

RESEARCH ARTICLE

Prey resources are equally important as climatic conditions for predicting the distribution of a broad-ranged apex predator

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Abstract

Aim: A current biogeographic paradigm states that climate regulates species distributions at continental scales and that biotic interactions are undetectable at coarse-grain extents. However, advances in spatial modelling show that incorporating food resource distributions are important for improving model predictions at large distribution scales. This is particularly relevant to understand the factors limiting the distribution of widespread apex predators whose diets are likely to vary across their range.

Location: Neotropical Central and South America.

Methods: The harpy eagle (*Harpia harpyja*) is a large raptor, whose diet is largely comprised of arboreal mammals, all with broad distributions across Neotropical lowland forest. Here, we used a hierarchical modelling approach to determine the relative importance of abiotic factors and prey resource distribution on harpy eagle range limits. Our hierarchical approach consisted of the following modelling sequence of explanatory variables: (a) abiotic covariates, (b) prey resource distributions predicted by an equivalent modelling for each prey, (c) the combination of (a) and (b), and (d) as in (c) but with prey resources considered as a single prediction equivalent to prey species richness.

Results: Incorporating prey distributions improved model predictions but using solely biotic covariates still resulted in a high-performing model. In the Abiotic model, Climatic Moisture Index (CMI) was the most important predictor, contributing 76% to model prediction. Three-toed sloth (*Bradypus* spp.) was the most important prey resource, contributing 64% in a combined Abiotic-Biotic model, followed by CMI contributing 30%. Harpy eagle distribution had high environmental overlap across all individual prey distributions, with highest coincidence through Central America, eastern Colombia, and across the Guiana Shield into northern Amazonia.

Main Conclusions: With strong reliance on prey distributions across its range, harpy eagle conservation programmes must therefore consider its most important food resources as a key element in the protection of this threatened raptor.

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KEYWORDS

biotic interactions, geographic range size, *Harpia harpyja*, harpy eagle, prey base, species distribution models

1 | INTRODUCTION

Within biogeographic theory, climate is hypothesized to be the main driver of species distributions at continental scales (Louthan et al., 2015; Wiens, 2011). This is evidenced through the fossil record (Davis & Shaw, 2001) and recent observed trends (Parmesan & Yohe, 2003; Walther et al., 2002). However, the relationship between distribution and climate may be either indirect (Rich & Currie, 2018), an oversimplification (Dallas et al., 2017), or due to historical biogeography (Heads, 2015). Whether biotic resources are more important determinants of species distributions than climatic conditions is still a central issue in ecology and biogeography (Andrewartha & Birch, 1954; Araújo & Rozenfeld, 2014; Heads, 2015; MacArthur, 1972; Wisz et al., 2013). The current paradigm postulates that biotic resources are most apparent at finer geographical scales (Pearson & Dawson, 2003; Peterson et al., 2011), but this assertion may not apply across all taxa.

Biotic effects may be lost at continental scales due to the coarse-grain extent, commonly termed the Eltonian Noise Hypothesis (Soberón & Nakamura, 2009). The Eltonian Noise Hypothesis postulates that because biotic interactions occur at a fine-scale individual level, modelling approaches will fail to recognize them when working at coarse continental scales. Alternatively, biotic resources may correlate closely with abiotic factors; thus, the biotic signal is lost in abiotic environmental space (Brewer & Gaston, 2003). The effect of biotic resources on species distributions can vary markedly across a given species geographic range (Thompson, 2005). Even so, the overriding assumption is that biotic resources require a fine-scale spatial structure to be noticeable (Soberón & Nakamura, 2009), because by definition biotic interactions occur at the individual level (Anderson, 2017). This assumption is applied to multiple biotic interactions such as the presence or absence of mutualists, competitors and predators.

The relationship between the range limits of animals, such as butterflies and nectivorous birds being driven by the distribution of their food plants, is well established (Kass et al., 2019; Wisz et al., 2013). However, whether the same processes act on the distribution of large vertebrate apex predators with more diverse diets is still unclear (Sih, 2005; With, 2019). It is well-known that apex predators can limit the distribution of their prey species (Holt & Barfield, 2009). However, an outstanding question for large vertebrates is whether the distribution of food resources limits the distribution of their main consumers (Aragón & Sánchez-Fernández, 2013; Louthan et al., 2015; Schweiger et al., 2015; Sih, 2005). The expectation would be for a high overlap between the abiotic conditions in the predator's distribution and those of its prey. Consumer (i.e. predator) distribution should be nested within their main resource

distributions (Holt, 1997), but conversely food resource distributions are not reliant on the distribution of their main consumers.

