University of Plymouth

PEARL https://pearl.plymouth.ac.uk

Faculty of Science and Engineering School of Biological and Marine Sciences

2022-08-02

Range-wide habitat use of the Harpy Eagle indicates four major tropical forest gaps in the Key Biodiversity Area network

Sutton, LJ

http://hdl.handle.net/10026.1/19931

10.1093/ornithapp/duac019
Ornithological Applications
Oxford University Press

All content in PEARL is protected by copyright law. Author manuscripts are made available in accordance with publisher policies. Please cite only the published version using the details provided on the item record or document. In the absence of an open licence (e.g. Creative Commons), permissions for further reuse of content should be sought from the publisher or author.

RESEARCH ARTICLE

Range-wide habitat use of the Harpy Eagle indicates four major tropical forest gaps in the Key Biodiversity Area network

ABSTRACT

Quantifying habitat use is important for understanding how animals meet their requirements for survival and provides information for conservation planning. Currently, assessments of range-wide habitat use that delimit species distributions are incomplete for many taxa. The Harpy Eagle (*Harpia harpyja*) is a raptor of conservation concern, widely distributed across Neotropical lowland forests, that currently faces threats from habitat loss and fragmentation. Here, we use penalized logistic regression to identify species-habitat associations and predict habitat suitability based on a new International Union for the Conservation of Nature range metric, termed Area of Habitat. From the species-habitat model, we performed a gap analysis to identify areas of high habitat suitability in regions with limited coverage in the Key Biodiversity Area (KBA) network. Range-wide habitat use indicated that Harpy Eagles prefer areas of 70-75 % evergreen forest cover, low elevation, and high vegetation species richness. Conversely, Harpy Eagles avoid areas of >10 % cultivated landcover and mosaic forest, and topographically complex areas. Our species-habitat model identified a large continuous area of potential habitat across the pan-Amazonia region, and a habitat corridor from the Chocó-Darién ecoregion of Colombia running north along the Caribbean coast of Central America. Little habitat was predicted across the Atlantic Forest biome, which is now severely degraded. The current KBA network covered 18 % of medium to high Harpy Eagle habitat exceeding a target biodiversity area representation of 10 %, based on species range size. Four major areas of high suitability habitat lacking coverage in the KBA network were identified in north and west Colombia, western Guyana, and north-west Brazil. We recommend these multiple gaps of habitat as new KBAs for strengthening the current KBA network. Modelled area of habitat estimates as described here are a useful tool for large-scale conservation planning and can be readily applied to many taxa.

Keywords: Area of Habitat, conservation planning, gap analysis, habitat use, *Harpia harpyja,* Harpy Eagle, Key Biodiversity Areas, Species Distribution Models

LAY SUMMARY

- Quantifying habitat use is key to understanding animals' requirements for survival and can inform spatial conservation planning by mapping species range limits
- Species that inhabit remote, hard-to-survey areas lack sufficient location data and there is a need to be able to predict into poorly sampled areas to estimate the potential area of habitat
- Using Species Distribution Models we identified Harpy Eagle range limits, habitat area and Key Biodiversity Area coverage across the species range
- Harpy Eagles prefer areas of 70-75 % evergreen forest cover, high vegetation species richness and low elevation
- Key Biodiversity Areas covered 18 % of highly suitable Harpy Eagle habitat but with key gaps in coverage in north and west Colombia, western Guyana, and north-west Brazil

- Our method of calculating habitat area estimates based on a predictive spatial model is a useful tool for large-scale conservation planning and can be readily applied to many taxa.

INTRODUCTION

Determining habitat resource use is a fundamental aspect of wildlife ecology and conservation planning (Manly et al. 2002; Morrison et al. 2006). However, our understanding of range-wide species-habitat associations across continental extents is incomplete, even for well-studied groups such as birds (Gregory and Baillie 1998; Engler et al. 2017; Lees et al. 2020). Currently, many taxa face increasing threats from human-driven habitat loss and fragmentation across their entire range (Powers and Jetz 2019). Therefore, developing a broad spatial quantification of habitat use is an effective starting point for conservation planning (Margules and Pressey 2000; Early et al. 2008). Once habitat use is identified for a focal species, the key variables characterising those habitats can be used to produce a mapped representation of habitat across the species' range (Hirzel et al. 2006). Management actions can then be directed to guide conservation planning to protect or enhance those areas (Margules and Pressey 2000; Suárez-Seoane et al. *2002*).

Recently, the International Union for the Conservation of Nature (IUCN) developed a new range size metric termed Area of Habitat (AOH, Brooks et al. 2019). AOH is defined as the habitat available to a species based on habitat preferences and elevational limits within the mapped distributional range of a focal species. Various approaches have been taken to estimate AOH which all use a similar method of matching and overlaying the known mapped range, landcover and elevation limits of a given species (Brooks et al. 2019). While the AOH method is useful and repeatable, IUCN methods may still have limitations by missing areas that have no occurrence data but may still contain preferred habitat (Ramesh et al. 2017).

On the other hand, Species Distribution Models (SDMs) are statistical methods that assess species' habitat requirements and predict distribution based on correlating environmental covariates with species occurrences (Elith and Leathwick 2009; Matthiopoulos et al. 2020; Valavi et al. 2021). Two example applications for SDMs are the re-evaluation of range sizes (e.g., Herkt et al. 2017), and the identification of gaps in protected or biodiversity area networks (e.g., de Carvalho et al. 2017). Indeed, SDMs can predict more complex and ecologically realistic geographic ranges compared to IUCN range maps (Breiner et al. 2017; Herkt et al. 2017). Using model-based interpolation based on the AOH guidelines but adapted to a correlative modelling approach like SDMs (Da Silva et al. 2020), may also be more effective for highlighting species-specific gaps in biodiversity area coverage by identifying higher coverage of suitable pixels (Di Marco et al. 2017).

Designation of biodiversity areas is a fundamental tool for conservation (IUCN 2016) and has been successful in reducing habitat loss and fragmentation for many taxa (Brooks et al. 2009). However, despite wide coverage in the global biodiversity area network, gaps in biodiversity area coverage still exist with new areas being continually added (KBA Standards and Appeals Committee 2019). Additionally, not all biodiversity areas are located in places deemed effective for conservation but are often designated by human socio-economic factors (Pringle 2017; Morán-Ordóñez 2020; Rodrigues and Cazalis 2020). Key Biodiversity Areas (KBAs, BirdLife

International 2020) are sites of international significance for the global persistence of biodiversity. KBAs also protect areas important for biodiversity and aim to overlap with the entire global protected area network (The World Database on Protected Areas, UNEP-WCMC & IUCN 2021; Donald et al. 2019). The KBA concept is largely based on Important Bird and Biodiversity Areas (IBAs), a template for KBAs which aims to identify and conserve sites of global importance for bird species (Donald et al. 2019). Indeed, the majority of terrestrial KBAs are designated based on birds and contain either: (1) populations of globally threatened species, (2) populations and communities of range- or biome-restricted species, or (3) substantial congregations of specific avian taxa.

Information on where to establish new KBAs identifies where the current biodiversity area networks miss key bird species and where these gaps need filling. Gap analysis is an established method to identify discontinuities in protected or biodiversity area networks (Scott et al. 1993) and has been effective in setting conservation planning priorities across a range of taxa (Margules and Pressey 2000). In particular, gap analysis has identified priority conservation areas for many taxa across the highly biodiverse Neotropics (e.g., de Carvalho et al. 2017; Bax and Francesconi 2019; Perrig et al. 2020). The Harpy Eagle (*Harpia harpyja*) is a large raptor historically distributed throughout Neotropical lowland tropical forest from southern Mexico to northern Argentina (Miranda et al. 2019; Sutton et al. 2021). The species was recently reclassified from ‘Near-Threatened’ to ‘Vulnerable’ by the IUCN Red List due to continued habitat loss and persecution (Birdlife International 2021). Harpy Eagles are now largely restricted to tropical lowland broadleaf forest but can also inhabit dry seasonal forest and fragmented habitat (Vargas González et al. 2006; Silva et al. 2013).

Despite this habitat specialization, the Harpy Eagle has a large range due to the extensive distribution of lowland tropical forest across the Neotropics. However, historical and ongoing deforestation has led to extirpations in parts of southern Mexico and Central America, and across the Atlantic Forest of Brazil (Vargas González et al. 2006; Silva et al. 2013; Meller and Guadagnin 2016). Current deforestation rates across the species' stronghold in Amazonia are also of significant concern for its future persistence (Banhos et al. 2016; Miranda et al. 2019). As an apex predator requiring large tracts of continuous tropical lowland forest for breeding and foraging (Vargas González et al. 2014; Miranda 2015), the Harpy Eagle may also act as a useful trigger species for designating new regional IBAs (BirdLife International 2020), under the assumption that triggering a regional IBA would be justification for inclusion as a KBA. Further, as a threatened species of conservation concern, it fulfils the criteria for designating new regional IBAs based on inferred habitat area (category B1a; BirdLife International 2020), with the assumption that the gap sites identified are predicted to hold significant numbers of a threatened species.

Here, a predictive Species Distribution Model (SDM) was developed to identify species-habitat associations (Matthiopoulos et al. 2020; Valavi et al. 2021) based on penalized logistic regression (Phillips et al. 2017). Estimating Harpy Eagle distribution based solely on habitat predictors at the continental scale should provide the most accurate and reliable estimate of range size due to the Harpy Eagle's generally high reliance on tropical lowland forest. Specifically, this study sets out a baseline assessment of large-scale habitat use defining potential Harpy Eagle distribution. A first estimate of modelled habitat suitability using a spatial framework based on the Area of Habitat metric was then used to predict areas of highest habitat suitability for the Harpy Eagle. Using this information, a broad-scale gap analysis was generated to identify priority areas of highest habitat suitability in regions with limited KBA network coverage. In short, this study applied statistical modelling to systematic conservation planning to determine: **(1)** how effective the current KBA network is for covering areas of Harpy Eagle habitat, and **(2)** where gap areas of highest habitat suitability for the Harpy Eagle are located for inclusion as proposed KBAs.

METHODS

Occurrence Data

Harpy Eagle occurrences were sourced from the Global Raptor Impact Network (GRIN, McClure et al. 2021), a data information system for population monitoring of all raptor species. For the Harpy Eagle, GRIN includes occurrence data from the Global Biodiversity Information Facility (GBIF 2019) and eBird (Sullivan et al. 2009), along with two additional occurrence datasets (Vargas González and Vargas 2011; Miranda et al. 2019). Though it is recommended to apply sampling regime filters to eBird occurrence data (Johnston et al. 2021), we opted to retain all eBird data points because the majority of our eBird occurrences did not have sufficient sampling regime metadata to employ these filters in the analysis (See Supplementary Material). In doing so we also sought to achieve a large enough sample size to capture the widest possible range of species-habitat associations needed for robust predictions (Gaul et al. 2020; Santini et al. 2021).

