Reduced range size and Important Bird and Biodiversity Area coverage for the Harpy Eagle (*Harpia harpyja*) predicted from multiple climate change scenarios

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Climate change is expected to have a profound impact on species distributions, contracting suitable climate space. Biodiversity areas are important to mitigate these negative effects but are static by design and thus do not account for future projections of species distributions. The Harpy Eagle *Harpia harpyja* has a broad range across lowland Neotropical forests and thus its distribution could be negatively affected by climate change when combined with current rates of habitat loss. To test this hypothesis, we use spatial point process models fitted with climatic, topographic, and landcover covariates to identify current distribution. We then project to 24 future climate scenarios, using three General Circulation Models (GCMs), and two emission scenarios between the years 2021 and 2100 averaged over four 20-year periods. Our current model identified a core range across Amazonia and the Guiana Shield, with evergreen forest (71 %), mean diurnal temperature range (13 %), and elevation

(6 %) the most important predictors. Reclassifying the current model to a binary prediction estimated a range size of ~7.6 million km^2, with the Important Bird and Biodiversity Area (IBA) network covering 18 % of habitat (~1.4 million km^2) within this range. By 2090, range size was predicted to decrease on average by 14.4 % under a higher emissions scenario, and 7.3 % under a lower emissions scenario. The IBA network would cover 14 % less area under a higher emissions scenario, and 3.3 % less distribution area under a lower emissions scenario by 2090. Southern Amazonia is predicted to have the greatest reduction in range size and subsequently highest loss of Harpy Eagle habitat within the IBA network. Our work demonstrates that the combination of climate change and subsequent habitat loss may result in substantial losses in distribution for this raptor across the southern edge of its range.

Keywords: biodiversity areas, conservation planning, global warming, *Harpia harpyja*, Species Distribution Models

Climate change is predicted to have a significant impact on the distribution of many bird species (Crick 2004), with individual species responding differently to a changing climate (Pearce-Higgins & Green 2014). Therefore, assessing the threat level to each species is required, along with a species-specific assessment of adaptability to change (Pettorelli 2012). Even though the exact mechanisms limiting species distributions are often unclear (Journé *et al.* 2020), ultimately climatic conditions interacting with vegetation often determine where terrestrial bird species are distributed (Huntley *et al.* 2007, Barnagaud *et al.* 2011). Increasing temperatures interacting with extreme climates are predicted to have the greatest impact on bird populations at higher latitudes or elevations, driving poleward and upslope elevational range shifts (Şekercioğlu *et al.* 2008, Freeman *et al.* 2018). However, in lowland tropical regions, where precipitation is a key determinant of avian distributions (Şekercioğlu *et al.* 2012), climate change may not necessarily result in poleward range shifts but in multi-directional range shifts and contractions (VanDerWal *et al.* 2013, de Moraes *et al.* 2020, Sutton *et al.* 2020).

Although temperature increases are predicted to be lower in the tropics compared to higher latitudes (IPCC 2014), populations of tropical bird species may be amongst the most vulnerable to climate change (Şekercioğlu *et al.* 2012). The expected negative effects of warming and drought on tropical species adapted to narrow thermal tolerances may lead to reductions in distribution and potential extinctions (Harris *et al.* 2011). In the Neotropics, rates of warming are expected to be highest in central South America (da Costa *et al.* 2010), with increasing drought conditions throughout the pan-Amazonian region, an area largely covered by climate-regulating tropical forests. Climate change may then result in an increase in tropical forest fragmentation (Coe *et al.* 2017). Within the Neotropical avifauna, hawks and eagles (family: Accipitridae) may be particularly affected by climate change, because they generally exist at low population densities (Whitacre 2012) and are sensitive to habitat loss and fragmentation (Newton 1979, Krüger & Radford 2008). Factoring in the potential for range shifts and contractions adds another potential threat to this group in increasingly human-dominated landscapes.

The Harpy Eagle *Harpia harpyja* is a large Neotropical raptor with a broad but currently contracting range across Central and South America, due to habitat loss and fragmentation (Miranda *et al.* 2019,, Sutton *et al.* 2021a,b). The Harpy Eagle is classified as ‘Near Threatened’ on the International Union for the Conservation of Nature (IUCN) Red List (Birdlife International 2017) but is considered endangered or locally extinct in most of southern Mexico and Central America, and in the Atlantic Forest of Brazil (Vargas González *et al.* 2006). Harpy Eagles are habitat specialists of lowland tropical forest (Sutton *et al.* 2021b), with habitat loss and persecution the current primary threats facing the species (Vargas González *et al.* 2006). Although the Harpy Eagle has a broad distribution, changing climatic conditions interacting with deforestation could result in range shifts or contraction. As a habitat-specialist raptor (Vargas González *et al.* 2020) with low reproductive output, the Harpy Eagle may be particularly susceptible to the effects of climate change (Huntley *et al.* 2006), because it may struggle to adapt rapidly enough to changing conditions and resources (Krüger & Radford 2008,, Miranda *et al.* 2021).

Species that inhabit lowland areas without extensive topographical diversity may need to move long distances to track their preferred climate (Anciães & Peterson 2009, Harris *et al.* 2011, Şekercioğlu *et al.* 2012). For the Harpy Eagle, climate change could result in potential shifts or contraction in the species’ range, following its strong reliance on lowland tropical forest and associated climate and resources (Miranda *et al.* 2019, Sutton *et al.* 2021a,b). When coupled with anthropogenic factors such as deforestation, which is increasing in lowland tropical forests (Hansen *et al.* 2008, Stabile *et al.* 2020), there might be considerably less habitat available for Harpy Eagle in the future (Sutton *et al.* 2021b). Biodiversity areas are important for preserving the most critical areas to mitigate the various threats facing many species, such as habitat loss (Donald *et al.* 2019). However, identifying the areas where species ranges are predicted to shift or contract in a changing climate is a key priority for biodiversity area designation and expansion to ensure continued coverage into the future (Blair *et al.* 2012, Şekercioğlu *et al.* 2012).

Important Bird and Biodiversity Areas (IBAs, BirdLife International 2019) are a key biodiversity area network, with extensive global coverage in areas of highest priority for endangered and endemic bird species (Donald *et al.* 2019). IBAs specifically target key areas that sustain the long-term viability of bird populations - a key issue for Harpy Eagles since they occur at low densities of 4-6 breeding pairs per 100 km^2 (Vargas González & Vargas 2011). As well as birds, IBAs also aim to protect areas of high biodiversity and are used as a template for Key Biodiversity Areas (KBAs, IUCN 2016) an entire global biodiversity area network (IUCN 2016, Donald *et al.* 2019). Therefore, how effective the IBA network will be for covering future Harpy Eagle distribution under climate change is a key question for setting spatial conservation planning priorities (Şekercioğlu *et al.* 2012).

Here, we use climatic, topographical, and landcover variables within Species Distribution Models (SDMS) to identify distributional constraints from Harpy Eagle occurrences. We then use climate projections to predict future distribution using a range of climate change scenarios. Specifically, we set out a baseline assessment of the range-wide impact of climate change on Harpy Eagle distribution using both lower and higher future emission scenarios between the years 2021-2100. Based on the future projections, we then identify areas where current IBA network coverage will continue or be lost. We aim to inform range-wide conservation planning by: **(1)** estimating the current distributional range for the Harpy Eagle, **(2)** predicting future distribution based on multiple climate change scenarios, and **(3)** quantifying how effective the current IBA network is for covering areas of future Harpy Eagle distribution.

Methods

Occurrences

We sourced Harpy Eagle occurrences from the Global Raptor Impact Network (GRIN, McClure *et al.* 2021) a data information system for all raptor species. For the Harpy Eagle, GRIN consists of occurrence data from the Global Biodiversity Information Facility (GBIF 2019), which are mostly eBird records (79 %, Sullivan *et al.* 2009), along with two additional datasets of observations (Vargas González & Vargas 2011, Miranda *et al.* 2019). Occurrences were cleaned by removing duplicate locations, and those with no geo-referenced coordinates. We only included occurrences recorded from 1970 onwards to temporally match the timeframe of the climatic predictors. We applied a 5-km spatial filter between each occurrence point which approximately matches the resolution of the raster data (~4.5 km) and reduces the effect of biased sampling (Kramer-Schadt *et al.* 2013). After data cleaning, we compiled a total of 1146 geo-referenced records. Applying the 5-km spatial filter resulted in a subset of 692 Harpy Eagle occurrences for use in the modelling.