Food resource distributions can be an important predictor for estimating avian distributions at regional or landscape scales (Aragón et al., 2018; Aragón & Sánchez-Fernández, 2013; de Araújo et al., 2014). However, whether the distribution of food resources can successfully predict the presence of a main consumer across continental extents (2000–10,000 km) has not been tested specifically for a terrestrial apex predator. The harpy eagle (*Harpia harpyja*) is a large Neotropical raptor with a continental range across Central and South America from southern Mexico to northern Argentina (Sutton et al., 2021, 2022a, 2022b; Vargas Gonzalez et al., 2006). Harpy eagles are distributed across lowland tropical forest (Miranda et al., 2019; Sutton et al., 2022a, 2022b; Vargas González & Vargas, 2011), and in seasonal forest enclaves (Silva et al., 2013). A recent review summarizing harpy eagle diet across its range established a trend towards a semispecialized diet (Miranda, 2015), mainly comprised of arboreal mammals, including sloths, primates and tree porcupines. However, birds, reptiles and terrestrial mammals may also be taken, albeit less frequently (Aguiar-Silva et al., 2015; Miranda, 2018; Miranda et al., 2020).

Species distribution models (SDMs) are spatial statistical models that establish the environmental range limits of a given species from environmental conditions and resources at known occurrences (Franklin, 2009; Peterson et al., 2011). SDMs have seen rapid advances over the past 20 years, yet there are still outstanding conceptual and methodical issues that need addressing to improve predictions (Guisan et al., 2017). An important current ecological question is whether including biotic interactions in SDMs can increase their predictive power (Anderson, 2017; Dormann et al., 2018; Stephenson et al., 2022; Wiens, 2011; Wisz et al., 2013). Incorporating food resource distributions into abiotic SDMs can improve model predictive performance, leading to more realistic predictions at regional scales (Aragón et al., 2018; Atauchi et al., 2018; Palacio & Girini, 2018). Moreover, including biotic resources in SDMs is especially relevant for species ranging over lower tropical latitudes with more benign abiotic conditions (Louthan et al., 2015). Indeed, it has long been hypothesized that species range limits in low-latitude areas are driven more by species interactions than climate (Biotic interactions hypothesis, Dobzhansky, 1950; MacArthur, 1972), with support for similar responses along altitudinal gradients (Dvorský et al., 2017; Normand et al., 2009). However, given that all taxa need suitable resources and conditions to survive, species distributions must be regulated by both conditions and resources regardless of scale (Godsoe et al., 2015). Thus, in this tropical forest predator-prey system, biotic resources and abiotic conditions are expected to exert varying but accountable effects on harpy eagle distribution.

Here, we used a hierarchical modelling approach with four SDMs fitted as functions of abiotic conditions and food resource covariates for the harpy eagle using: (1) climatic and topographical covariates (Abiotic model), (2) solely food resource distribution covariates (Biotic model), (3) including food resource distributions individually, and (4) as predicted prey species richness (both Abiotic-Biotic models). Last, pair-wise niche overlaps in geographical space were calculated and all distributions were correlated to determine commonality in distribution for all species in this predator-prey system. Specifically, we sought to establish whether including food resource distributions were more important for predicting distribution at continental scales and meaningfully improved climate-derived model predictions. Further, we quantified the level of niche overlap between the harpy eagle and its main prey in this lowland tropical forest predator-prey system and predicted areas of highest environmental suitability for the harpy eagle and its main food resources.