Duplicate records and those with no geo-referenced location were removed and only occurrences recorded from year 2000 onwards were included to temporally match the timeframe of the habitat covariates. A 5-km spatial filter was applied between each occurrence point, which approximately matches the spatial resolution of the raster data (~4.5-km), resulting in one occurrence per pixel grid cell reducing the effect of biased sampling (Kramer-Schadt et al. 2013). We used this resolution and spatial filter distance because it is an appropriate spatial resolution for identifying environmental variation across lowland tropical regions (Fick & Hjimans 2017), to address continent-scale management issues. A total of 1021 geo-referenced records were compiled after data cleaning. Applying the 5-km spatial filter resulted in a filtered subset of 591 Harpy Eagle occurrence records for use in the calibration models (Fig. 1).

Habitat Covariates

To predict occurrence, habitat covariates representing landcover, topography and vegetation heterogeneity were downloaded from the EarthEnv (www.earthenv.org) and ENVIREM (Title and Bemmels 2018) repositories. Six continuous covariates were used at a spatial resolution of 2.5 arc-minutes (~4.5-km resolution): cultivated landcover, elevation, evergreen forest, habitat homogeneity (i.e., vegetation species richness, structure, composition and diversity), mosaic forest (i.e, a mosaic of mixed forest, shrubland and woody savanna) and Terrain Roughness Index (Table S1; See Supplementary Material). Covariates were selected a prioiri based on the IUCN Area of Habitat criteria from landcover and topographic factors related empirically to Harpy Eagle distribution and tropical forest raptor abundance in previous studies (Robinson

1994; Anderson 2001; Vargas González and Vargas 2011; Miranda et al. 2019; Vargas González et al. 2020; Sutton et al. 2021). Raster layers were cropped to a background region using a delimited polygon consisting of all known range countries (including Formosa, Jujuy, Misiones and Salta provinces in northern Argentina, and Chiapas, Oaxaca, and Tabasco states in southern Mexico).

Species Distribution Model

We fitted an SDM using penalized elastic net logistic regression (Fithian and Hastie 2013), via maximum penalized likelihood estimation (Hefley and Hooten 2015) in the R package *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 (Gastón and García-Viñas 2011; Helmstetter et al. 2020). The *maxnet* package uses penalized logistic regression to fit the SDM based on the maximum entropy algorithm, MAXENT (Phillips et al. 2017), which is mathematically equivalent to estimating the parameters for an inhomogeneous Poisson process (IPP; Fithian and Hastie 2013; Renner and Warton 2013; Hefley and Hooten 2015; Renner et al. 2015). In its original implementation MAXENT imposed a 'lasso' (least absolute shrinkage and selection operator) regularization penalty, where only the most significant covariates are retained, with uninformative covariates set at zero. Instead, 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. Elastic net regularization improves predictive accuracy compared to the lasso, in both simulated and real data examples (Zou and Hastie 2005) and may be viewed as a generalization of the lasso. We parametrized the penalized logistic regression model using infinite weighting within the IPP framework because this is the most effective method to model presence-background data as used here (Warton and Shepherd 2010; Hefley and Hooten 2015). Within the *maxnet* package the complementary log-log (cloglog) link function was selected as a continuous index of habitat suitability, with 0 = low suitability and 1 = high suitability. Phillips et al. (2017) demonstrated the cloglog link is equivalent to an IPP and can be interpreted as a measure of relative occurrence probability proportional to a species potential abundance. We used a tuned penalized logistic regression algorithm because this approach outperforms other SDM algorithms (Valavi et al. 2021), including ensemble averaged methods (Hao et al. 2020).

We used 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; Figure S1). Optimal-model selection was based on Akaike's Information Criterion (Akaike 1974) corrected for small sample sizes (AIC_c; Hurvich and Tsai 1989), to determine the most parsimonious model from two key *maxnet* parameters: regularization beta multiplier (β; level of coefficient penalty) and feature classes (response functions, Warren and Seifert 2011; Phillips et al. 2017). Eighteen candidate models of varying complexity were built by conducting a grid search using a range of regularization multipliers from 1 to 5 in 0.5 increments, and two feature classes (response functions: Linear, Quadratic) in all possible combinations using the '*trainMaxNet'* function in the R package *enmSdm* (Smith 2019). We considered all models with a $\Delta AIC_c < 2$ as having strong support (Burnham and Anderson 2004), and the model with the lowest β was selected to avoid overfitting. We used response curves and parameter estimates to measure variable performance in the optimal calibration model.

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 from 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). The optimal model was tested 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 and Barve, 2013).

Range Size and Gap Analysis

To calculate Area of Habitat in suitable pixels and assess the effectiveness of the KBA network, we reclassified the continuous prediction to a binary threshold prediction. All pixels equal to or greater than the median pixel value of 0.345 from the continuous model were used as a suitable threshold for conservation planning (Liu et al. 2005; Rodríguez-Soto et al. 2011; Portugal et al. 2019). We selected the median because this threshold is not reliant on measuring predictive ability based on unknown pseudo-absences (Merow et al. 2013), unlike measures that use specificity (Liu et al. 2013). The KBA network polygons (as of September 2020; BirdLife International 2020) were then clipped to the reclassified area, establishing those KBAs covering pixels of habitat suitability $\geq$ 0.345 threshold. To visualise KBA network coverage, we reclassified the continuous prediction into four discrete quantile habitat classes (No habitat: 0.0 - 0.067; Low: 0.068 - 0.344; Medium: 0.345 - 0.701; High: 0.702 - 1.000).

The clipped KBA network polygons were then overlaid onto the discrete class map identifying those pixels of medium to high habitat $\geq$ 0.345 threshold which were within the clipped KBA network polygons. We used the threshold range size to calculate a protected area 'representation target', quantifying how much protected area representation is needed for a species dependent on its range size following the formulation of Rodrigues et al. (2004),

$$\text{Target} = \max(0.1, \min(1, -0.375 \times \log10(\text{range size}) + 2.126)) \qquad (1)$$

where 'Target' is equal to the percentage of protected target representation required for the species 'range size', as used in subsequent applications of the formula (Butchart et al. 2015; Di Marco et al. 2017). As can be verified by inserting different range size values, this formula yields a target of 10 % for species with a range size >250,000 km^2 and increasing proportional representation for smaller range sizes up to a target of 100 % if range size <1000 km^2. We used the current KBA coverage to calculate the difference between the current level of KBA coverage compared to the target level representation.

Lastly, we calculated two IUCN range metrics from our modelled 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 our modelled AOH binary 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). Extent of Occurrence (EOO) was calculated by fitting a minimum convex polygon (MCP) around the furthest boundaries of the projected habitat of the 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 area within the MCP that could not be occupied over the ocean. All range metric calculations were performed using an Equatorial Lambert Azimuth Equal-Area projection. 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 and Rundle 2019) and *sp* (Bivand et al. 2013) packages.

RESULTS

Species Distribution Model

Six candidate models had an $\Delta AIC_c \leq 2$, and the model with the lowest regularization multiplier (β) was selected (Model 6 in Table S2, see Supplementary Material). The best-fit SDM (ΔAIC_c = 1.19) had linear and quadratic terms and β = 2.5 as model parameters, with high calibration accuracy (mean CBI = 0.960), and was robust against random expectations (pROC = 1.431, SD± 0.055, range: 1.244 – 1.594). From the penalized linear beta coefficients, Harpy Eagles were positively associated with evergreen forest (0.065) and most negatively associated with habitat homogeneity (-3.849), followed by mosaic forest (-0.026), Terrain Roughness Index (-0.023) cultivated land (-0.010) and elevation (-0.001).

The largest continuous area of habitat extended across Amazonia and the Guiana Shield (Figure 2). A habitat corridor was identified through Central America along the Caribbean coast, extending south into the Chocó-Darién ecoregion along the Pacific coast of Colombia (Figure S2). Little habitat was predicted across the largely deforested Atlantic Forest region in Brazil. From the SDM response functions, evergreen forest had peak suitability at 70-75 % forest cover, with highest suitability for topographic areas of both low elevation and terrain ruggedness (Figure 3). Habitat suitability was highest in areas of low homogeneity < 0.2 (i.e., highly heterogenous species-rich vegetation), areas with < 10 % human cultivated landcover, and zero or low percentage of mosaic forest.

Range Size and Gap Analysis

The reclassified binary model (median threshold = 0.345) calculated an Area of Habitat equalling 7,479,752 km^2 (Figure 4). The current KBA network covered 18.1 % (1,352,879 km^2) of this habitat area in the medium to high discrete quantile classes (Figure 5), 8.1 % greater than the target representation (10 %). Four major gaps (Figure 5, blue circles/ellipses) for high class habitat without extensive KBA coverage were identified in: (**1**) the Chocó-Darién ecoregion in western Colombia (Fig. 6), (**2**) the Magdalena-Urabá moist forests of northern Colombia (Fig. 6), (**3**) north-east Amazonas state in Brazil, and (**4**) north and west Guyana. From our AOH model, maximum Extent of Occurrence (EOO) was 18,130,602 km^2 and minimum EOO 14,738,408 km^2, with an AOO of 708,697 occupied cells.

DISCUSSION

Our results indicate that Harpy Eagle populations are more likely to be associated with dense (70-75%) evergreen forest cover, low elevation, and high vegetation species richness across their range. Conversely, Harpy Eagles seem to avoid extensive areas of cultivated land, mosaic forest, and high terrain complexity. Using the AOH parameters as the basis for the habitat model predicted a large area of habitat across the pan-Amazonia region, and a habitat corridor extending from the Pacific coast of Colombia, north along the Caribbean coast of Central America. Almost no habitat was predicted across the Atlantic Forest region, which is now severely degraded. The current KBA network coverage exceeded the target biodiversity area representation (10 %), covering 18 % of medium to high Harpy Eagle habitat. Considering the large range of the Harpy Eagle, the current KBA extent is encouraging but misses key areas of potentially important habitat. Four areas of high suitability habitat were identified as gaps in the KBA network for north and west Colombia, western Guyana, and north-west Brazil. We recommend establishing new KBAs in these four areas, further strengthening the current KBA network across the region.

Despite the high predictive performance of our continuous model and the ability of the reclassified discrete model to identify previously unprotected areas of key habitat, we recognise there are limitations to our approach. Thresholding continuous SDMs is common practice but not always appropriate (Guillera-Arroita et al. 2015; Santini et al. 2021). However, in this context thresholding was justifiable to achieve our aim of calculating discrete habitat classes for use in spatial conservation planning (Guillera-Arroita et al. 2015). Using a Bayesian approach with a range of continuous probabilities would be a useful future step forward to account for any uncertainty in model outputs (Carlson 2020). The use of presence-background data in SDMs is widespread but has been fraught with statistical issues related to sampling bias since their inception (Ranc et al. 2017). However, recent advances implementing the unifying inhomogeneous Poisson process framework which models points as a log-linear intensity function of the covariates, as used here, can effectively account for sampling bias that may skew model predictions (Renner et al. 2015; Isaac et al. 2019).