Environmental covariates

We used nine continuous covariates (Table 1) at a spatial resolution of 2.5 arc-minutes (~4.5-km), a suitable resolution for capturing environmental variation across climatically-stable lowland regions with low terrain complexity (Fick & Hjimans 2017). We selected covariates *a prioiri* based on Harpy Eagle biology (Vargas González & Vargas 2011, Miranda *et al.* 2019, Vargas González *et al.* 2020, Sutton *et al.*

2021a,b), following established SDM protocols for biological relevance (Hirzel & Le Lay 2008, Fourcade *et al.* 2016) and model simplicity to avoid over-fitting (Merow *et al.* 2014). Raster layers were cropped using a delimited polygon consisting of all known range countries and Formosa, Jujuy, Misiones and Salta provinces in northern Argentina, and Chiapas, Oaxaca, and Tabasco states in southern Mexico. These provinces and states are respectively the southern and northern limits of the species range. This allowed us to extend into potential future areas of marginal habitat on the distribution edges. This provides more realistic model predictions by focusing on the accessible area available to the Harpy Eagle (Barve *et al* 2011). Further, reducing the background area used for testing points used in model evaluation also limits model overfitting (Radosavljevic & Anderson 2014). All covariates showed low collinearity and thus all nine were included as predictors in model calibration, with Variance Inflation Factors (VIFs) lower than 6 (Dormann *et al.* 2013).

Five climatic covariates, specifically related to temperature and precipitation conditions that influence Harpy Eagle distribution, were downloaded from the WorldClim v2.1 database (Fick & Hjimans 2017). WorldClim variables are interpolated from average monthly weather station climate data (9000-60,000 stations) between years 1970-2000. WorldClim v2.1 improves on the previous WorldClim v1.4 by incorporating remote-sensed satellite data for areas with low weather station density. Two topographical covariates were sourced from the ENVIREM (Title & Bemmels 2018) and EarthEnv (www.earthenv.org) databases, used to provide measures of topographical heterogeneity, where species may find refugia from future climatic conditions (Austin & Van Niel 2010, Meineri & Hylander 2017).

Elevation and Terrain Roughness Index (TRI) are both key topographic variables influencing Harpy Eagle distribution (Vargas González & Vargas 2011, Vargas González *et al.* 2020, Sutton *et al.* 2021a,b) and including topography in climate change SDMs can improve model predictions (Luoto & Heikkinen 2008, Virkkala *et al.* 2010). Elevation was derived from a digital elevation model product from the 250-m Global Multi-Resolution Terrain Elevation Data 2010 (GMTED2010, Danielson & Gesch 2011). TRI was derived from the 30 arc-sec resolution Shuttle Radar Topographic Mission (SRTM30, Becker *et al.* 2009).

The two measures of percentage landcover (Evergreen forest and Cultivated) are consensus products derived from satellite remote-sensing post-1990, integrating GlobCover (v2.2), MODIS land-cover product (v051), GLC2000 (v1.1) and DISCover (v2) at 30 arc-sec (~1km) spatial resolution. Both 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 & Jetz (2014). Landcover covariates were included following IUCN guidelines for modelling climate change distributions (IUCN 2019), with both evergreen forest and cultivated land key predictors for Harpy Eagle distribution (Sutton *et al.* 2021b). Including landcover in SDMs improves future climate change predictions (Pearson *et al.* 2004, Stanton *et al.* 2012), accounting for the dynamic nature between climate and land use, and despite the limitations of using current land use in future predictions (Beale *et al.* 2008, Renwick *et al.* 2012, Stanton *et al.* 2012, Platts *et al.* 2019).

Species Distribution Models

We fitted SDMs using a point process modelling (PPM) framework employing the maximum entropy software, MAXENT (v3.4.1, Phillips *et al.* 2017). Internal model parameters were set to fit a PPM model treating occurrences as point intensity rather than grid cells, following the methodology set out by Renner *et al.* (2015). Recent theoretical work has demonstrated the equivalence of MAXENT to an inhomogeneous Poisson process (IPP, Fithian & Hastie 2013, Renner & Warton 2013),), which is the most appropriate method for fitting presence-only data SDMs (Warton & Shepherd 2010). Within the MAXENT software, we selected the complementary log-log (cloglog) transform as a continuous index of environmental suitability, with 0 = low suitability and 1 = high suitability. Phillips *et al.* (2017) demonstrated the cloglog transform is equivalent to an IPP and can be interpreted as a measure of relative occurrence probability proportional to a species relative abundance.

We used a random sample of 10,000 background points as pseudo-absences (Barbet-Massin *et al.* 2012) and to sufficiently sample the background calibration environment (Guevara *et al.* 2018). Convergent threshold was set at 10^{-5} and iterations increased to 5000 from the default (500) allowing for model convergence. 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 key MAXENT parameters: regularization multiplier and feature classes (Warren & Seifert 2011). Tuning MAXENT parameters results in more biologically relevant response curves, limits sampling bias, and reduces over-fitting in presence-only predictions (Merow *et al.* 2013, Radosavljevic & Anderson 2014). We used only Linear and Quadratic feature classes to produce less complex and more realistic predictions (Merow *et al.* 2013, Guevara *et al.* 2018). Omitting Threshold and Product feature classes generally increases model performance and gives more biologically meaningful model interpretations (Phillips *et al.* 2017). Hinge features were used initially but resulted in unrealistic, cranked response curves, so were omitted from model calibration (Guevara *et al.* 2018).

For the current distribution, we built eighteen candidate models of varying complexity by comparing a range of regularization multipliers from 1 to 5.0 in 0.5 increments, and two feature classes (Linear and Quadratic) in all possible combinations using the 'block' method of cross-validation (*k* = 5) in the ENMeval package in R (Muscarella *et al.* 2014). Block partitioning masks the geographical structure of the data according to latitude and longitude lines, dividing all occurrences into four spatially independent bins of equal numbers. Masking the geographical structure of test-data means the models are projected onto an evaluation region not included in the calibration process. All occurrence and background test points are assigned to their respective bins dependent on location, further reducing spatial autocorrelation between testing and training localities (Muscarella et al. 2014, Radosavljevic and Anderson 2014). We chose the block method because it reduces the possibility of encountering non-analogue climate conditions when transferring model predictions in time (Radosavljevic and Anderson 2014).

For future predictions, we built twenty-four SDMs using three earth system General Circulation Models (GCMs, Table 2) from the Coupled Model Intercomparison Project Phase 6 (CMIP6, Eyring *et al.* 2016). We used two future emission scenarios averaged over four time periods: 2021-2040 (henceforth 2030), 2041-2060 (henceforth 2050), 2061-2080 (henceforth 2070) and 2081-2100 (henceforth 2090). We used a range of projections to assess the magnitude of climate change from the short to long term, accounting for variation in model output sensitivity, and any uncertainty in single model predictions (,Lutz *et al.* 2016). Data were downloaded from the WorldClim database (v2.1, Fick & Hjimans 2017) for two CMIP6 emission scenarios or Shared Socioeconomic Pathways (SSPs): SSP245 and SSP585. SSP245 represents limiting warming to < 3°C by 2100, and SSP585 corresponds to a 'worst-case scenario' where no climate policy actions are implemented with CO_2 emissions reaching > 120 gigatonnes annually by 2100 (Riahi *et al.* 2017). Finer resolutions (e.g., 30 arc-seconds) of future climatic data are currently unavailable for CMIP6 projections in WorldClim v2.1, but 2.5 arc-minutes was used as a suitable resolution for the broad scale analysed here. All internal MAXENT parameters used for the current distribution model were kept for the future distribution models and predicted using the 'projection layers' function in the MAXENT software.

Model evaluation

We evaluated optimal model selection using both threshold-independent and threshold-dependent measures (Radosavljevic & Anderson 2014). Area Under the Curve (AUC) is a non-parametric, threshold-independent measure representing an overall value of model performance across all thresholds, with AUC = 1.0 being the maximum predictive performance, and an AUC = 0.5 being no better than a random prediction (Franklin 2009). AUC_{DIFF}, the difference in AUC values from the training and test models (AUC_{TRAIN} - AUC_{TEST}) was used to quantify model over-fitting (Muscarella *et al.* 2014), with a value close to zero indicating a low over-fit model (Warren & Seifert 2011). We used AUC metrics as a measure of optimal model selection, best suited to comparing a range of candidate models and not as a test of final model predictive performance (Lobo *et al.* 2008, Jiménez-Valverde 2012).

Omission rates report the proportion of training points that are outside of the model when converted into a threshold binary prediction, evaluating discriminatory ability at a specified threshold. Lower omission rates show improved discrimination between suitable and unsuitable pixels (indicating higher performance), whilst overfitted models show higher omission rates than expected by theory (Radosavljevic & Anderson 2014). We calculated a single threshold-dependent measure based on the 10% training presence omission rate (OR10) threshold. For low over-fit models the expectation for OR10 is a value of 0.10 (Muscarella *et al.* 2014). We used response curves, percent contribution and permutation importance as estimates for variable performance within the optimal calibration model. Percent contribution is the proportion of each variable to model training gain dependent on the algorithm, whereas permutation importance is independent of the algorithm path and represents the importance of a given value on the AUC training values (Phillips *et al.* 2006). Pair-wise niche overlap metrics were calculated for all future continuous distributions to quantify how predictions from the three GCMs differed in geographic space using Schoener's *D* (Schoener 1968, Warren *et al.* 2008), which ranges from 0 (no overlap) to 1 (identical predictions).