2 | METHODS

2.1 | Occurrence data

We sourced harpy eagle occurrences from the Global Raptor Impact Network (GRIN, McClure et al., 2021) a data information system for monitoring populations of all raptor species. For the harpy eagle, GRIN consists of occurrence data from two previous distribution assessments (Miranda et al., 2019; Vargas González & Vargas, 2011), which give precise point localities for nests and sightings. In addition, we downloaded presence-only data from the Global Biodiversity Information Facility (GBIF, 2022) but omitted eBird (Sullivan et al., 2009) data points, due to concerns over location accuracy because of the checklist system used in the eBird dataset. Food resource occurrence data were compiled from GBIF (2019a, 2019b, 2019c, 2019d, 2019e, 2019f), using the five most frequent prey by genus (Miranda, 2015): three and two-toed sloth *Bradypus* & *Choloepus* spp. (respectively; 53.2%), capuchin monkey *Cebus* & *Sapajus* spp. (8.0%), howler monkey *Alouatta* spp. (7.3%), and tree porcupine *Coendou* spp. (5.3%).

Food resources were combined into their respective genera (1) to obtain a higher number of occurrence records for each model, and (2) as an appropriate broad-scale representation of food resource distribution. Two genera were used for capuchin monkey based on

a recent taxonomic assessment, with *Sapajus* (or robust capuchin) found south of the Amazon river and *Cebus* (or gracile capuchin) north of the Amazon river (Lynch Alfaro et al., 2012). Combined these five food resource genera comprise 73.8% by frequency and 75.6% of biomass, representing the majority of food resources taken by the harpy eagle across its range. We omitted all other known prey types because including these would create unnecessary noise in our predictions and our focus was on correlating harpy eagle occurrence with its main food resources important for conservation applications.

We cleaned occurrences by removing duplicate records, those with no geo-referenced location and only those occurrences recorded from 1960 onwards, to temporally match the timeframe of the environmental covariates. Finally, a manual check for unlikely outliers was performed in the Quantum Geographic Information System software (v3.2.2., QGIS, 2022). For all species occurrences, a 5-km spatial filter was applied between each occurrence point using the 'geoThin' function in the R package 'enmSdm' (Smith, 2019). Using a 5-km filter approximately matches the resolution of the environmental raster data (~4.5-km) and reduces the effect of biased sampling (Kramer-Schadt et al., 2013). After data cleaning, a total of 609 geo-referenced records were compiled for the harpy eagle. Applying the 5-km spatial filter resulted in 488 harpy eagle occurrence records for use in the calibration models. Occurrence records used for the food resource species calibration models are given in Table 1.

2.2 | Environmental covariates

We downloaded 37 bioclimatic and topographical abiotic raster layers from the WorldClim (v1.4, Hijmans et al., 2005) and ENVIREM (Title & Bemmels, 2018) databases at a spatial resolution of 2.5 arc-minutes (~4.5-km resolution). WorldClim variables ($n = 19$) are generated through interpolation of average monthly weather station climate data from 1960 to 1990, with ENVIREM variables derived from the WorldClim v1.4 bioclimatic layers. Raster layers for both the harpy eagle and food resource models were cropped to a polygon representing the accessible area for all species (Barve et al., 2011). We based this on the Neotropical ecoregions (Dinerstein et al., 2017) where harpy eagles are known to occur (Vargas Gonzalez et al., 2006). This polygon was then cropped to

TABLE 1 Number of unfiltered and

filtered occurrences for food resource genera used in the food resource distribution models (GBIF, 2019a, 2019b, 2019c, 2019d, 2019e, 2019f).

Food resource genus	Primary diet type	Unfiltered	Filtered
Howler monkey <i>Alouatta</i>	Folivore/Frugivore	1841	1003
Capuchin monkey <i>Cebus</i> & <i>Sapajus</i>	Omnivore	1160	691
Three-toed sloth <i>Bradypus</i>	Folivore	547	276
Two-toed sloth <i>Choloepus</i>	Folivore	389	223
Tree porcupine <i>Coendou</i>	Folivore	269	204

the current political borders 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) where the harpy eagle is currently distributed (Vargas Gonzalez et al., 2006). This improves model predictive power by only including those ecoregions where harpy eagles would most likely be found and reducing the background area used for testing points used in model evaluation (Barve et al., 2011; Radosavljevic & Anderson, 2014).