Habitat Use

Broad and fine scale species-habitat assessments often result in different variables emerging as important, potentially leading to contrasting recommendations for conservation (Gregory and Baillie 1998). However, our results show general similarities to habitat models from previous studies at both broad and fine scales. The SDM was consistent with predicted Harpy Eagle habitat from an earlier broad-scale SDM (Miranda et al. 2019). This was expected because both SDMs used measures of forest cover as landcover predictors but different modelling methodologies. This reinforces the consistency in SDM outputs for the Harpy Eagle from a range of algorithms and gives confidence in SDM predictions that have been criticised for lacking ecological realism (Fourcade et al. 2017). Building on the Miranda et al. (2019) model, the SDM here also predicted a distinct corridor of habitat extending from the Chocó-Darién ecoregion of west Colombia north through Central America along the Caribbean coast (Figure 6). This suggests that including a habitat heterogeneity covariate, along with topographic and landcover predictors, was able to identify key areas of habitat undetectable from other texture measures used in that study.

Habitat heterogeneity is a key landscape characteristic, here representing vegetation species richness, important for determining general biodiversity patterns (Stein et al. 2014), including for lowland tropical forest raptors (Jullien and Thiollay 1996; Anderson 2001). Areas of high species-rich vegetation provide more diverse niche space, promoting greater species coexistence and thus increased species diversity (Tews et al. 2004). For the Harpy Eagle, areas of higher habitat heterogeneity may be preferred over more homogenous areas because they contain a greater density and diversity of prey species (Miranda 2018). Further, a diverse forest canopy structure may also facilitate aerial attacks on canopy prey, by providing more hunting perches (Vargas González et al. 2014). Moreover, the SDM confirmed the restricted elevational distribution for the Harpy Eagle, consistent with a landscape-level SDM (Vargas González et al. 2020). This may be similarly linked to the Harpy Eagles' preference for nesting in large, canopy-emergent trees, and the abundance of its main prey of arboreal mammals, both of which occur in greater abundance at lower elevations (Miranda 2015; Miranda et al. 2020).

Harpy Eagles are dependent on large tracts of lowland tropical forest for breeding and foraging (Vargas González et al. 2014; Miranda et al. 2019). Indeed, breeding success was higher in areas with > 70 % forest cover in northern Mato Grosso, Brazil (Miranda et al. 2021), consistent with the range-wide response to evergreen forest cover here. Perhaps as important, strong negative associations were identified with >10 % cultivated landcover and mosaic forest, showing that Harpy Eagles avoid areas of high human impact and sporadic forest cover. This implies that, as deforestation increases across the species' range, the Harpy Eagle may struggle to adapt to large areas of human disturbance and heavily fragmented landscapes (Miranda et al. 2021).

Area of Habitat

Our method of calculating the Area of Habitat metric refines previous range size estimates (Birdlife International 2021; Sutton et al. 2021) and provides a baseline area of habitat map for the Harpy Eagle. There was 4.6 % less area in our modelled AOH range polygon (7,479,752 km^2), than in the current IUCN range map (7,838,093 km^2; Fig. 4). Therefore, we recommend this new AOH estimate be incorporated into future IUCN assessments for the species. Our modelled AOH polygon also had 24 % less area compared to a binary SDM map using solely climatic and topographic predictors (9,844,399 km^2; Sutton et al. 2021). If we assume that the SDM from Sutton et al. (2021) based on climate and terrain is representative of the Harpy Eagle pre-industrial range (in the absence of satellite-derived landcover not available for pre-industrial times), then the species' habitat range has shrunk by nearly a quarter during the industrial period to the present.

One limitation of the analyses was the timeframe of the remote-sensing data used for the covariates. Both the landcover and vegetation covariates are a consensus product collected between the years 1992-2005, with land use having changed in parts of Neotropics since then (Powers and Jetz 2019). Therefore, the Area of Habitat prediction should be viewed as a conservative baseline assessment, knowing that landcover can change rapidly. Processing large areas of current remote-sensed landcover data at continental-scales can be challenging due to the high computing power required; the EarthEnv habitat variables are recommended as a readily available dataset to use for first estimates of modelled AOH at large scales (Tuanmu and Jetz 2014, 2015).

Current and predicted future habitat loss may lead inevitably to declines in populations of some species, increasing their extinction risk (Powers and Jetz 2019). Continued habitat loss and fragmentation is likely to have a negative impact on the future persistence of many birds across the highly biodiverse Neotropics (Bird et al. 2011). The Harpy Eagle is a good example, despite its large range precluding high extinction risk (Gaston and Fuller 2009). Continued habitat loss and fragmentation through agricultural development and logging across its geographic range (Vargas González et al. 2006; Miranda et al. 2020) should raise the alarm about the species' future (Krüger and Radford 2008; Miranda et al. 2019). The declining range of the Harpy Eagle is demonstrated by the few breeding and sighting records in the largely deforested Atlantic Forest (Meller and Guadagnin 2016; Suscke et al. 2017), and parts of southern Mexico and Central America (Vargas González et al. 2006), reflected in the results from the SDM. Our results should therefore serve as a forewarning of what could happen across parts of the core habitat area in Amazonia where deforestation has steadily increased since 2000 (Hansen et al. 2008), with current deforestation rates across the Brazilian Amazon increasing since 2013 (Silva Junior et al. 2021).

As a baseline assessment, our SDM should be viewed as a *maximum extent of habitat*, knowing that deforestation is an ongoing process across the pan-Amazonia region (Bird et al. 2011; Hansen et al. 2020). Approximately 18 % of tropical forest in Amazonia had been cleared by 2011 (Bird et al. 2011), with predictions of up to 40 % of forest cover lost by 2050 (Soares-Filho et al. 2006). Recently, those tropical forests of highest structural integrity most associated with preferred Harpy Eagle habitat (tall, closed canopy forest and low human pressure; Vargas González et al. 2014; Miranda et al. 2020) were identified as largely limited to the Amazon basin (Hansen et al. 2020). These forests generally remain intact due to their remoteness (Soares-Filho et al. 2006), but with the majority having no formal protection. Strengthening biodiversity and protected area networks should be given high priority in policy decisions (Butchart et al. 2015), along with effective biodiversity area-based conservation outside of, but concurrent with, formally protected areas (Pringle 2017; Maxwell et al. 2020).

Gap Analysis

Although the current coverage of the KBA network within our modelled AOH range (~18 %) exceeded the representative biodiversity area target based on species range size set here (10 %), it is substantially lower than the proportion of IBA network coverage for threatened bird species overall in Amazonia (54.9 %, Bird et al. 2011). Of the four key gaps identified here only gap 3 in north-west Amazonas state in Brazil has any form of current protection as an area of indigenous land (UNEP-WCWC & IUCN 2020). The three remaining gap areas have little formal protection or KBA coverage, despite both the Chocó-Darién ecoregion (gap 1) and Guyana (gap 4) having extensive Harpy Eagle habitat. In the case of Guyana it is likely that most habitat is 'passively' protected due to the inaccessibility of the region. However, solely relying on remoteness may be short-sighted and extending the current KBAs east and west of Guyana to cover a larger portion of the Guiana Shield is recommended. To this aim, given that on average ~49 % of the area of each KBA/IBA globally has formal protection (Waliczky et al. 2019), intersecting KBA coverage with nationally protected areas across the Harpy Eagle range would be a useful next step in protected area assessment for the species (Butchart et al. 2012).

The Chocó-Darién ecoregion is one of 25 global biodiversity hotspots prioritized for conservation (Myers et al. 2000). Based on satellite remote-sensing, deforestation for agricultural expansion has steadily increased in the region over the past two decades (Fagua et al. 2019; Fagua and Ramsey 2019). Approximately 42 % of forest remains intact, making this an area of high importance for protection not only for the Harpy Eagle but for all the associated fauna, flora, and crucial ecological processes. Establishing and reinforcing the current KBA network throughout the Chocó-Darién ecoregion could be important for habitat continuity essential to dispersing Harpy Eagles (Urios et al. 2017) between Central and South America. The Darién region of Panama (in the north of the Chocó-Darién ecoregion) has a high density of breeding Harpy Eagles and is considered the current stronghold of the species in Central America (Vargas González and Vargas 2011). A small population still exists in the highly deforested Chocó humid forest region of north-west Ecuador in the south of the Chocó-Darién ecoregion (Zhang 2020). Designating new KBAs in the Chocó-Darién ecoregion corridor could thus sustain habitat for fragmented Harpy Eagle populations, maintaining genetic diversity and thus potential adaptation to environmental change (Lerner et al. 2009; Banhos et al. 2016; Maxwell et al. 2020). Indeed, genetic diversity decreased in fragmented Harpy Eagle populations inhabiting deforested regions of the southern Amazon and Atlantic Forest of Brazil (Banhos et al. 2016), reinforcing the need to protect and link habitat patches throughout its whole distribution.

Habitat loss is a principal threat to the long-term survival of the Harpy Eagle and protecting large areas of tropical forest habitat for the species should be a high priority (Banhos et al. 2016). Continued deforestation resulting in habitat loss and fragmentation across the Harpy Eagle range should raise the alarm about the species' future conservation status. Using targeted forest protection through responsible community land use and broad-scale conservation planning is needed to reduce current deforestation rates (Kramer et al. 1997; Bird et al. 2011; Butchart et al. 2015). While the current KBA network coverage for the Harpy Eagle exceeds the representation target, our models identified gaps in the KBA network that ought to be prioritised for enlarging the KBA network estate. As demonstrated here, our method of calculating modelled Area of Habitat estimates based on SDMs are a useful tool for large-scale conservation planning and can be readily applied to many taxa.

LITERATURE CITED

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

Amatulli, G., Domisch, S., Tuanmu, M. N., Parmentier, B., Ranipeta, A., Malczyk, J. and Jetz, W. (2018). A suite of global, cross-scale topographic variables for environmental and biodiversity modeling. *Scientific Data*. 5: 180040.

Anderson, D.L. (2001). Landscape Heterogeneity and Diurnal Raptor Diversity in Honduras: The Role of Indigenous Shifting Cultivation 1. *Biotropica*. 33: 511-519.

Banhos, A., Hrbek, T., Sanaiotti, T.M. and Farias, I.P. (2016). Reduction of genetic diversity of the Harpy Eagle in Brazilian tropical forests. *PloS one*. 11: e0148902.

Barbet-Massin, M., Jiguet, F., Albert, C.H., and Thuiller, W. (2012). Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution*. 3: 327-338.

Barve, N. and Barve, V. (2013). ENMGadgets: tools for pre and post processing in ENM workflows. https://github.com/narayanibarve/ENMGadgets.

Bax, V. and Francesconi, W. (2019). Conservation gaps and priorities in the Tropical Andes biodiversity hotspot: Implications for the expansion of protected areas. *Journal of Environmental Management*. 232: 387-396.

Bellamy, C., Boughey, K., Hawkins, C., Reveley, S., Spake, R., Williams, C. and Altringham, J. (2020). A sequential multi-level framework to improve habitat suitability modelling. *Landscape Ecology*. 35: 1001-1020.

Bird, J.P., Buchanan, G.M., Lees, A.C., Clay, R.P., Develey, P.F., Yépez, I. and Butchart, S.H. (2012) Integrating spatially explicit habitat projections into extinction risk assessments: a reassessment of Amazonian avifauna incorporating projected deforestation. *Diversity and Distributions* 18: 273-281.