We tested final model 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 – 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). We used Continuous Boyce index (CBI) as a threshold-independent evaluation metric (Hirzel *et al.* 2006), measuring how much environmental suitability predictions differ from a random distribution of observed presences (Boyce et al. 2002). It is consistent with a Spearman correlation (r_S) with values of CBI ranging from -1 to +1, with positive values indicating predictions consistent with observed presences, values close to zero no different than a random model, and negative values indicating areas with frequent presences having low environmental suitability. CBI evaluation was calculated on 20% test data with a moving window for threshold-independence and 101 defined bins in the R package enmSdm (Smith 2019).

Binary models

To calculate current and future distribution area, all continuous models were reclassified as binary threshold predictions. From the three GCM future predictions for each 20-year time interval, we calculated mean predictions from the continuous outputs for each future emissions scenario. All pixels equal to or greater than the median value of 0.396 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). The IBA network polygons (as of September 2019, BirdLife International 2019) were then clipped to the reclassified area, establishing those IBAs covering pixels of habitat suitability ≥ 0.396 threshold. The IBA shapefile was cropped to the Harpy Eagle range extent, and then intersected with each mean binary prediction to calculate IBA coverage (km^2). Geospatial analysis, modelling and visualisation were conducted 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), sp (Bivand *et al.* 2013) and wesanderson (Ram & Wickham 2018) packages.

Results

Current Distribution Model

The best-fit model ($\Delta\text{AIC}_\text{c}$ = 0.0) had feature class parameters Linear and Quadratic, with a regularization multiplier of β = 1. Optimal model selection metrics using 'block' cross-validation had moderate to high predictive performance (AUC_TRAIN = 0.780, AUC_TEST = 0.755). Model overfitting was low (AUC_DIFF = 0.025), with discrimination ability close to the expected omission rate threshold (OR10 = 0.15). The final predictive model was robust against random expectations (pROC = 1.482 ±0.052, range=1.321-1.629), with high calibration accuracy between predicted environmental suitability and test occurrence points (CBI = 0.928). The current distribution model defined a large continuous range across Amazonia and the Guiana Shield, with a corridor running north from the Chocó region of Colombia through Central America along the Caribbean coast (Fig. 1). Distribution across the largely deforested Atlantic Forest region in Brazil was patchy and fragmented, mainly confined to the far south-east of the region. The reclassified binary threshold prediction (median = 0.396) estimated a range size of climatically suitable habitat totalling 7,617,932 km^2. Within this distributional area the current IBA network covered 18.2 % (1,388,412 km^2) of habitat for the Harpy Eagle (Fig. S1).

Covariate Importance

Four covariates contributed 92.9 % to model prediction (Table 3), with evergreen forest the highest contributor (71.2 %), followed by mean diurnal temperature range (12.9 %), elevation (5.6 %), and isothermality (3.2 %). Evergreen forest had peak suitability at 60-70 % proportion forest cover, with peak suitability for zero to low proportion of cultivated land (Fig. 2). Mean diurnal temperature range had a suitability range of 5 °C, as expected in the relatively stable climatic conditions of lowland tropical forests. Topographic areas had highest suitability in the range 0-500 m elevation and low terrain roughness with TRI peak suitability ~100. Isothermality peaked at 40-50 %, reflecting the constant annual temperatures Harpy Eagles experience in lowland tropical forests. Precipitation in the wettest month peaked at 500-600 mm/month, with highest suitability for precipitation in the warmest quarter of 700-800 mm.

Future distribution models

The mean binary GCM predictions showed a decline in range size in both emission scenarios (Table 4). Under the lower emissions scenario (SSP245), mean range size is predicted to decrease by 2 to 7 % from 2030 to 2090 (Table 4, Fig. S2). Under the higher emissions scenario (SSP585), mean range size is predicted to decrease by 5 to 14 % from 2030 to 2090 (Table 4, Fig. S3). From all individual future predictions there was high correlation between GCMs in where future geographic space is likely to persist (Table S1), but with some variation in the amount of area predicted to contract (Tables S2-S3). Using the CanESM5 climate projection as the most sensitive GCM, all future climate scenarios predicted a consistent contraction in range size across southern and central Amazonia (Figs. 3-4). A core distribution area is predicted to persist over the period 2030-2050 across the wider pan-Amazonian region and Guiana Shield under both emission scenarios. However, from 2070 to 2090 under the higher emissions scenario (Fig. 4), the distribution area is likely to be restricted to northern Amazonia, the Guiana Shield, and the Caribbean coast of Central America. Southern and south-western Amazonia is predicted to have the greatest reductions in distribution area, but with an area adjacent to the east Andean slope in Bolivia and Peru persisting to 2090 under the higher emissions scenario.

IBA network coverage

Using the mean GCM projections under the lower emissions scenario (SSP245), the current IBA network would provide similar coverage from 2030 to 2050 with percentage losses relative to current distribution between 0.2 and 1.3 % (Table 5). By 2070, there would be 4.1 % less distribution area covered, but only 3.3 % less distribution area by 2090 (Table 5). Under the higher emissions scenario, decreases in IBA network coverage of 2.7 and 2.2 % are predicted for 2030 and 2050 respectively, with 6 % less coverage by 2070 and 14 % less IBA coverage by 2090 (Table 5). To identify a ‘worst-case scenario’ for 2090 we used the CanESM5 climate projection as the most sensitive GCM under the SSP585 higher emissions scenario. This climate change outcome would result in 29 % reduction in range size to 5 441 364 km^2 (Table 4, Table S3), with the current IBA network coverage reduced by 32 % to 946 779 km^2. Most biodiversity area losses are predicted within south-west Brazil across the states of Acre, Rondônia, Mato Grosso and southern Amazonas, and the bordering regions in eastern Bolivia and Peru (Fig. 5, Table S4). However, a broad area adjacent to the east Andean slope in Bolivia and Peru would still retain IBA coverage.

Discussion

Our results demonstrate that climate change could lead to range size contraction for the Harpy Eagle and subsequently reduce coverage within the current IBA network, mainly across the southern extent of the species range. The reclassified binary model estimated a current distribution area totalling ~7.6 million km^2, with the current IBA network covering 18 % (~1.4 million km^2) of this area. By 2090, mean range size was predicted to decrease by 14 % under the higher emissions scenario, and 7 % under the lower emissions scenario. By 2090 under the higher emissions scenario, core refugia were predicted to remain across northern Amazonia, the Guiana Shield, and the Caribbean coast of Central America. By 2090, there would be 14 % less mean distribution area covered by the IBA network under a higher emissions scenario and 3 % less IBA coverage under the lower emissions scenario. Southern Amazonia is predicted to have the greatest reductions in distribution area for the Harpy Eagle and subsequently highest loss of habitat within the IBA network, in line with the current pace of shifting local climates (Mahlstein *et al.* 2013).

Current distribution

Methodology to estimate current and future species distributions using SDMs was established mainly using climatic variables (Pearson & Dawson 2003, Thuiller 2004, Hijmans & Graham 2006,), especially at continental extents where climate is expected to exert the strongest influence on distribution (Huntley *et al.* 2007). Evergreen forest was the most important predictor, followed by mean diurnal temperature range and elevation. It is recognised that species range limits are dependent on the interaction of multiple factors including land cover (Renwick *et al.* 2012, Stanton *et al.* 2012) and topography (Luoto & Heikkinen 2008, Virkkala *et al.*

2010, Hof *et al.* 2012). The models presented demonstrate that including land cover results in a more restricted range estimate for the Harpy Eagle compared to using solely climatic and topographical predictors (as in Sutton *et al.* 2021a). Because the Harpy Eagle is a habitat specialist of lowland tropical forests (Miranda *et al.* 2019, Vargas González *et al.* 2020, Sutton *et al.* 2021b), it follows that high proportion of evergreen forest, lower elevation, and stable temperatures would have the greatest influence on determining the species geographic range. Thus, the interaction between vegetation, climate, and topography best explains Harpy Eagle range limits, over a model relying solely on climate and topography (Sutton *et al.* 2021a).