Before building each model, all covariates for both the harpy eagle and food resource models were tested for multicollinearity underlying occurrences using variance inflation factor (VIF, Hair et al., 2006) in the R package 'fuzzySim' (Barbosa, 2015, 2018). VIF is based on the square of multiple correlation coefficients, regressing a single predictor variable against all other covariates. A step-wise elimination of highly correlated variables was used retaining covariates with a VIF threshold of <10 (Dormann et al., 2013), and Spearman's correlation coefficient of $r_s \leq |0.7|$ retained for consideration as covariates. We selected environmental covariates for the food resource distribution models based on species biology and reducing collinearity between environmental covariates underlying the occurrences of each specific food resource genus (Meineri et al., 2012). Using this method, all five food resource models used a different set of environmental covariates (Table S1), resulting in low collinearity between the final food resource model raster covariates (all tests $VIF = <10$; Table S2).

For the Abiotic-Biotic SDMs, these five covariates defining modelled food resource distributions were included in the harpy eagle model calibration as raster layers as has been done in previous studies (Araújo & Luoto, 2007; Gherghel et al., 2018; Preston et al., 2008; Stephenson et al., 2022). Finally, we combined all individual food resource models into a stacked SDM and the continuous suitability values summed for a continuous estimate of food resource species richness in the range of 0.0–5.0. We standardized all raster values for the food resource distribution predictions prior to summing and stacking the rasters with a mean of one and standard deviation of zero, thus treating all prey species equally in the stacking.

For the Abiotic model (A) two climatic variables, Climatic Moisture Index (CMI) and minimum temperature warmest month, and one topographic variable, Terrain Roughness Index (TRI), were included as covariates. We selected all three covariates a priori because combined they contributed 96% to model prediction from a previous SDM (Sutton et al., 2021) and because all three presented a low level of spatial autocorrelation with the filtered harpy eagle occurrences when assessed with a Mantel correlogram (Figure S1). Food resource distributions were used in three further models, with SDMs fitted using the same methodology as for the Abiotic model. First, only food resource distribution covariates were used in a Biotic model (B). Second, modelled food resource raster predictions were included as individual biotic covariates along with the abiotic covariates in an Abiotic + Biotic model (A+B). Finally, the predicted species richness was used as the sole biotic predictor along with the abiotic covariates in an Abiotic + (Biotic) Species Richness model

(A + SR), for a comparison to using individual prey genera (model B) as covariates. Geospatial analysis and modelling was 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 & Rundel, 2019) and 'sp' (Bivand et al., 2013) packages.

2.3 | Species distribution models

We fitted SDMs using penalized elastic-net logistic regression (Fithian & Hastie, 2013), within a point process model (PPM) framework in the R package 'maxnet' (Phillips et al., 2017). Penalized logistic regression imposes a penalty (termed regularization) to the model shrinking the coefficients of covariates that contribute the least to model prediction towards zero (or exactly zero). The complementary log-log (cloglog) transform was selected as a continuous index of environmental suitability, with 0 = low suitability and 1 = high suitability. The 'maxnet' package is based on the maximum entropy algorithm MAXENT, equivalent to an inhomogeneous Poisson process (IPP; Fithian & Hastie, 2013; Renner & Warton, 2013; Renner et al., 2015). 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 potential abundance. We used a tuned penalized logistic regression algorithm because this modelling approach outperforms other SDM methods (Valavi et al., 2021), including ensemble-averaged models (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). 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 beta multiplier (β ; level of coefficient penalty) and feature classes (response functions, Warren & Seifert, 2011). For all SDMs, eighteen candidate models of varying complexity were built by conducting a grid search comparing a range of regularization multipliers from 1 to 5 in 0.5 increments and two feature classes (response functions: Linear and Quadratic) in all possible combinations using the 'checkerboard2' method of cross-validation (k -folds = 5) using a hierarchical 5×5 aggregation factor within the 'ENMeval' package in R (Muscarella et al., 2014).

We only used linear and quadratic features to produce less complex and more realistic predictions (Guevara et al., 2018; Merow et al., 2013). The checkerboard cross-validation method of 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. By masking the geographical structure of test data, 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, thus further reducing spatial autocorrelation between

testing and training localities (Radosavljevic & Anderson, 2014). We used the 'checkerboard2' method because this is an appropriate approach when correlating multiple species distributions in the same analogue environmental space but not transferring models into nonanalogue conditions across space and time (Muscarella et al., 2014). We used response curves, parameter estimates and per cent contribution to model prediction to measure variable performance within the optimal calibration models.