BirdLife International. (2021). *Harpia harpyja*. *The IUCN Red List of Threatened Species* 2021:

e.T22695998A197957213. https://dx.doi.org/10.2305/IUCN.UK.2021-3.RLTS.T22695998A197957213.en. Accessed 10 December 2021.

BirdLife International (2020). *Guidelines for the application of the IBA criteria.* BirdLife International, Cambridge, UK. Available at: http://datazone.birdlife.org/site/ibacriteria

BirdLife International. (2020). *World Database of Key Biodiversity Areas*. Developed by the KBA Partnership: BirdLife International, International Union for the Conservation of Nature, American Bird Conservancy, Amphibian Survival Alliance, Conservation International, Critical Ecosystem Partnership Fund, Global Environment Facility, Global Wildlife Conservation, NatureServe, Rainforest Trust, Royal Society for the Protection of Birds, Wildlife Conservation Society and World Wildlife Fund. September 2020 version. Available at http://www.keybiodiversityareas.org/site/requestgis

Bivand, R., Keitt, T. and 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. and Gomez-Rubio, V. (2013). *Applied spatial data analysis with R.* 2nd Ed. Springer, NY, USA.

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

Boyce, M.S. (2006). Scale for resource selection functions. *Diversity and Distributions*. 12: 269-276.

Boyce, M.S. and McDonald, L.L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution*. 14: 268-272.

Boyce, M.S., Vernier, P.R., Nielsen, S.E. and Schmiegelow, F.K. (2002). Evaluating resource selection functions. *Ecological Modelling.* 157: 281-300.

Bradter, U., Mair, L., Jönsson, M., Knape, J., Singer, A. and Snäll, T. (2018). Can opportunistically collected Citizen Science data fill a data gap for habitat suitability models of less common species? *Methods in Ecology and Evolution*. 9: 1667-1678.

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

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. and Li, B.V. (2019). Measuring terrestrial area of habitat (AOH) and its utility for the IUCN Red List. *Trends in Ecology and Evolution*. 34: 977-986.

Brooks, T.M., Wright, S.J., and Sheil, D. (2009). Evaluating the success of conservation actions in safeguarding tropical forest biodiversity. *Conservation Biology*. 23: 1448-1457.

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

Butchart, S.H., Clarke, M., Smith, R.J., Sykes, R.E., Scharlemann, J.P., Harfoot, M., Buchanan, G.M., Angulo, A., Balmford, A., Bertzky, B., Brooks, T.M., Carpenter, K.E., Comeros-Raynal, M.T., Cornell, J., Ficetola, G.F., Fishpool, L.D.C., Fuller, R.A., Geldmann, J., Harwell, H., Hilton-Taylor, C., Hoffmann, M., Joolia, A., Joppa, L., Kingston, N., May, I., Milam, A., Polidoro, B., Ralph, G., Richman, N., Rondinini, C., Segan, D.B., Skolnik, B., Spalding, M.D., Stuart, S.N., Symes, A., Taylor, J., Visconti, P., Watsom, J.E.M., Wood, L. and Burgess, N.D. (2015).

Shortfalls and solutions for meeting national and global conservation area targets. *Conservation Letters*. 8: 329-337.

Butchart, S.H., Scharlemann, J.P., Evans, M.I., Quader, S., Arico, S., Arinaitwe, J., ... and Woodley, S. (2012). Protecting important sites for biodiversity contributes to meeting global conservation targets. *PloS one*. 7: e32529.

Carlson, C.J. (2020). Embarcadero: Species distribution modelling with Bayesian additive regression trees in R. *Methods in Ecology and Evolution*. 11: 850-858.

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

De Carvalho, D.L., Sousa-Neves, T., Cerqueira, P.V., Gonsioroski, G., Silva, S. M., Silva, D.P. and Santos, M.P.D. (2017). Delimiting priority areas for the conservation of endemic and threatened Neotropical birds using a niche-based gap analysis. *PloS one*. 12: e0171838. DOI: 10.1371/journal.pone.0171838

Da Silva, F.P., Fernandes-Ferreira, H., Montes, M.A. and da Silva, L G. (2020). Distribution modeling applied to deficient data species assessment: A case study with Pithecopus nordestinus (Anura, Phyllomedusidae). *Neotropical Biology and Conservation*. 15: 165-175.

Di Marco, M., Watson, J.E., Possingham, H.P. and Venter, O. (2017). Limitations and trade-offs in the use of species distribution maps for protected area planning. *Journal of Applied Ecology*. 54: 402-411.

Donald, P.F., Fishpool, L.D., Ajagbe, A., Bennun, L.A., Bunting, G., Burfield, I.J., Butchart, S.H., Capellan, S., Crosby, M.J., Dias, M.P. and Diaz, D. (2019). Important Bird and Biodiversity Areas (IBAs): the development and characteristics of a global inventory of key sites for biodiversity. *Bird Conservation International*. 29: 177-198.

Early, R., Anderson, B. and Thomas, C.D. (2008). Using habitat distribution models to evaluate large-scale landscape priorities for spatially dynamic species. *Journal of Applied Ecology*. 45: 228-238.

Elith, J. and Leathwick, J. R. (2009). Species distribution models: ecological explanation and prediction across space and time. *Annual review of ecology, evolution, and systematics*. 40: 677-697.

Engler, J.O., Stiels, D., Schidelko, K., Strubbe, D., Quillfeldt, P. and Brambilla, M. (2017). Avian SDMs: current state, challenges, and opportunities. *Journal of Avian Biology*. 48: 1483-1504.

Fagua, J.C., Baggio, J.A., and Ramsey, R.D. (2019). Drivers of forest cover changes in the Chocó-Darien Global Ecoregion of South America. *Ecosphere*. 10: e02648.

Fagua, J.C. and Ramsey, R.D. (2019). Geospatial modeling of land cover change in the Chocó-Darien global ecoregion of South America; One of most biodiverse and rainy areas in the world. *PloS one*. 14: e0211324.

Fick, S.E. & Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*. 37: 4302-4315.

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

Fourcade, Y., Besnard, A.G. and Secondi, J. (2017). Paintings predict the distribution of species, or the challenge of selecting environmental predictors and evaluation statistics. *Global Ecology and Biogeography*. 27: 245-256.

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

Garshelis, D.L. (2000). Delusions in habitat evaluation: measuring use, selection, and importance. In: Boitani, L. and Fuller, T.K. (Eds.). *Research techniques in animal ecology: controversies and consequences*. Columbia University Press, New York, USA.

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

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

Gaul, W., Sadykova, D., White, H.J., Leon-Sanchez, L., Caplat, P., Emmerson, M. C. and Yearsley, J.M. (2020). Data quantity is more important than its spatial bias for predictive species distribution modelling. *PeerJ*. 8: e10411.

Global Biodiversity Information Facility. (2019). GBIF Occurrence Download. https://doi.org/10.15468/dl.6ikhnj

Gregory, R.D. and Baillie, S.R. (1998). Large-scale habitat use of some declining British birds. *Journal of Applied Ecology*. 35: 785-799.

Guevara, L., Gerstner, B.E., Kass, J.M. and Anderson, R.P. (2018). Toward ecologically realistic predictions of species distributions: A cross-time example from tropical montane cloud forests. *Global Change Biology*. 24: 1511-1522.

Guillera-Arroita, G., Lahoz-Monfort, J.J., Elith, J., Gordon, A., Kujala, H., Lentini, P.E., McCarthy, M.A., Tingley, R. and Wintle, B.A. (2015). Is my species distribution model fit for purpose? Matching data and models to applications. *Global Ecology and Biogeography*. 24: 276-292.

Hao, T., Elith, J., Lahoz-Monfort, J.J. and Guillera-Arroita, G. (2020). Testing whether ensemble modelling is advantageous for maximising predictive performance of species distribution models. *Ecography*. 43: 549-558.

Hansen, M.C., Stehman, S.V., Potapov, P.V., Loveland, T.R., Townshend, J.R., DeFries, R.S., Pittman, K.W., Arunarwati, B., Stolle, F., Steininger, M.K. and Carroll, M. (2008). Humid tropical forest clearing from 2000 to 2005 quantified by using multitemporal and multiresolution remotely sensed data. *Proceedings of the National Academy of Sciences*. 105: 9439-9444.

Hefley, T.J. and Hooten, M.B. (2015). On the existence of maximum likelihood estimates for presence-only data. *Methods in Ecology and Evolution*. 6: 648-655.

Helmstetter, N.A., Conway, C.J., Stevens, B.S. and 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.

Herkt, K.M.B., Skidmore, A.K. and Fahr, J. (2017). Macroecological conclusions based on IUCN expert maps: A call for caution. *Global Ecology and Biogeography*. 26: 930-941.

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. and Elith, J. (2017). Dismo: Species Distribution Modeling. R package version 1.1-4. https://CRAN.R-project.org/package=dismo.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C. and Guisan, A. (2006). Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling.* 199: 142-152.

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

Isaac, N.J., Jarzyna, M.A., Keil, P., Dambly, L.I., Boersch-Supan, P.H., Browning, E., Freeman, S.N., Golding, N., Guillera-Arroita, G., Henrys, P.A., Jarvis, S., Lahoz-Monfort, J., Pagel, J., Pescott, O.L. Schmucki, R., Simmonds, E.G. and O'Hara, R.B. (2019). Data integration for large-scale models of species distributions. *Trends in Ecology and Evolution*. 35: 56-67.

IUCN. (2016). *A Global standard for the identification of Key Biodiversity Areas, Version 1.0*. IUCN, Gland, Switzerland.

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

Johnston, A., Hochachka, W.M., Strimas-Mackey, M.E., Ruiz Gutierrez, V., Robinson, O.J., Miller, E.T., Auer, T., Kelling, S.T. and Fink, D. (2021). Analytical guidelines to increase the value of community science data: An example using eBird data to estimate species distributions. *Diversity and Distributions*. 27: 1265-1277.

Jullien, M. and Thiollay, J. M. (1996). Effects of rain forest disturbance and fragmentation: comparative changes of the raptor community along natural and human-made gradients in French Guiana. *Journal of Biogeography*. 23: 7-25.

KBA Standards and Appeals Committee (2019). *Guidelines for using a Global Standard for the Identification of Key Biodiversity Areas*. Version 1.0. Prepared by the KBA Standards and Appeals Committee of the IUCN Species Survival

Commission and IUCN World Commission on Protected Areas. Gland, Switzerland: IUCN.

Kramer, R., van Schaik, C. and Johnson, J. (1997). *Last Stand. Protected areas and the defense of tropical biodiversity.* Oxford University Press.

Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A.K., Augeri, D.M. and Cheyne, S.M. (2013). The importance of correcting for sampling bias in MaxEnt species distribution models. *Diversity and Distributions.* 19: 1366-1379.

Krüger, O. and Radford, A.N. (2008). Doomed to die? Predicting extinction risk in the true hawks Accipitridae. *Animal Conservation*. 11: 83-91.