In lowland tropical regions, daily and seasonal temperatures are relatively constant (Nieuwolt 1977) and a narrow mean diurnal temperature range of 5 °C also makes a large contribution to model prediction. This narrow temperature range tolerance is common amongst many tropical bird species (Şekercioğlu *et al.* 2008), and ultimately may be a key factor in how a changing climate may affect the distribution of many tropical species that have evolved within narrow thermal limits (Harris *et al.* 2011, Şekercioğlu *et al.* 2012). Aside from temperature, precipitation has been identified as potentially important for restricting tropical bird species ranges (Şekercioğlu *et al.* 2012,). For the Harpy Eagle, both monthly and seasonal rainfall contributed only small percentages to model prediction (Table 3 and Fig. 2). This suggests that precipitation may not be a direct determinant of Harpy Eagle distribution, but that moist tropical forests dependent on high rainfall constitute a more useful proximate predictor. Indeed, the causal chain may well be inverted as > 70 % forest cover may be required to maintain the forest-dependent rainfall regime in Amazonia (Silva Dias *et al.* 2002, Soares-Filho *et al.* 2006).

Future distributions

Unlike the general poleward shifts in distribution predicted for many temperate bird species, the core climate refugia for the Harpy Eagle will remain in equatorial regions of its range and is not predicted to shift, following current climate velocities (Mahlstein *et al.* 2013). By 2090 the main distribution strongholds will remain across northern Amazonia, the Guiana Shield, and parts of Central America assuming that land cover remains static, which seems unlikely. Including land use has gained wide support when predicting future distributions, even when land cover is a static variable derived from current land use layers (e.g., Pearson *et al.* 2004, Renwick *et al.* 2012, Stanton *et al.* 2012, Platts *et al.* 2019). Thus, including current land cover restricts the future models to those future areas predicted suitable both climatically and from land use, despite its unrealistic static nature for future predictions. Incorporating future land use scenarios (e.g., Hurtt *et al.* 2016) within our modelling framework would improve model predictions using a more dynamic approach (Beale *et al.* 2008, Huntley *et al.* 2010). Accounting for the rapid change in human-mediated land use (Powers & Jetz 2019), in particular across the Neotropics (Borges & Loyola 2020), would improve future forecasting efforts when combined with future climate change projections.

Biodiversity areas

Protecting large areas of key habitat is important for species conservation (Rodrigues & Cazalis 2020) and should be prioritised in an ongoing effort to identify gaps in coverage, establishing an effective interconnected network (Rodrigues *et al.* 2004a, Rodrigues *et al.* 2004b). Although the current IBA network exceeds the biodiversity area target representation (10 %) for covering Harpy Eagle habitat (~18 %, Sutton *et al.* 2021b), future coverage under climate change may see IBA coverage reduced in the south of the species range, along with associated impacts of climate change such as wildfires. Brazil is predicted to lose most distribution area for the Harpy Eagle within the IBA network, across the states of Acre, Rondônia, and Mato Grosso. Unfortunately, this area is one of the main agricultural frontiers in Brazil, where the 'arc of deforestation' is advancing rapidly (Coe *et al.* 2017, Miranda *et al.* 2020). Additionally, the forest-dependent rainfall regime is already increasing the extent of the dry season in this region, with the rainy season shortened by 1.81 days per year over the period 1998-2012 (Leite-Filho *et al.* 2019). Expanding biodiversity areas and connecting habitat, combined with area-based community conservation across these states would be an effective and economical conservation strategy over the long-term, even if future climate is deemed less favourable (Hannah *et al.* 2007).

Whilst the core refugia predicted for the Harpy Eagle across northern Amazonia and the Guiana Shield will still retain some level of coverage within the IBA network, this is based on current land cover remaining static until 2090. Due to accelerated rates of forest change this future land use scenario is unlikely (Powers & Jetz 2019), thus expanding IBAs across northern Amazonia, the Guiana Shield, and further north into Central America, will be required to maintain a sufficient level of IBA coverage for the Harpy Eagle. Priority gaps in the IBA/KBA network have already been identified for the Harpy Eagle in north-west Amazonia, Guyana, and the Chocó- Darién ecoregion in Colombia (Sutton *et al.* 2021b). Establishing new IBAs in all these areas seems even more necessary now given the core climate refugia projected to remain in these regions. Spatial conservation planning would still be focused on current threats such as habitat loss but would incorporate a long-term climate change ‘no regrets’ principle (Hannah *et al.* 2007, Pearce-Higgins & Green 2014) based on best-practice modelling for potential future distribution. In addition to the significance of this research for the conservation of Harpy Eagles, their position as apex predators used as flagship species may provide the necessary incentive to protect valuable habitat for many other species.

Though the models here had high predictive power, we recognise limitations to this approach. The interpretation of our future distribution models should be taken as a *maximum range extent*, knowing that forest cover is predicted to decrease and cultivated land increase over the time period analysed here (Powers & Jetz 2019, Lima *et al.* 2020). Indeed, shifting seasonality in the tropics combined with rapid land use change is predicted to have a strongly negative impact on the range limits for many tropical taxa (Sodhi *et al.* 2012). Taking a process-based approach by sustaining the underlying mechanisms for adaptation is critical (Tobias *et al.* 2013). Maintaining habitat heterogeneity and connectivity between key areas of protected habitat linked to area-based conservation can prevent species extinction (Tobias *et al.* 2013). Thus, to be effective, biodiversity areas need protective status to ensure coverage across areas of extensive habitat heterogeneity, topographical diversity, and wide elevational ranges (Sodhi *et al.* 2012). Therefore, including all these environmental variable types within the modelling process, as demonstrated here, is crucial to identify those areas predicted to remain most suitable into the future.

Changing climates have shaped species distributions over the aeons, yet the current magnitude and rate of human-mediated climate change, combined with habitat loss, may result in significant contraction and shift in species range limits, if not extinction (Parmesan & Yohe 2003, Travis 2003, Sodhi *et al.* 2011). When combined with the more immediate threat of rapid habitat loss occurring over shorter time scales, a changing climate may result in substantial losses in distribution in the long-term for this raptor across the southern edge of its range. Thus, maintaining and expanding a network of large-sized IBAs that contain high habitat and climatic heterogeneity may be a solution within a fixed reserve network that is robust to future climate change (Carroll *et al.* 2010,). This would not only benefit the Harpy Eagle, but as a large apex predator requiring large tracts of continuous tropical forest, it would benefit all the associated tropical forest biota within those biodiversity areas.

Acknowledgements

We thank all individuals and organisations who contributed occurrence data to the Global Raptor Impact Network (GRIN) information system. LJS thanks The Peregrine Fund for providing financial assistance for his studentship. EBPM work is supported by Rufford Foundation, ONF Brasil, Rainforest Biodiversity Group, Idea Wild, Explorer’s Club Exploration Fund, Cleveland Metroparks Zoo, and SouthWild.com. We thank the M.J. Murdock Charitable Trust for funding and the Information Technology staff and Research Library interns at The Peregrine Fund for support. We thank Rebecca Kimball, José Antonio Sánchez-Zapata and two anonymous reviewers for comments and suggestions that helped improve the manuscript.

Data Accessibility Statement

The data that support the findings of this study are openly available on the data repository *figshare* 10.6084/m9.figshare.16707244

Conflict of Interest statement

The authors have no conflicts of interest to declare.

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Tables

Table 1. Environmental variables used as predictors in current and future Species Distribution Models for the Harpy Eagle.

Predictor	Source	Citation
Mean diurnal temperature range (°C)	WorldClim v2.1	Fick & Hjimans 2017
Isothermality (%)	WorldClim v2.1	Fick & Hjimans 2017
Temperature seasonality (SD, °C)	WorldClim v2.1	Fick & Hjimans 2017
Precipitation wettest month (mm)	WorldClim v2.1	Fick & Hjimans 2017
Precipitation warmest quarter (mm)	WorldClim v2.1	Fick & Hjimans 2017
Terrain Roughness Index (TRI)	ENVIREM	Title & Bemmels 2018
Elevation (m)	EarthEnv	Amatulli *et al.* 2018
Evergreen forest (%)	EarthEnv	Tuanmu & Jetz 2014
Cultivated (%)	EarthEnv	Tuanmu & Jetz 2014

Table 2. General Circulation Models (GCMs) from the Coupled Model Inter-comparison Project Phase 6 (CMIP6) used to predict future Harpy Eagle distribution.

General Circulation Model (GCM)	Acronym	Citation
Canadian Earth System Model v5	CanESM5	Swart *et al.* 2019
CNRM Earth System Model v2.1	CNRM-ESM2-1	Séférian *et al.* 2020
Model for Interdisciplinary Research on Climate - Earth System v2 for Long-term simulations	MIROC-ES2L	Hajima *et al.* 2020

Table 3. Percent contribution and permutation importance for variables used as environmental predictors in the continuous model for the Harpy Eagle. All values are %.