2.4 | Model evaluation

We evaluated model performance using both threshold-independent and threshold-dependent measures (Radosavljevic & Anderson, 2014). Omission rates are a threshold-dependent measure that reports the proportion of training points that are outside of the model when converted into a binary prediction. Omission rates evaluate discriminatory ability and overfitting at specified thresholds. Lower omission rates show improved discrimination between suitable and unsuitable habitats (indicating higher performance), whilst overfitted models show higher omission rates than expected by theory (Radosavljevic & Anderson, 2014). A single threshold-dependent measure was calculated based on the 10% training presence omission rate (OR10) threshold. For low overfit models, the expectation for OR10 is a value close to 0.10 (Muscarella et al., 2014).

We used Continuous Boyce Index (CBI, Hirzel et al., 2006) as a threshold-independent measure of how predictions differ from a random distribution of observed presences (Boyce et al., 2002). CBI is consistent with a Spearman correlation (r_s) with CBI values 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 predicted environmental suitability. CBI was calculated using fivefold cross-validation on 20% of test data with a moving window for threshold independence and 101 defined bins in the R package 'enmSdm' (Smith, 2019). We evaluated models 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% of test data to determine significant ($\alpha = 0.05$) pROC values >1.0 in the R package 'ENMGadgets' (Barve & Barve, 2013).

2.5 | Geographical overlap and correlation

We measured pair-wise geographic overlaps between the harpy eagle and the five prey distributions using Schoener's D (Schoener, 1968; Warren et al., 2008), which ranges from 0 (no overlap) to 1 (identical overlap). To estimate the areas where all six species coincide, the three harpy eagle SDM predictions that used biotic covariates

(models B, A+B and A+SR) were first stacked and their respective CBI scores used to calculate a weighted mean ensemble prediction. Second, the five prey distribution SDMs were also stacked into a single raster. Last, we then predicted a measure of commonality in species distribution by intersecting the harpy eagle ensemble prediction, with the stacked prey distribution rasters with a threshold of 0.5 using the 'stability' function in the R package 'sdStaf' (Atauchi, 2018).

3 | RESULTS

3.1 | Food resource distribution models

Optimal model selection ($\Delta AIC_c = 0.0$) for the capuchin monkey, howler monkey and three-toed sloth distribution models had feature classes linear and quadratic and a regularization multiplier $\beta = 1$. The best-supported two-toed sloth model had a $\beta = 1.5$ and the best-supported tree porcupine model had a $\beta = 3.5$, both with linear and quadratic feature class functions. Discrimination ability (OR10) for all models was at or close to the expected threshold of 0.10 (Table 2). Final best-fit models were robust to random expectations (range: pROC = 1.324–1.683) with high model calibration accuracy (range: CBI = 0.803–0.992). Capuchin monkey had the broadest distribution, followed by howler monkey and tree porcupine (Figure 1). Three-toed and two-toed sloths were largely restricted to Central America, Colombia, Amazonia and the Guiana Shield. Prey species richness was highest in Panama, north along the Caribbean coast of Central America, and south along the Pacific coast of Colombia. A broad belt of high prey species richness was predicted across northern Amazonia, east into the Guiana Shield and across the central Amazon.

3.2 | Harpy eagle distribution models

All four best-supported harpy eagle models ($\Delta AIC_c = 0.0$) had feature classes linear and quadratic and a regularization multiplier

TABLE 2 Evaluation metrics for prey distribution models used as biotic covariates in the harpy eagle distribution models.

Food resource SDM	FC	RM	OR10	CBI	pROC
Capuchin monkey	LQ	1.0	0.104	0.803	1.424
Howler monkey	LQ	1.0	0.108	0.992	1.533
Three-toed sloth	LQ	1.0	0.122	0.960	1.604
Tree porcupine	LQ	3.5	0.098	0.977	1.324
Two-toed sloth	LQ	1.5	0.104	0.965	1.683

Note: All models selected with $\Delta AIC_c = 0.0$.

Abbreviations: CBI, Continuous Boyce Index; FC, feature classes: Linear (L) and quadratic (Q); OR10, 10% training presence omission rate threshold; pROC, partial Receiver Operating Characteristic ratios; RM, regularization multiplier.