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

Lees, A.C., Rosenberg, K.V., Ruiz-Gutierrez, V., Marsden, S., Schulenberg, T. S. And Rodewald, A. D. (2020). A roadmap to identifying and filling shortfalls in Neotropical ornithology. *The Auk*. 1-17. DOI: 10.1093/auk/ukaa048

Lerner, H.R., Johnson, J.A., Lindsay, A.R., Kiff, L.F. and Mindell, D.P. (2009). It's not too late for the Harpy Eagle (*Harpia harpyja*): high levels of genetic diversity and differentiation can fuel conservation programs. *PloS One*. 4: e7336.

Levin, S.A. (1992). The problem of pattern and scale in ecology. *Ecology*. 73: 1943-1967.

Liu, C., Berry, P.M., Dawson, T.P. and Pearson, R.G. (2005). Selecting thresholds of occurrence in the prediction of species distributions. *Ecography*. 28: 385-393.

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

Manly, B F.L., McDonald, L., Thomas, D.L., McDonald, T.L. and Erickson, W.P. (2002). *Resource selection by animals: statistical design and analysis for field studies*. 2^{nd} edition. Kluwer Academic Publishers.

Margules, C.R. and Pressey, R.L. (2000). Systematic conservation planning. *Nature*. 405: 243-253.

Matthiopoulos, J., Fieberg, J. and 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.

Maxwell, S.L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A.S., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E. and Maron, M. (2020). Area-based conservation in the twenty-first century. *Nature*. 586: 217-227.

McClure, C.J.W., Anderson, D.L., Buij, R., Dunn, L., Henderson, M.T., McCabe, J., ... and 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.

Meller, D.A., and Guadagnin, D.L. (2016). Rediscovery of the Harpy Eagle *Harpia harpyja* (Accipitriformes: Accipitridae) for Rio Grande do Sul state, Brazil. *Ornithology Research*. 24: 53-57.

Merow, C., Smith, M.J. and 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, E.B.P. (2015). Conservation implications of Harpy Eagle *Harpia harpyja* predation patterns. *Endangered Species Research*. 29: 69-79.

Miranda, E.B.P. (2018). Prey composition of Harpy Eagles (*Harpia harpyja*) in Raleighvallen, Suriname. *Tropical Conservation Science*, 11: 1-8. DOI: 10.1177/1940082918800789

Miranda, E.B.P., Menezes, J.F., Farias, C.C., Munn, C. and Peres, C.A. (2019). Species distribution modeling reveals strongholds and potential reintroduction areas for the world's largest eagle. *PloS one*. 14: e0216323.

Miranda, E.B.P., Peres, C.A., Carvalho-Rocha, V., Miguel, B.V., Lormand, N., Huizinga, N., Munn, C.A., Semedo, T.B.F., Ferreira, T.V., Pinho, J.B., Piacentini, V.Q., Marini, M.A. and Downs, C.T. (2021). Tropical deforestation induces thresholds of reproductive viability and habitat suitability in Earth's largest eagles. *Scientific Reports.* 11: 1-17.

Miranda, E.B.P., Peres, C.A., Marini, M.Â., and Downs, C.T. (2020). Harpy Eagle (*Harpia harpyja*) nest tree selection: Selective logging in Amazon forest threatens Earth's largest eagle. *Biological Conservation*. 250: 108754.

Morán-Ordóñez, A. (2020). Conservation of "new" species within and beyond protected areas. *Animal Conservation*. 23: 353-354.

Morrison, M.L., Marcot, B. and Mannan, W. (2006). *Wildlife-habitat relationships: concepts and applications*. Island Press. Washington D.C., USA.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. and Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*. 403: 853-858.

Perrig, P.L., Lambertucci, S.A., Cruz, J., Alarcón, P.A., Plaza, P.I., Middleton, A.D., Blanco, G., Sánchez-Zapata, J.A., Donázar, J.A. and Pauli, J.N. (2020).

Identifying conservation priority areas for the Andean condor in southern South America. *Biological Conservation*. 243: 108494.

Peterson, A.T., Papeş, M. and Soberón, J. (2008). Rethinking receiver operating characteristic analysis applications in ecological niche modeling. *Ecological Modelling.* 213: 63-72.

Peterson, A.T., Soberón, J., Pearson, R.G., Anderson, R.P., Martinez-Meyer, E., Nakamura, M. and Araújo, M.B. (2011). *Ecological Niches and Geographic Distributions*. Monographs in Population Biology 49. Princeton University Press, NJ, USA.

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

Portugal, M.P., Morato, R.G., de Barros, K.M.P.M., Rodrigues, F.H.G. and Jacobi, C.M. (2019). Priority areas for jaguar *Panthera onca* conservation in the Cerrado. *Oryx*. 1-12.

Powers, R.P. and Jetz, W. (2019). Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nature Climate Change*. 9: 323-329.

Pringle, R.M. (2017). Upgrading protected areas to conserve wild biodiversity. *Nature*. 546: 91-99.

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

Radosavljevic, A. and Anderson, R.P. (2014). Making better Maxent models of species distributions: complexity, overfitting and evaluation. *Journal of Biogeography.* 41: 629-643.

Ramesh, V., Gopalakrishna, T., Barve, S. and Melnick, D.J. (2017). IUCN greatly underestimates threat levels of endemic birds in the Western Ghats. *Biological Conservation*. 210: 205-221.

Ranc, N., Santini, L., Rondinini, C., Boitani, L., Poitevin, F., Angerbjörn, A. and Maiorano, L. (2017). Performance tradeoffs in target-group bias correction for species distribution models. *Ecography*. 40: 1076-1087.

Renner, I.W., Elith, J., Baddeley, A., Fithian, W., Hastie, T., Phillips, S.J., Popovic, G. and Warton, D.I. (2015). Point process models for presence-only analysis. *Methods in Ecology and Evolution*. 6: 366-379.

Renner, I.W. and Warton, D.I. (2013). Equivalence of MAXENT and Poisson point process models for species distribution modeling in ecology. *Biometrics*. 69: 274-281.

Robinson, S.K. (1994). Habitat selection and foraging ecology of raptors in Amazonian Peru. *Biotropica*. 26: 443-458.

Rodrigues, A.S., Akcakaya, H.R., Andelman, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Chanson, J.S., Fishpool, L.D., Da Fonseca, G.A., Gaston, K.J. and Hoffmann, M. (2004). Global gap analysis: priority regions for expanding the global protected-area network. *BioScience*. 54: 1092-1100.

Rodrigues, A.S. and Cazalis, V. (2020). The multifaceted challenge of evaluating protected area effectiveness. *Nature Communications*. 11: 1-4.

Rodríguez-Soto, C., Monroy-Vilchis, O., Maiorano, L., Boitani, L., Faller, J.C., Briones, M.A., Nunez, R., Rosas-Rosas, O., Ceballos, G. and Falcucci, A.

(2011). Predicting potential distribution of the jaguar (*Panthera onca*) in Mexico: identification of priority areas for conservation. *Diversity and Distributions*. 17: 350-361.

Santini, L., Benítez-López, A., Maiorano, L., Čengić, M. and Huijbregts, M.A. (2021). Assessing the reliability of species distribution projections in climate change research. *Diversity and Distributions*. 27: 1035-1050.

Scott, J.M., Davis, F., Csuti, B., Noss, R., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards Jr, T.C. and Ulliman, J. (1993). Gap analysis: a geographic approach to protection of biological diversity. *Wildlife Monographs*. 123: 1-41.

Silva, D.A., de Melo, F.R., and Júnior, I.G.G. (2013). Historical and recent records of the Harpy Eagle (*Harpia harpyja*) in the Cerrado biome of the state of Goiás, Brazil. *Revista Brasileira de Ornitologia-Brazilian Journal of Ornithology*. 21: 260-263.

Silva Junior, C.H., Pessoa, A., Carvalho, N.S., Reis, J.B., Anderson, L.O. & Aragao, L.E. (2021). The Brazilian Amazon deforestation rate in 2020 is the greatest of the decade. *Nature Ecology & Evolution*. 5: 144-145.

Smith, A.B. (2019). enmSdm: Tools for modeling niches and distributions of species. R package v0.3.4.6. https://github.com/adamlilith/enmSdm/

Soares-Filho, B.S., Nepstad, D.C., Curran, L.M., Cerqueira, G.C., Garcia, R.A., Ramos, C.A., Voll, E., McDonald, A., Lefebvre, P. and Schlesinger, P. (2006). Modelling conservation in the Amazon basin. *Nature*. 440: 520-523.

Stein, A., Gerstner, K. and Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*. 17: 866-880.

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

Suárez-Seoane, S., Osborne, P.E. and 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.

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

Suscke, P., Verderane, M., de Oliveira, R.S., Delval, I., Fernández-Bolaños, M. and Izar, P. (2017). Predatory threat of Harpy Eagles for yellow-breasted capuchin monkeys in the Atlantic Forest. *Primates*. 58: 141-147.

Sutton, L.J. (2022). Data from: Range-wide habitat use of the Harpy Eagle indicates four major tropical forest gaps in the Key Biodiversity Area network . *Ornithological Applications*. https://doi.org/10.5061/dryad.v41ns1rzt

Sutton, L.J., Anderson, D.L., Franco, M., McClure, C.J.W., Miranda, E.B.P, Vargas, F.H., Vargas González, J. de J. and Puschendorf, R. (2021). Geographic range estimates and environmental requirements for the Harpy Eagle derived from spatial models of current and past distribution. *Ecology and Evolution.* 11: 481-497. DOI: https://doi.org/10.1002/ece3.7068

Tews, J., Brose, U., Grimm, V., Tielbörger, K., Wichmann, M.C., Schwager, M. and Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *Journal of Biogeography*. 31: 79-92.

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

Tuanmu, M.N. and Jetz, W. (2015). A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*. 24: 1329-1339.

UNEP-WCMC & IUCN (2020). Protected Planet: Brazil; The World Database on Protected Areas (WDPA). Cambridge, UK. Available at: www.protectedplanet.net/country/BRA

UNEP-WCMC & IUCN (2021). The World Database on Protected Areas (WDPA). UNEP-WCMC & IUCN, Cambridge, UK. Available at: www.protectedplanet.net

Urios, V., Muñiz-López, R. and Vidal-Mateo, J. (2017). Juvenile dispersal of Harpy Eagles (*Harpia harpyja*) in Ecuador. *Journal of Raptor Research*. 51: 439-445.

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

Vargas González , J. de J., McCabe, J.D., Anderson, D.L., Curti, M., Cárdenas, D.C. and Vargas, F.H. (2020). Predictive Habitat Model Reveals Specificity in a Broadly Distributed Forest Raptor, The Harpy Eagle. *Journal of Raptor Research*. 54: 349-363.

Vargas González, J. de J. and Vargas, F.H. (2011). Nesting density of Harpy Eagles in Darien with population size estimates for Panama. *Journal of Raptor Research*. 45: 199-211.

Vargas González, J. de J., Vargas, F.H., Carpio, D. and McClure, C.J.W. (2014). Características de la vegetación en sitios de anidación del águila arpía (*Harpia harpyja*) en Darién, Panamá. *Ornitologia Neotropical.* 25: 207-218. (In Spanish).