Predictor	Percent contribution	Permutation importance
Evergreen forest (%)	71.2	34.9
Mean diurnal temperature range (°C)	12.9	19.1
Elevation (m)	5.6	15.1
Isothermality (%)	3.2	10.1
Precipitation wettest month (mm)	2.2	6.3
Cultivated (%)	1.7	5.0
Terrain Roughness Index (TRI)	1.5	2.9
Temperature seasonality (SD, °C)	1.3	5.8
Precipitation warmest quarter (mm)	0.3	1.0

Table 4. Predicted change (%) in future range size for the Harpy Eagle for four 20-year periods (2030-2090) using lower (SSP245) and higher (SSP585) emissions climate change scenarios from three General Circulation Models (GCMs).

	2030		2050		2070		2090	
GCM / SSP	245	585	245	585	245	585	245	585
CanESM5	-3.9	-12.7	-9.7	-15.7	-13.5	-19.4	-20.8	-28.6
CRNM-ESM2-1	-0.9	-0.3	0.2	-0.3	0.2	-0.7	1.6	-4.7
MIROC-ES2L	-0.7	-3.2	-5.1	-2.5	-5.5	-6.1	-2.3	-10.1
Mean	-1.8	-5.4	-4.9	-6.1	-6.3	-8.7	-7.3	-14.4

Table 5. Mean area and percent change from area of predicted future Harpy Eagle distribution within the current IBA network employing lower (SSP245) and higher (SSP585) climate change scenarios for four 20-year periods (2030-2090).

SSP245	Year	Area (km^2)	% change
	2030	1 385 341	-0.2
	2050	1 370 469	-1.3
	2070	1 331 280	-4.1
	2090	1 342 220	-3.3
SSP585			
	2030	1 351 043	-2.7
	2050	1 357 640	-2.2
	2070	1 304 577	-6.0
	2090	1 194 030	-14.0

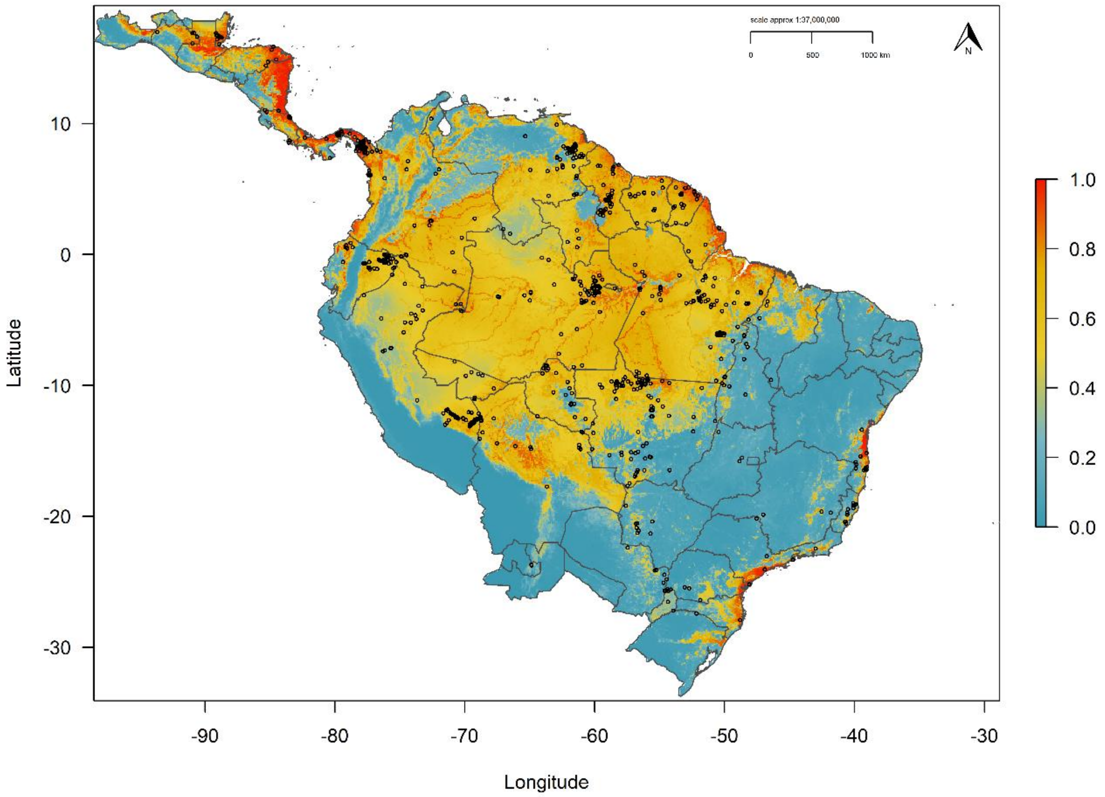

Figure 1. Predicted continuous distribution model for the Harpy Eagle. Map denotes cloglog prediction with values closer to 1 having higher environmental suitability for Harpy Eagle occurrence. Black points define known Harpy Eagle occurrences.

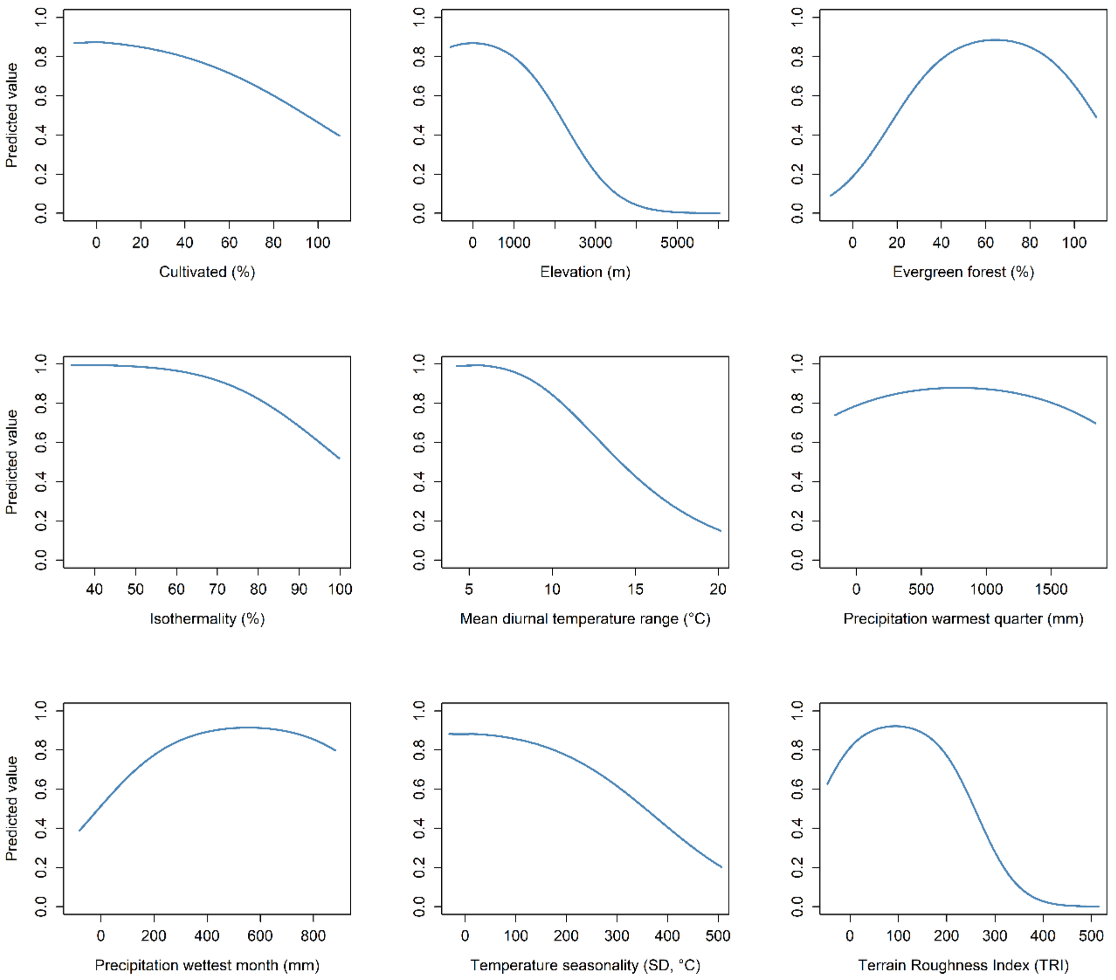

Figure 2. Response curves for each environmental variable used as predictors in the current distribution model for the Harpy Eagle.

