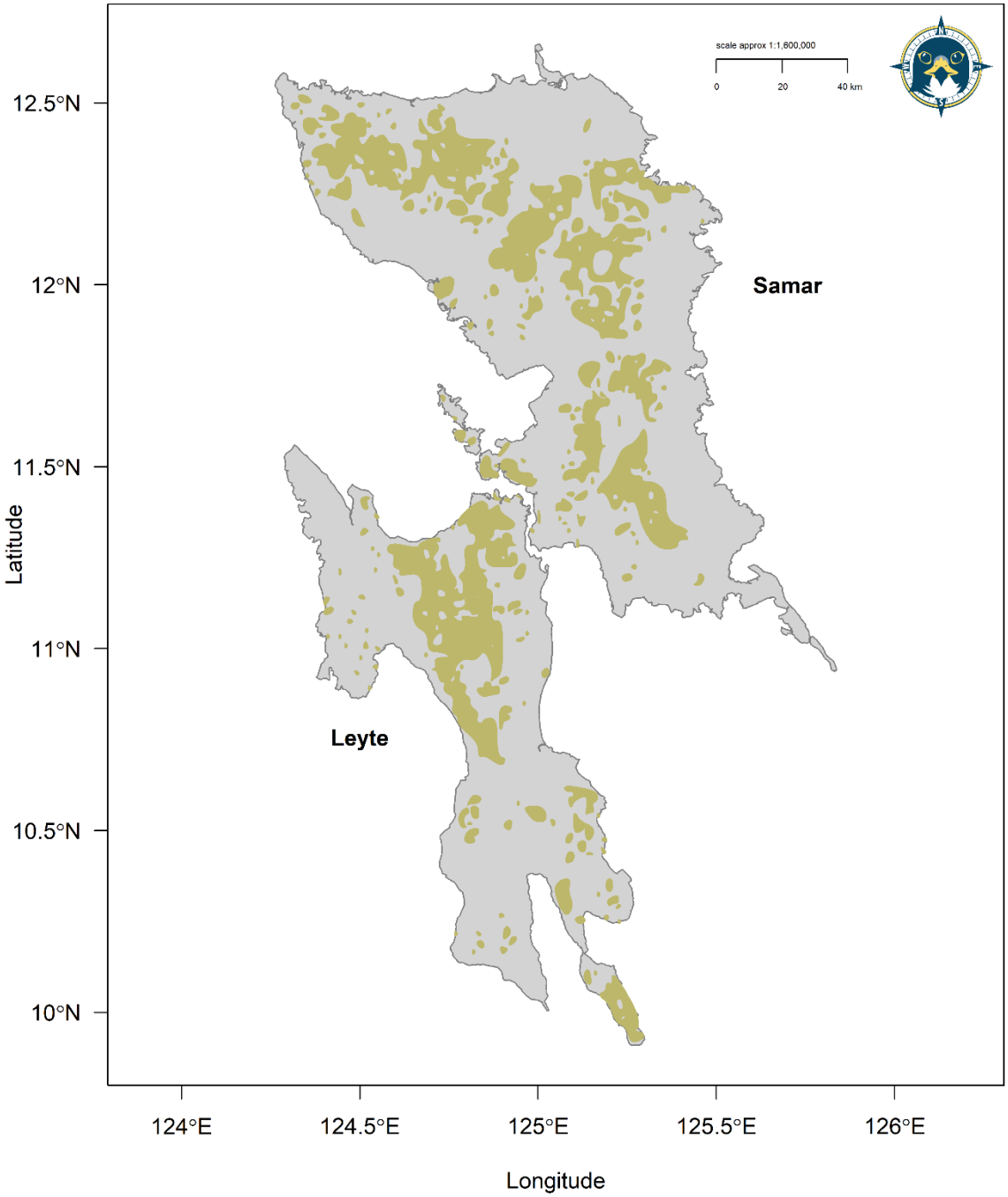

Figure S7. Reclassified binary *model* AOH area (dark khaki) for the Philippine Eagle on the islands of Leyte and Samar in the Eastern Visayas.