Vargas González, J. de J., Whitacre, D., Mosquera, R., Albuquerque, J., Piana, R., Thiollay, J.M., Márquez, C., Sánchez, J.E., Lezama-López, M., Midence, S., Matola, S., Aguilar, S., Rettig, N. and Sanaiotti, T. (2006). Estado y distribucion actual del aguila arpia (*Harpia harpyja*) en Centro y Sur America. *Ornitologia Neotropical*. 17: 39-55. (In Spanish).

Waliczky, Z., Fishpool, L.D., Butchart, S.H., Thomas, D., Heath, M.F., Hazin, C., Donald, P.F., Kowalska, A., Dias, M.P. and Allinson, T.S. (2019). Important Bird and Biodiversity Areas (IBAs): their impact on conservation policy, advocacy and action. *Bird Conservation International*. 29: 199-215.

Warren, D.L. and 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.

Warton, D.I. and 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.

Zhang, S. (2020). An Apex Predator in Peril in the Western Lowlands of Ecuador: Mapping the Population Distribution of Harpy Eagles (*Harpia harpyja*) in a Highly Deforested Region*. Independent Study Project (ISP) Collection*. 3326. https://digitalcollections.sit.edu/isp_collection/3326

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

FIGURES

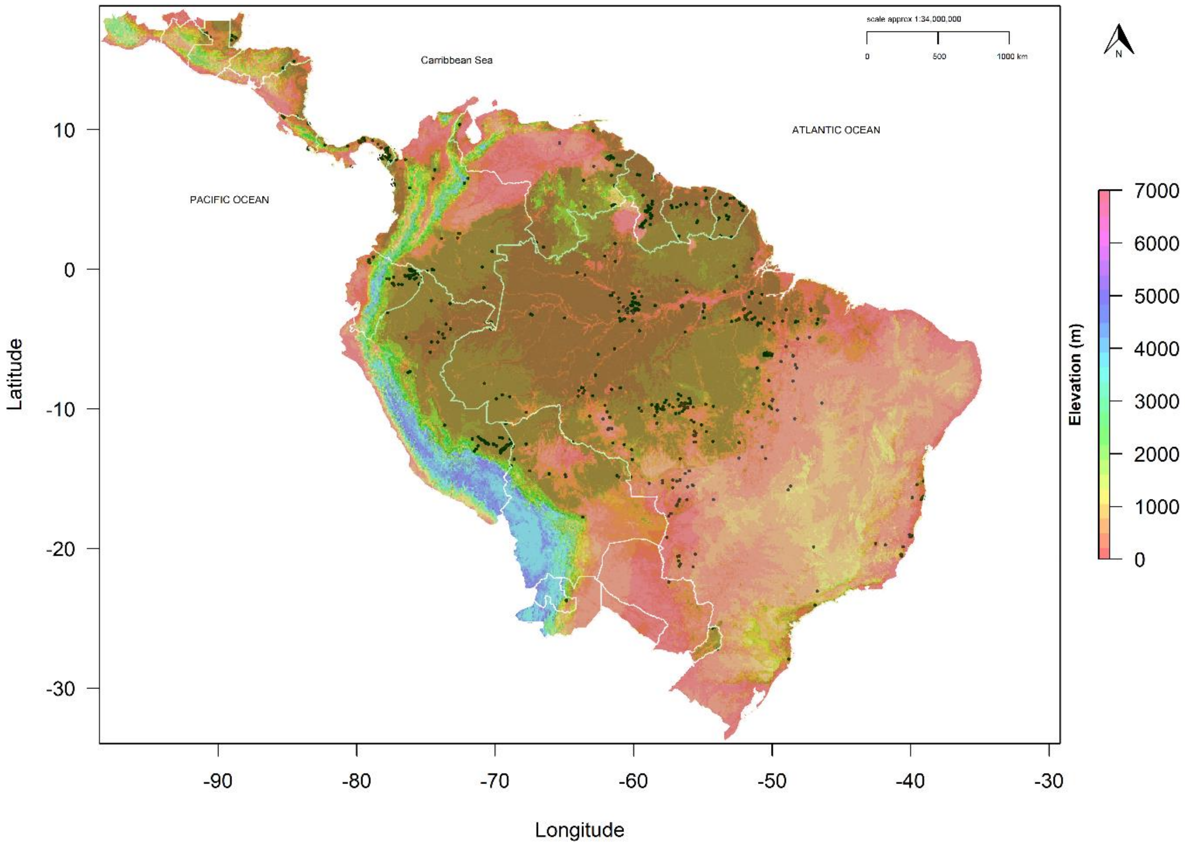

Figure 1. Distribution of spatially filtered Harpy Eagle occurrences (black points) across the study extent, showing the relationship to elevation and evergreen forest cover (brown). White borders define national boundaries within the study extent.

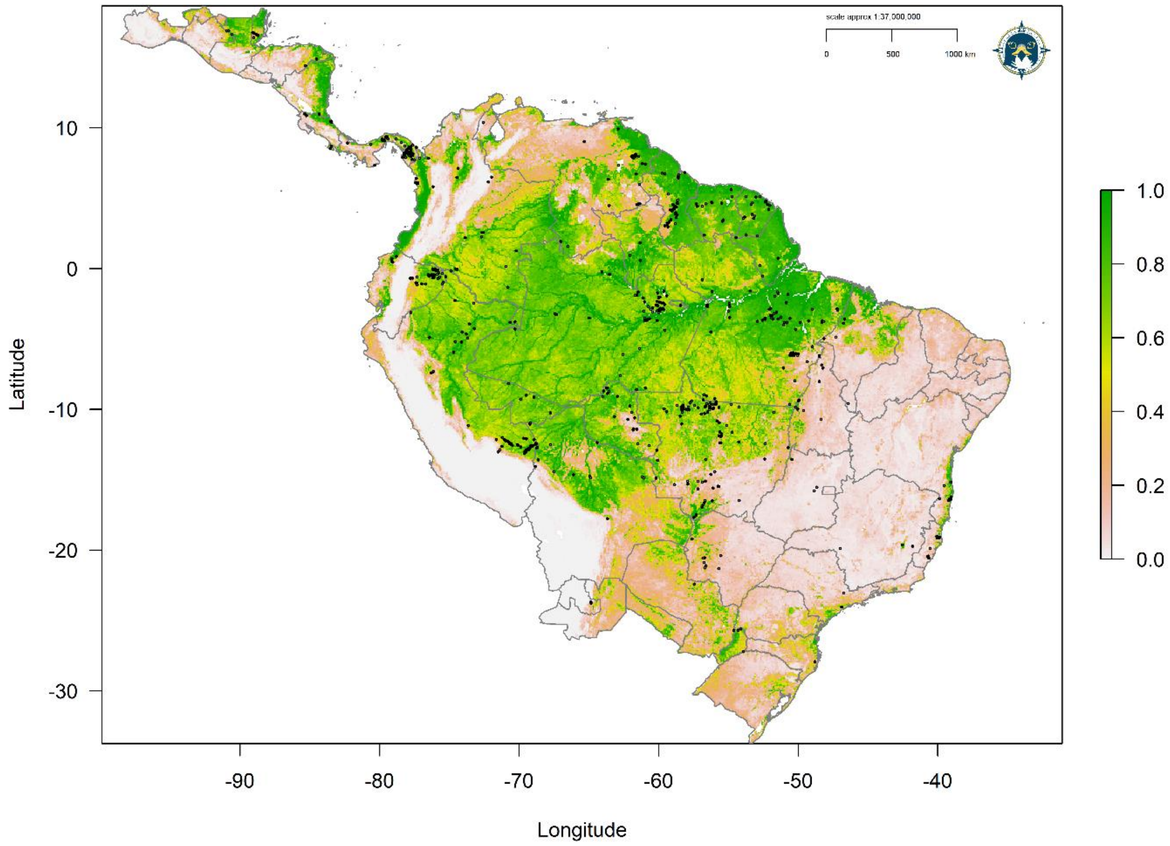

Figure 2. Species Distribution Model for the Harpy Eagle. Map denotes cloglog prediction with darker green areas (values closer to 1) having highest suitability and expected abundance. Gray borders define national boundaries within the study extent and internal state boundaries for Brazil. Black points define Harpy Eagle occurrences using a 5-km spatial filter. See Figure S2 in Supplement for map showing cropped model prediction for Central America without Harpy Eagle occurrences for clarity.

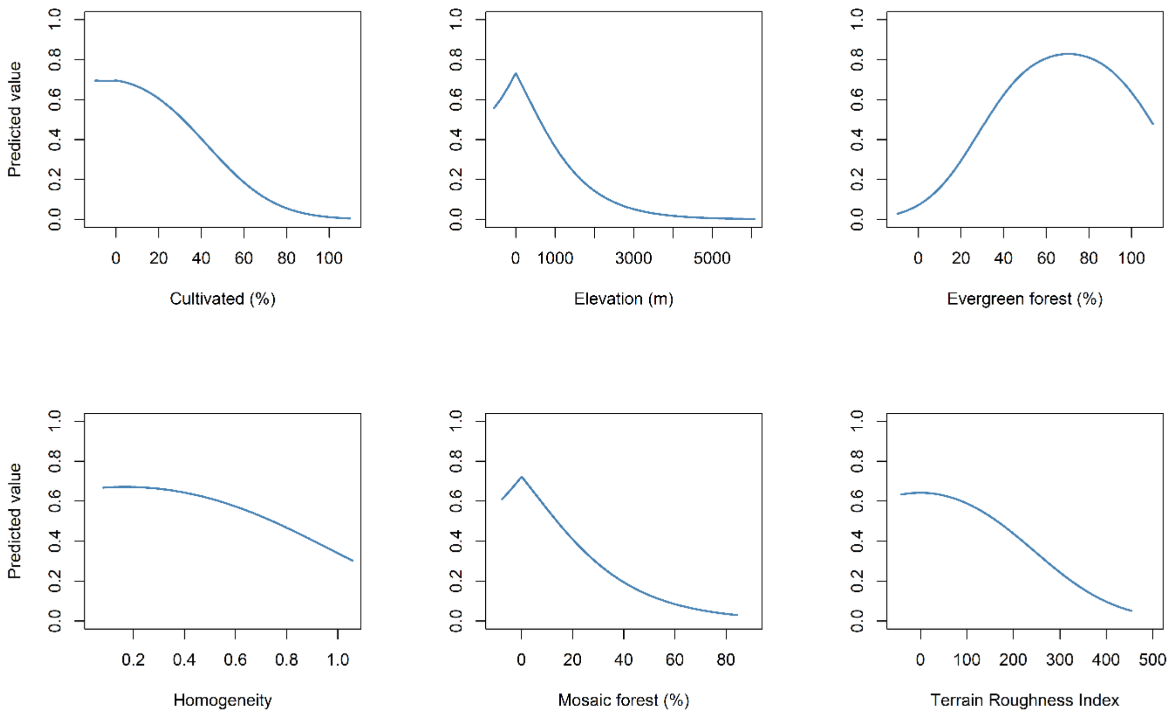

Figure 3. Penalized logistic regression response curves for each habitat covariate from the Harpy Eagle Species Distribution Model. The response curves show the contribution to model prediction (y-axis) as a function of each continuous habitat covariate (x-axis). Maximum values in each response curve define the highest predicted relative suitability. The response curves reflect the partial dependence on predicted suitability for each covariate and the dependencies produced by interactions between the selected covariate and all other covariates.