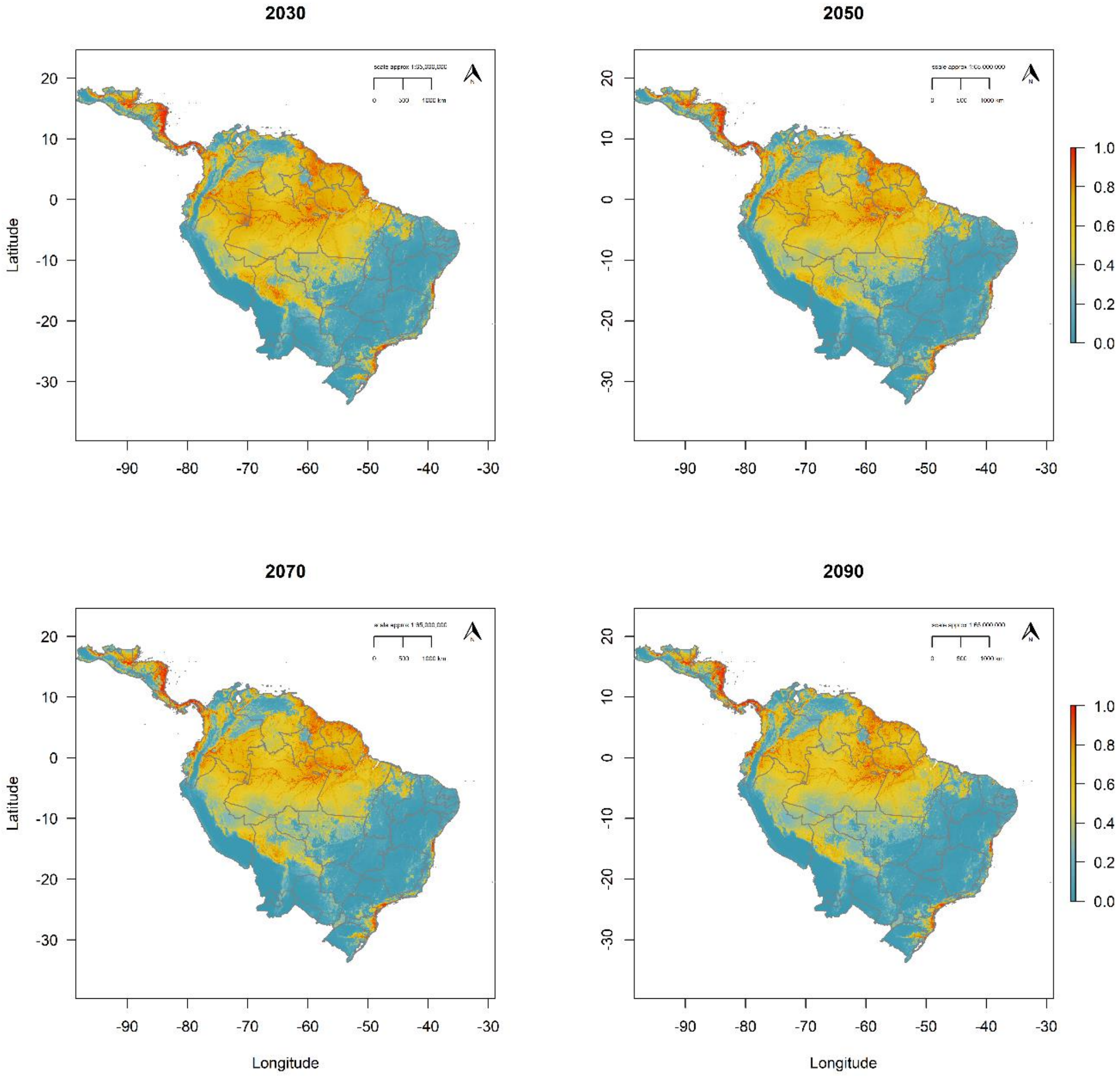

Figure 3. Continuous predictions from the CanESM5 general circulation model for Harpy Eagle distribution using the SSP245 lower emissions scenario across four future climate change timeframes.

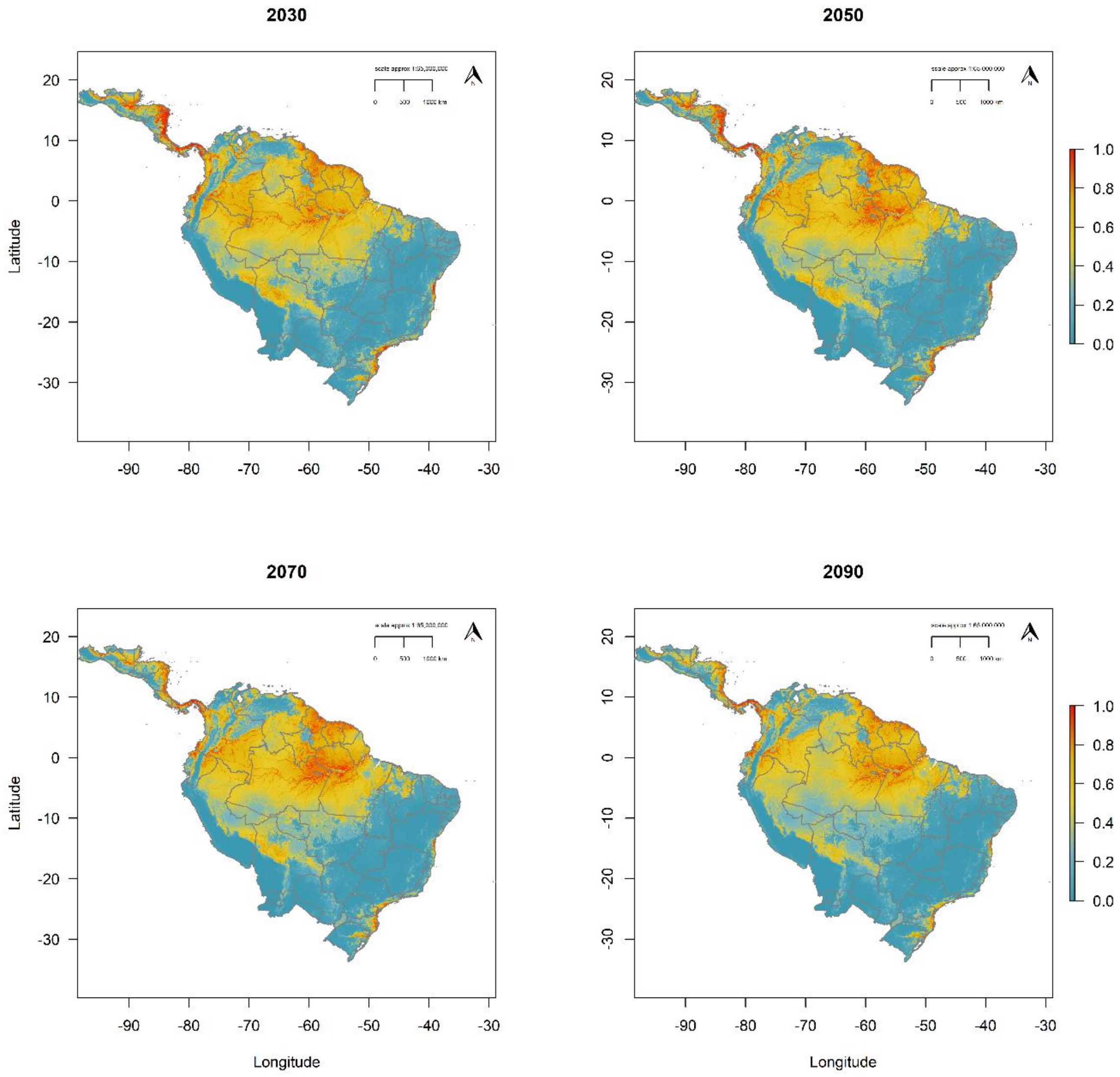

Figure 4. Continuous predictions from the CanESM5 general circulation model for Harpy Eagle distribution using the SSP585 higher emissions scenario across four future climate change timeframes.

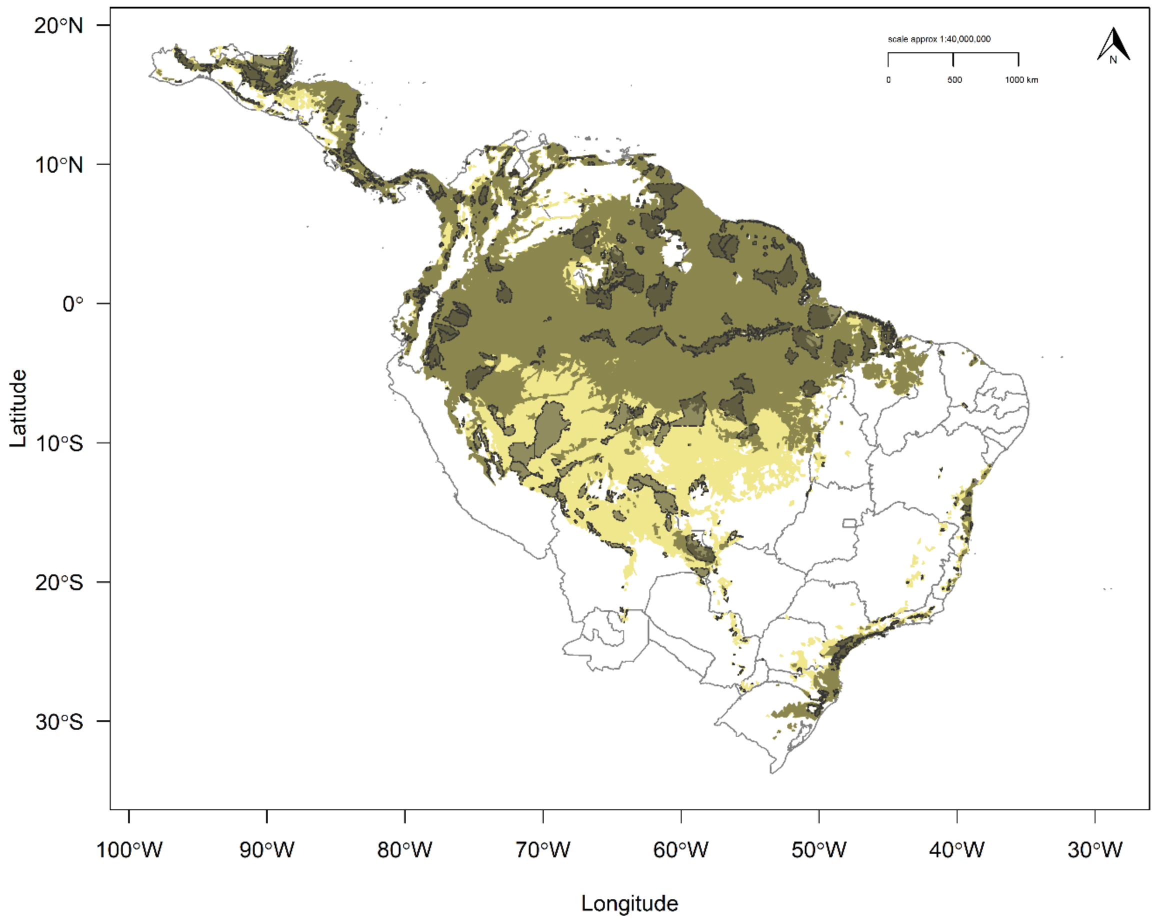

Figure 5. Reclassified ‘worst-case scenario’ binary prediction for 2090 under the higher emissions scenario (SSP585) using the CanESM5 Global Circulation Model (GCM) projection. Dark khaki area is predicted distribution under the CanESM5 climate projection, pale khaki areas are where climate space is predicted to be lost. Dark grey polygons show continued coverage of the current Important Bird and Biodiversity Area (IBA) network and pale grey polygons where future Harpy Eagle distribution will be lost within the IBA network.

Supplementary Online Material

Appendix 1 Supplementary Tables

Table S1. Geographical niche overlap calculated for predicted future distributions for the Harpy Eagle from 2030-2090 using three paleoclimate General Circulation Models (GCMs). SSP245 refers to the lower emissions Shared Socioeconomic Pathway scenario, and SSP585 refers to the higher emissions Shared Socioeconomic Pathway scenario.

SSP245

Year	GCM	CanESM5	CNRM-ESM2
2030	CNRM-ESM2	0.948	
	MIROC-ES2L	0.941	0.967
2050	CNRM-ESM2	0.950	
	MIROC-ES2L	0.951	0.952
2070	CNRM-ESM2	0.937	
	MIROC-ES2L	0.942	0.953
2090	CNRM-ESM2	0.918	
	MIROC-ES2L	0.921	0.955

SSP585

Year	GCM	CanESM5	CNRM-ESM2
2030	CNRM-ESM2	0.937	
	MIROC-ES2L	0.943	0.956
2050	CNRM-ESM2	0.928	
	MIROC-ES2L	0.927	0.955
2070	CNRM-ESM2	0.908	
	MIROC-ES2L	0.908	0.944
2090	CNRM-ESM2	0.901	
	MIROC-ES2L	0.887	0.932

Table S2. Predicted change in future distribution area (km^2) for the Harpy Eagle (and corresponding percentage from current distribution) using a lower emissions (SSP245) CMIP6 climate change scenario from three General Circulation Models (GCMs).

Year	GCM	Future area (km^2)	Change (km^2)	Change (%)
2030	CanESM5	7 318 047	-299 885	-3.9
	CRNM-ESM2-1	7 550 583	-67 350	-0.9
	MIROC-ES2L	7 566 312	-51 620	-0.7
	Mean	7 478 314	-139 618	-1.8
2050	CanESM5	6 882 584	-735 348	-9.7
	CRNM-ESM2-1	7 631 332	13 400	0.2
	MIROC-ES2L	7 232 711	-385 221	-5.1
	Mean	7 248 876	-369 056	-4.9
2070	CanESM5	6 588 509	-1 029 423	-13.5
	CRNM-ESM2-1	7 636 476	18 544	0.2
	MIROC-ES2L	7 197 029	-420 904	-5.5
	Mean	7 140 671	-477 261	-6.3
2090	CanESM5	6 034 912	-1 583 020	-20.8
	CRNM-ESM2-1	7 713 258	95 326	1.3
	MIROC-ES2L	7 445 726	-172 206	-2.3
	Mean	7 064 632	-553 300	-7.3

Table S3. Predicted change in future distribution area (km^2) for the Harpy Eagle (and corresponding percentage from current distribution) using a higher emissions (SSP585) CMIP6 climate change scenario from three General Circulation Models (GCMs).

Year	GCM	Future area (km^2)	Change (km^2)	Change (%)
2030	CanESM5	6 651 210	-966 722	-12.7
	CRNM-ESM2-1	7 597 088	-20 844	-0.3
	MIROC-ES2L	7 376 030	241 902	-3.2
	Mean	7 208 109	-248 555	-5.4
2050	CanESM5	6 425 874	-1 192 058	-15.7
	CRNM-ESM2-1	7 598 186	-19 747	-0.3
	MIROC-ES2L	7 429 399	-188 533	-2.5
	Mean	7 151 153	-466 799	-6.1
2070	CanESM5	6 142 061	-1 475 871	-19.4
	CRNM-ESM2-1	7 565 340	-52 592	-0.7
	MIROC-ES2L	7 151 584	-466 348	-6.1
	Mean	6 952 995	-664 937	-8.7
2090	CanESM5	5 441 364	-2 176 568	-28.6
	CRNM-ESM2-1	7 261 414	-356 519	-4.7
	MIROC-ES2L	6 850 089	-767 843	-10.1
	Mean	6 517 622	-1 100 310	-14.4

Table S4. Important Bird and Biodiversity Areas (IBAs) predicted to lose all current Harpy Eagle habitat under the worst-case higher emissions scenario (SSP585) for 2090 using the CanESM5 Global Circulation Model (GCM) projection. See attached Excel file for details.

Appendix 2 Supplementary Figures

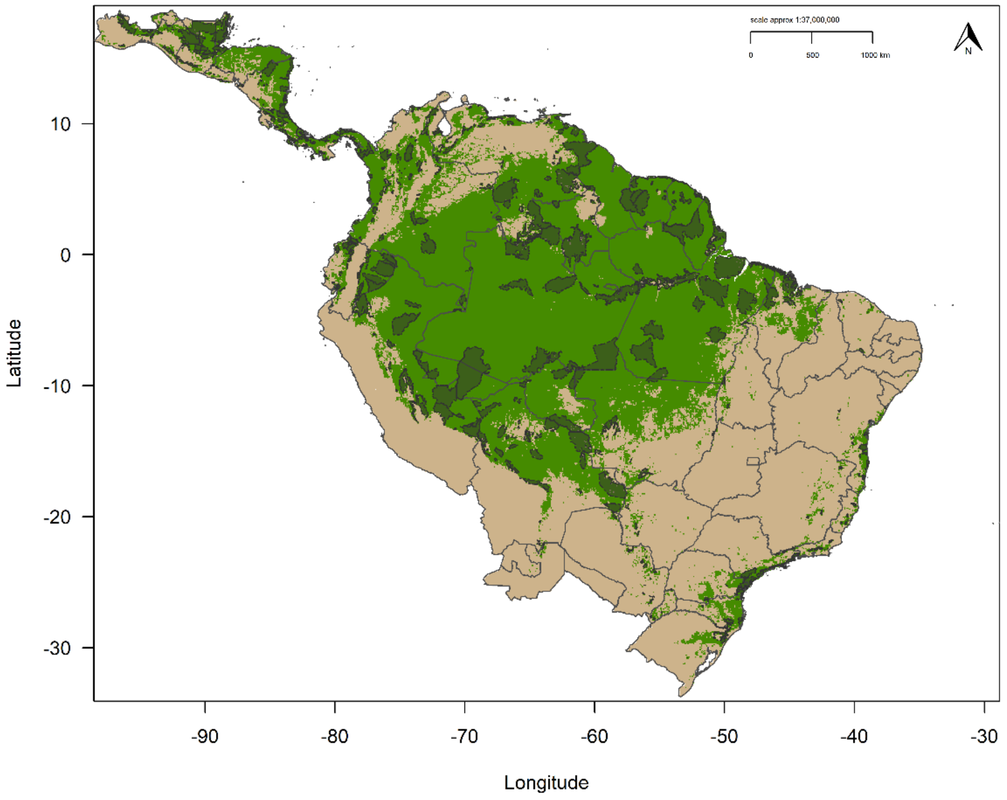

Figure S1. Binary prediction reclassified using the median threshold (0.396). Green areas are predicted Harpy Eagle habitat, beige areas predicted unsuitable habitat. Black bordered polygons define the current Important Bird and Biodiversity Area (IBA) network within the median threshold prediction.