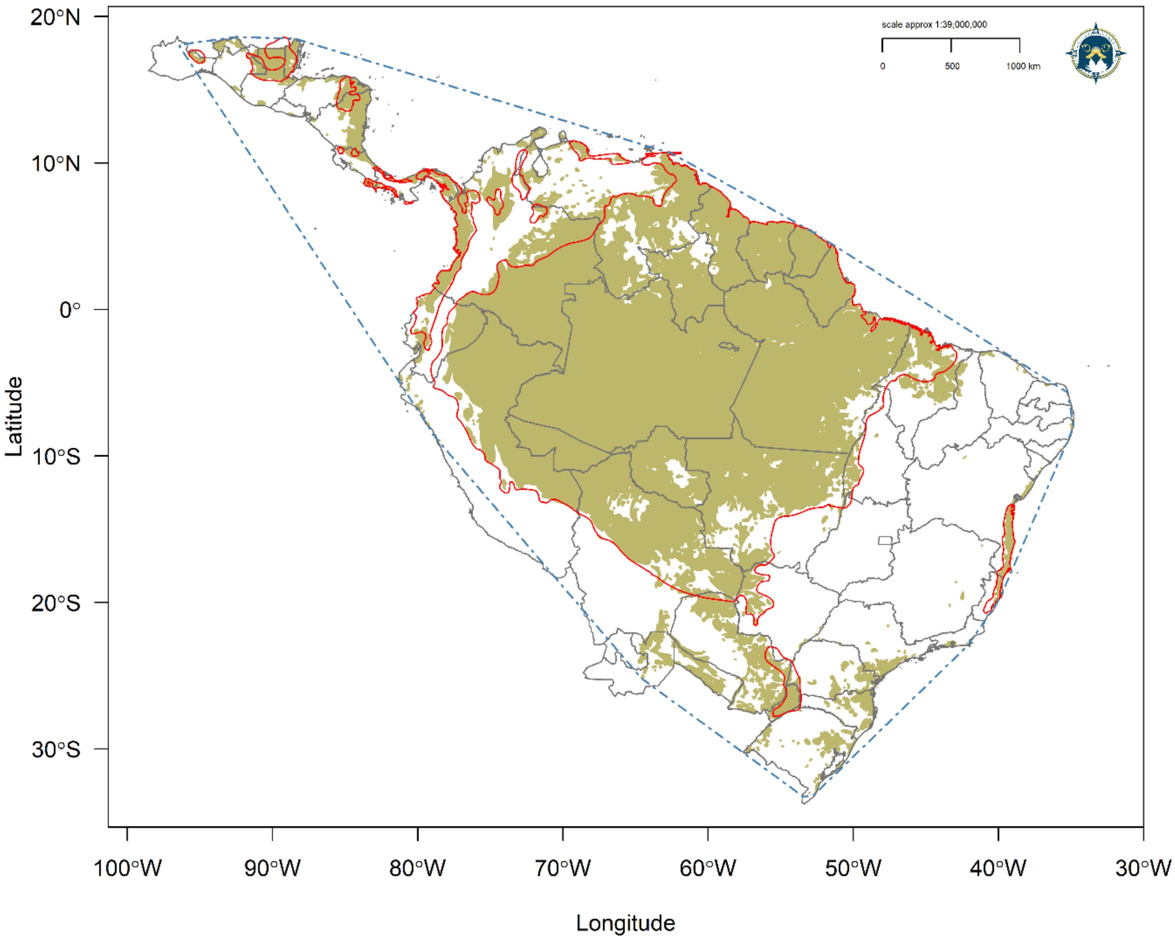

Figure 4. Reclassified binary Species Distribution Model (threshold = 0.345) for the Harpy Eagle. Dark khaki area is habitat above the 0.345 threshold, white areas below the threshold. Red polygons define current IUCN range map for the Harpy Eagle as a comparison to the SDM prediction. Blue hashed polygon represents the Harpy Eagle Extent of Occurrence (EOO) range metric. Gray borders define national boundaries within the study extent and internal state boundaries for Brazil.

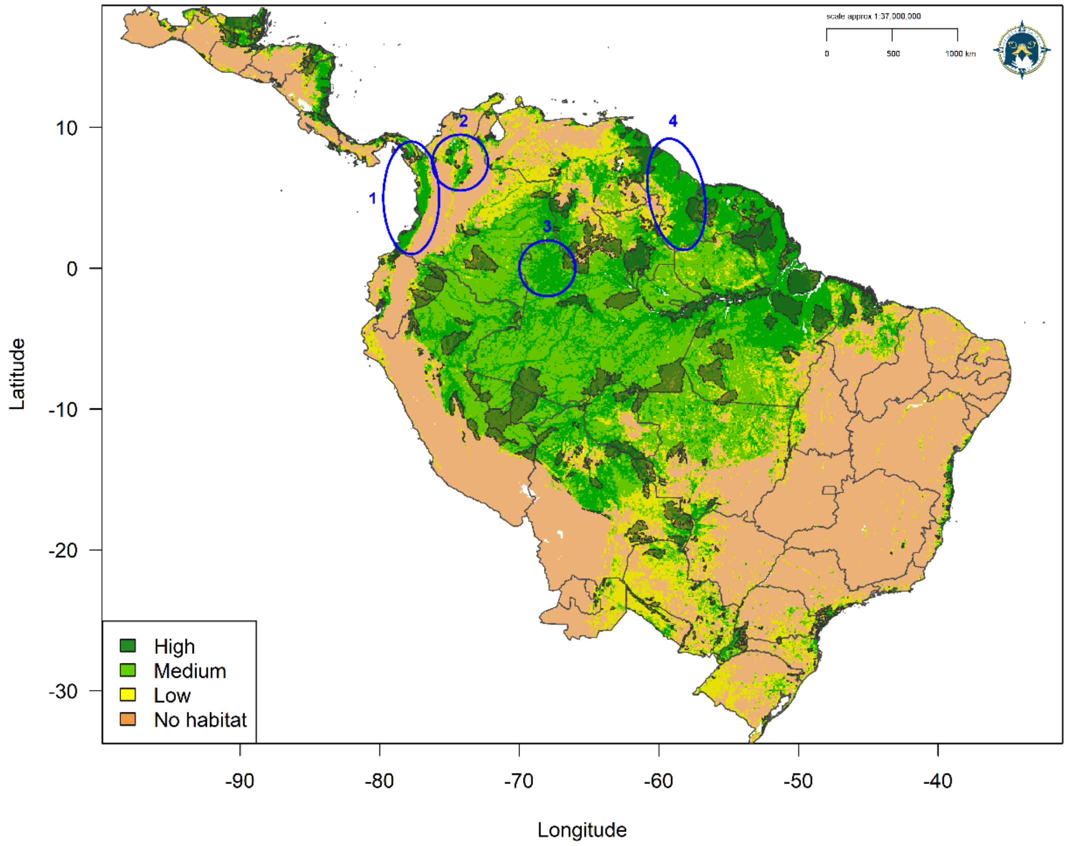

Figure 5. Key Biodiversity Area (KBA) network gap analysis for Harpy Eagle habitat. Map denotes cloglog prediction reclassifed into four discrete quantile threshold classes (brown = no habitat; yellow = low, pale green = medium; dark green = high). Black bordered polygons denote current KBA network. Blue ellipses identify priority KBA network coverage gaps: (**1**) Chocó-Darién ecoregion in Colombia, Ecuador and Panama, (**2**) Magdalena-Urabá moist forests in northern Colombia, (**3**) north-east Amazonas state in Brazil, (**4**) north and west Guyana. Gray borders define national boundaries within the study extent and internal state boundaries for Brazil.

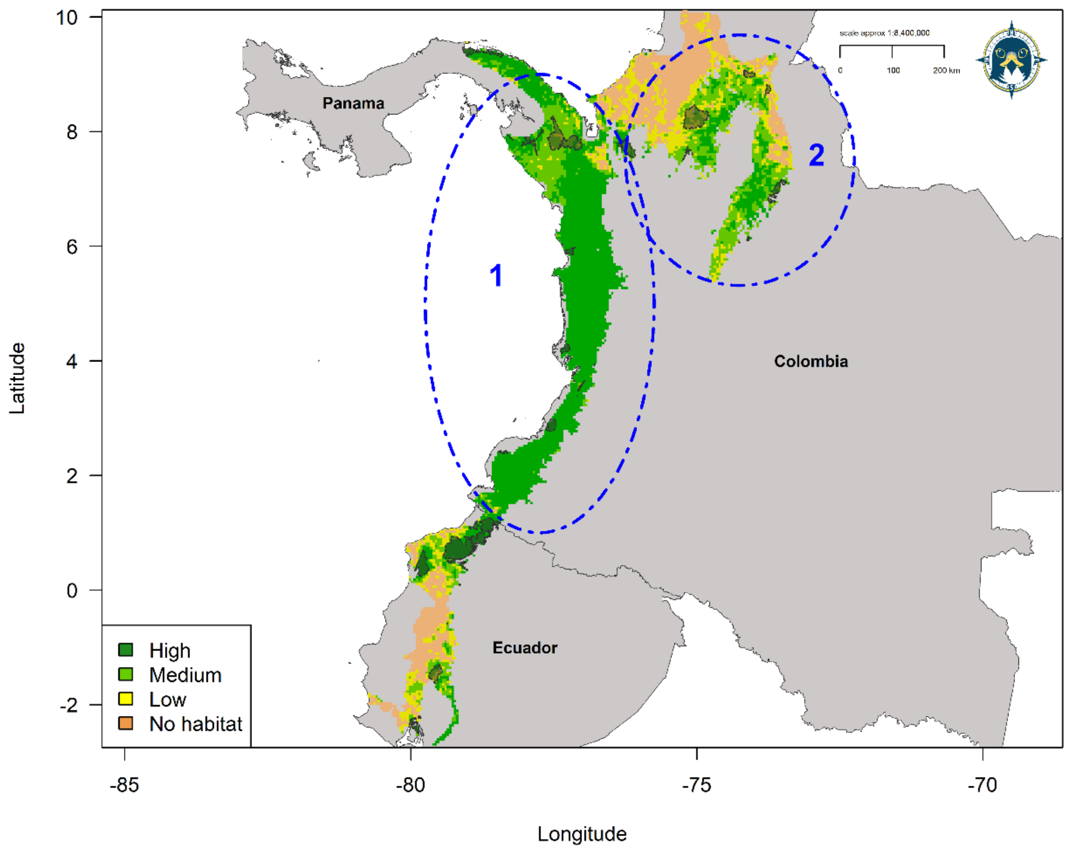

Figure 6. Key Biodiversity Area (KBA) network gap analysis for Harpy Eagle habitat projected into the Chocó-Darién ecoregion. Map denotes cloglog prediction reclassifed into four discrete quantile threshold classes (brown = no habitat; yellow = low, pale green = medium; dark green = high). Black bordered transparent polygons denote current KBA network. Hashed blue ellipses identify priority KBA network coverage gaps: (**1**) Chocó-Darién region in Colombia, Ecuador, and Panama, (**2**) Magdalena-Urabá moist forests in northern Colombia.

SUPPLEMENTARY MATERIAL

Occurrence data

From the 591 filtered occurrences we had 188 eBird records in total, with 57 of these with sampling regime metadata to define as quality records based on checklists with a sampling duration on >5 mins and <240 mins and a distance effort of <5 km (Johnston et al. 2021). We recognise the potential issues this raises with regard to precisely defining the environmental conditions and resources at occurrence points. However, because of the broad scale of our analysis we opted to retain all eBird occurrence data because using just the quality-controlled eBird occurrences would result in less data to build an appropriate continental-scale model. Further, the majority of our occurrence data were sourced from three other datasets that do not contain these sampling protocol data fields but give precise point localities for nests and sightings, rendering these quality checks across our entire dataset obsolete.

Habitat Covariates

Elevation and Terrain Roughness Index (TRI) are both key topographic variables influencing Harpy Eagle distribution (Vargas González and Vargas 2011; Vargas González et al. 2020; Sutton et al. 2021). Elevation was derived from a digital elevation model (DEM) product from the 250m Global Multi-Resolution Terrain Elevation Data 2010 (GMTED2010, Danielson and Gesch 2011). TRI was derived from the 30 arc-sec resolution Shuttle Radar Topographic Mission (SRTM30, Becker et al. 2009). Homogeneity is a biophysical similarity measure closely related to vegetation species richness (i.e., vegetation structure, composition and diversity) derived from textural features of Enhanced Vegetation Index (EVI) between adjacent pixels; 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 (Table S1).

The three measures of percentage landcover (Evergreen Forest, Mosaic Forest, Cultivated) are consensus products integrating GlobCover (v2.2), MODIS land-cover product (v051), GLC2000 (v1.1) and DISCover (v2) at 30 arc-sec (~1km) spatial resolution. Mosaic forest is derived from the EarthEnv variable ‘Mixed trees’ and represents a mosaic of mixed forest, shrubland and woody savanna, with cultivated representing a mix of cropland, tree cover and managed vegetation (Table S1). All landcover layers were resampled to a spatial resolution of 2.5 arc-minutes using bilinear interpolation. Full details on methodology and image processing can be found in Tuanmu and Jetz (2014) for the landcover layers, and Tuanmu and Jetz (2015) for the habitat heterogeneity texture measure. All selected covariates showed low collinearity and thus all six were included as predictors in model calibration (Variance Inflation Factor (VIF) < 5; Table S3). Finally, we summarized the environmental range of all habitat covariates used in our models at the species occurrences, pseudo-absences and background region to account for instances of extrapolation (Table S4).

LITERATURE CITED

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. and Ladner, R. (2009). Global bathymetry and elevation data at 30 arc seconds resolution: SRTM30_PLUS. *Marine Geodesy*. 32: 355-371.

Danielson, J.J. and Gesch, D.B. (2011). *Global multi-resolution terrain elevation data 2010 (GMTED2010)* (p. 26). US Department of the Interior, US Geological Survey.

Johnston, A., Hochachka, W.M., Strimas-Mackey, M.E., Ruiz Gutierrez, V., Robinson, O.J., Miller, E.T., Auer, T., Kelling, S.T. and Fink, D. (2021). Analytical guidelines to increase the value of community science data: An example using eBird data to estimate species distributions. *Diversity and Distributions*. 27: 1265-1277.

Sutton, L.J., Anderson, D.L., Franco, M., McClure, C.J.W., Miranda, E.B.P, Vargas, F.H., Vargas González, J. de J. and Puschendorf, R. (2021). Geographic range estimates and environmental requirements for the Harpy Eagle derived from spatial models of current and past distribution. *Ecology and Evolution.* 11: 481-497. DOI: https://doi.org/10.1002/ece3.7068

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

Tuanmu, M.N. and Jetz, W. (2015). A global, remote sensing-based characterization of terrestrial habitat heterogeneity for biodiversity and ecosystem modelling. *Global Ecology and Biogeography*. 24: 1329-1339.

Vargas González , J. de J., McCabe, J.D., Anderson, D.L., Curti, M., Cárdenas, D.C. and Vargas, F.H. (2020). Predictive Habitat Model Reveals Specificity in a Broadly Distributed Forest Raptor, The Harpy Eagle. *Journal of Raptor Research*. 54: 349-363.

Vargas González, J. de J. and Vargas, F.H. (2011). Nesting density of Harpy Eagles in Darien with population size estimates for Panama. *Journal of Raptor Research*. 45: 199-211.

Table S1. Habitat covariates used in all spatial modelling analyses for the Harpy Eagle, with citations for the sources of the environmental data used.

Covariate	Source	Citation	Resolution	Year(s)
Cultivated (%)	EarthEnv	Tuanmu & Jetz 2014	30 arc secs	1992-2005
Elevation (m)	EarthEnv	Amatulli et al. 2018	2.5 arc mins	2010
Evergreen forest (%)	EarthEnv	Tuanmu & Jetz 2014	30 arc secs	1992-2005
Homogeneity (0.0-1.0)	EarthEnv	Tuanmu & Jetz 2015	2.5 arc mins	2001-2005
Mosaic forest (%)	EarthEnv	Tuanmu & Jetz 2014	30 arc secs	1992-2005
Terrain Roughness Index	ENVIREM	Title & Bemmels 2018	30 arc secs	2000

Table S2. Model selection metrics for all six candidate models with $\Delta AIC_c < 2$. RM = regularization multiplier (β), FC = feature classes, LQ = Linear, Quadratic.

Model	RM	FC	AIC_c	ΔAIC_c
1	4.0	LQ	7574.316	0.000
2	3.5	LQ	7574.389	0.070
3	4.5	LQ	7574.561	0.245
4	3.0	LQ	7574.785	0.470
5	5.0	LQ	7575.125	0.809
6	2.5	LQ	7575.509	1.193

Table S3. Multi-collinearity test using stepwise elimination Variance Inflation Factor (VIF) analysis. Variables with VIF < 5 have low correlation with other variables, and thus are suitable for inclusion in calibration models when further evaluated for ecological relevance.

Covariate	VIF
Homogeneity	1.65
Terrain Ruggedness Index	1.76
Elevation	2.41
Mosaic forest	2.54
Cultivated	2.62
Evergreen forest	4.64

Table S4. Environmental range of habitat covariates at species occurrences, pseudo-absences and the background region used in Species Distribution Models for the Harpy Eagle. Values are mean (min-max).

Covariate	Occurrences	Pseudo-absences	Background region
Cultivated (%)	9 (0-70)	20 (0-99)	20 (0-100)
Elevation (m)	245 (3-2336)	538 (0-5368)	550 (0-5850)
Evergreen forest (%)	77 (0-100)	48 (0-100)	48 (0-100)
Homogeneity (0-1)	0 (0-1)	0 (0-1)	0.4 (0.1-1)
Mosaic forest (%)	5 (0-54)	13 (0-78)	13 (0-83)
Terrain Roughness Index (0-Inf)	22 (0-217)	27 (0-586)	27 (0-615)

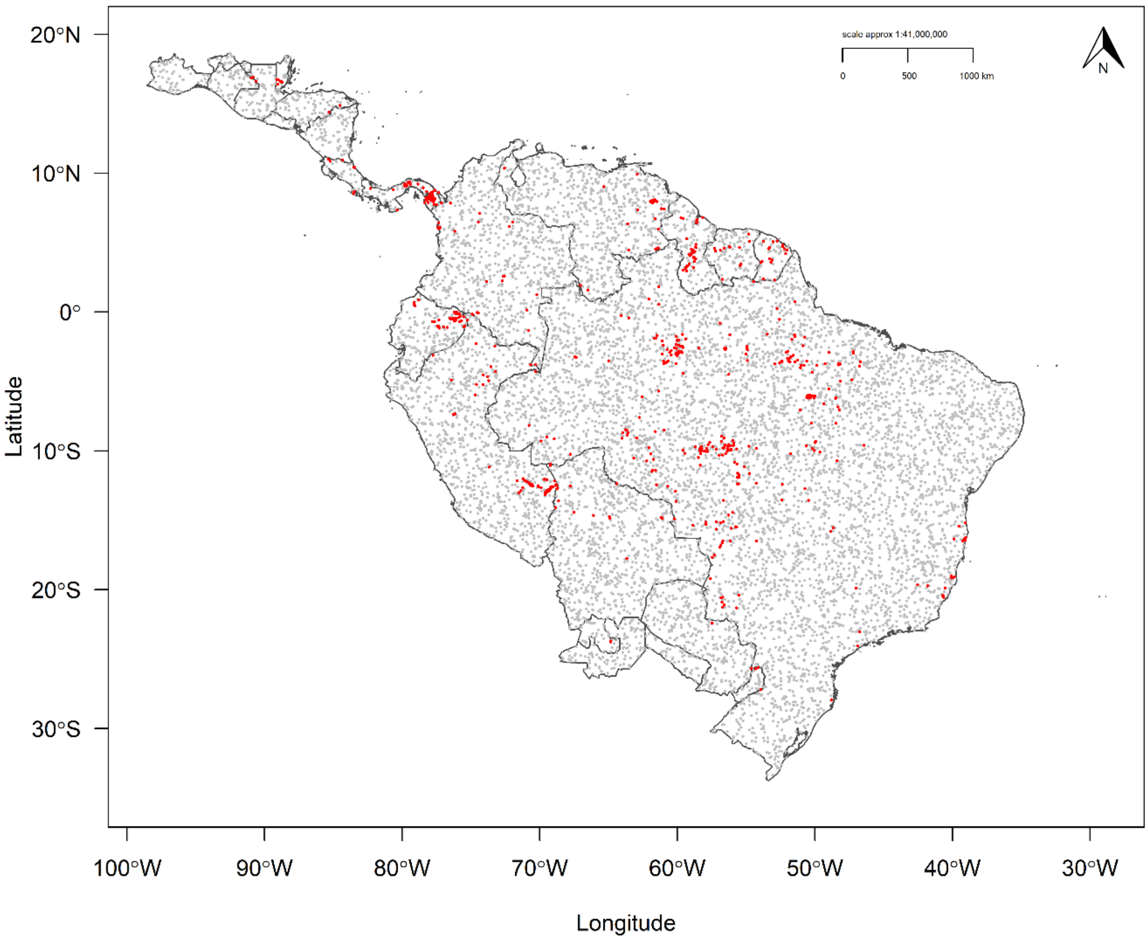

Figure S1. Distribution of random background points (*n* = 10,000, gray points) across the study extent used as pseudo-absences in Species Distribution Models for the Harpy Eagle. Red points denote spatially filtered Harpy Eagle occurrences.

Figure S2. Cropped Species Distribution Model for the Harpy Eagle across Central America. Map denotes cloglog prediction with darker green areas (values closer to 1) having highest suitability and expected abundance. Gray borders define national boundaries.