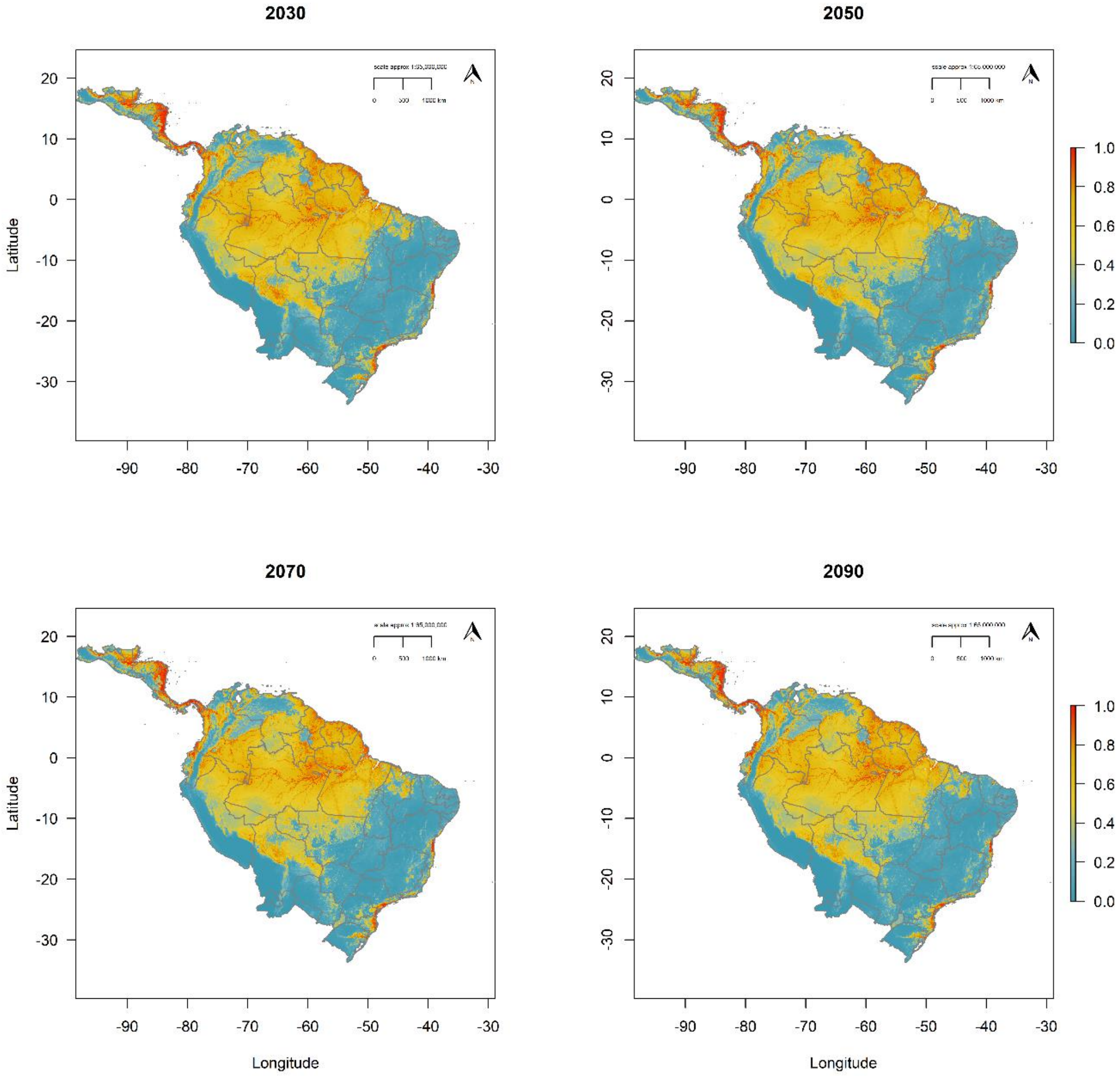

Figure S2. Continuous mean predictions from the three general circulation models for Harpy Eagle distribution using the SSP245 lower emissions scenario across four future climate change timeframes.

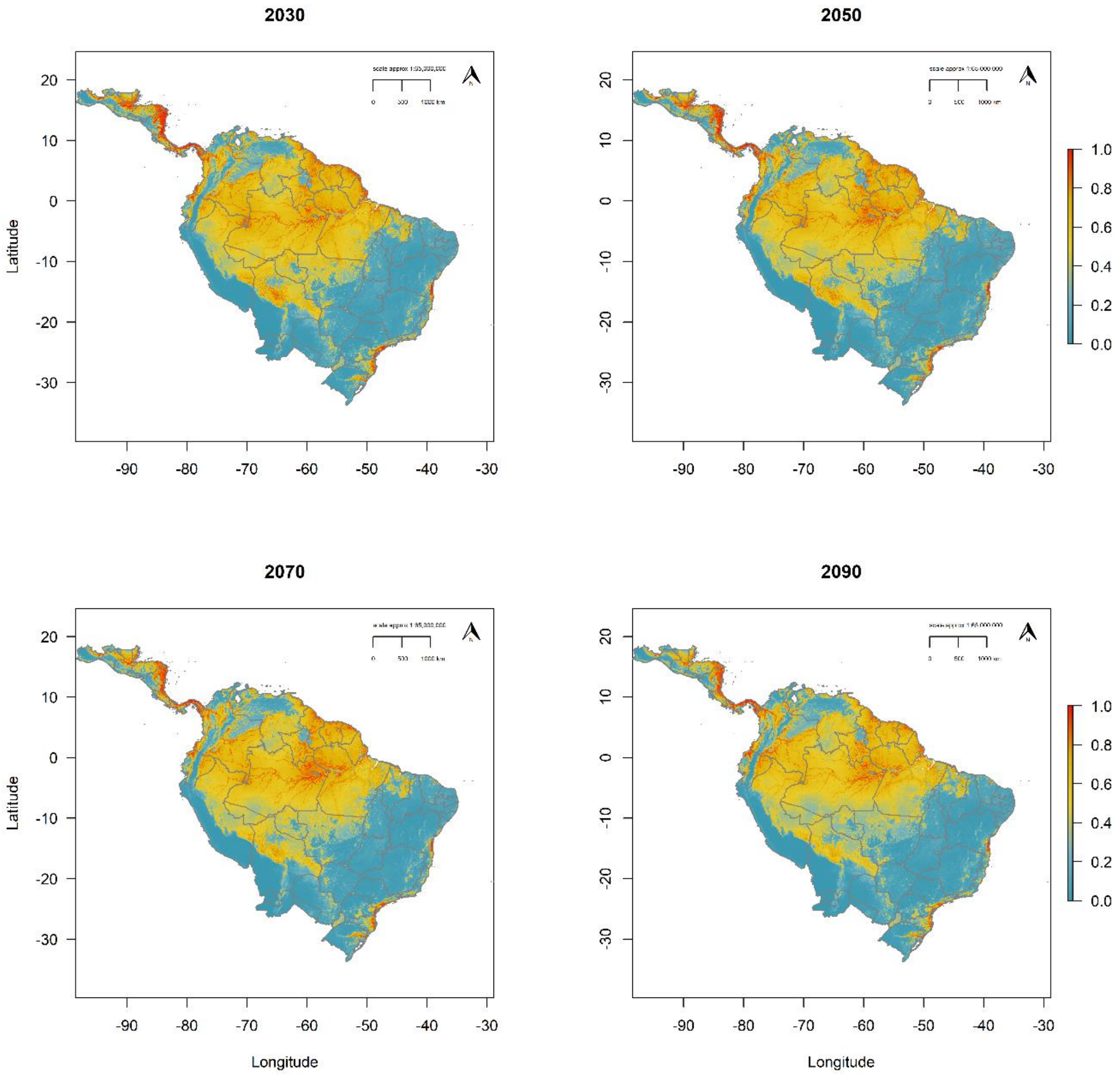

Figure S3. Continuous mean predictions from the three general circulation models for Harpy Eagle distribution using the SSP585 higher emissions scenario across four future climate change timeframes.

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