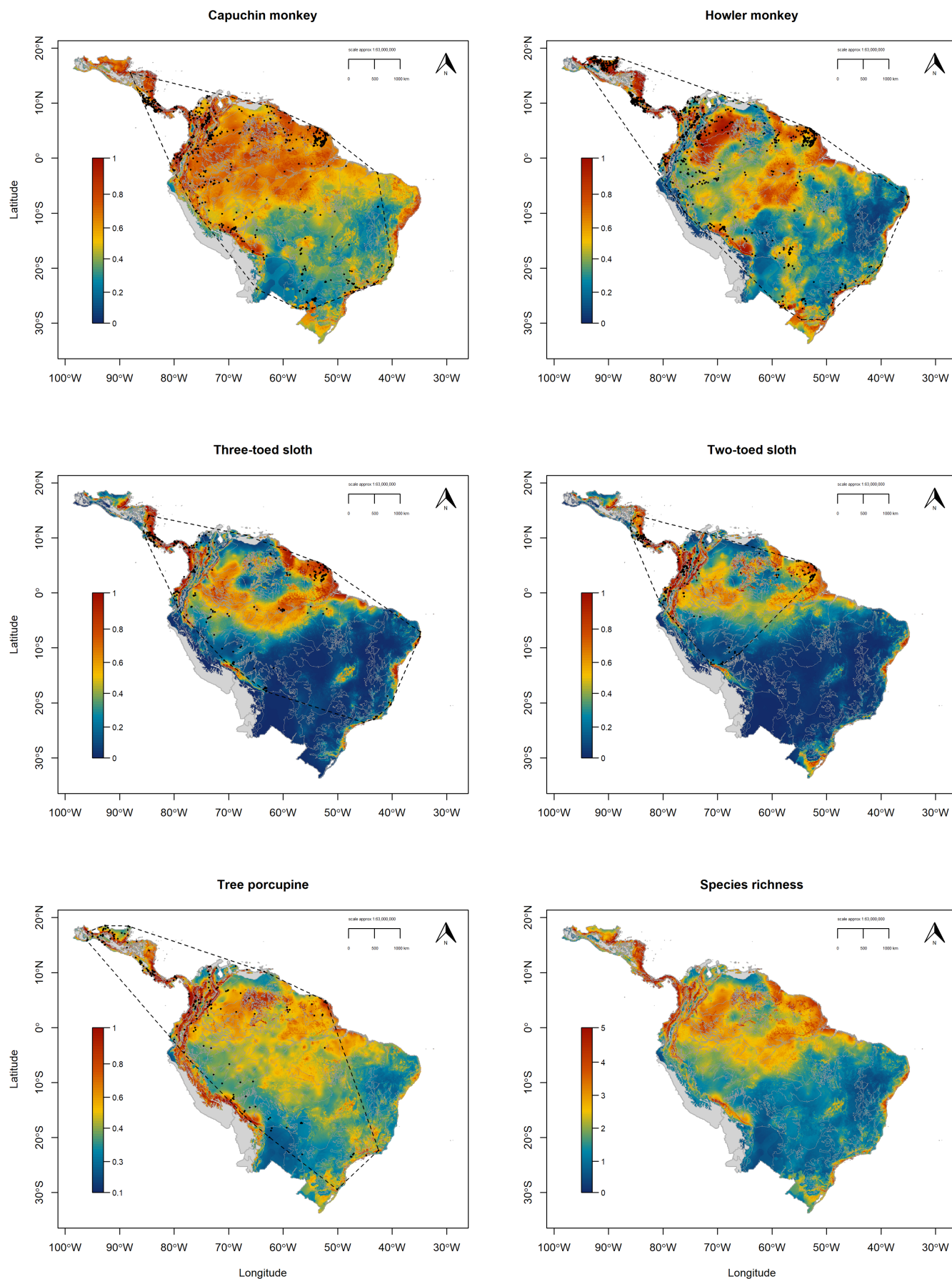


FIGURE 1 Predicted distributions for the five primary prey genera for the harpy eagle and combined into a summed prediction of prey species richness. Maps denote cloglog prediction with red areas (values closer to 1) having highest suitability. Grey borders represent ecoregions, and black points are each respective prey species' occurrences fitted with minimum convex hulls.

TABLE 3 Model selection and evaluation metrics for all four harpy eagle SDMs ranked by AIC_c.

SDM	AIC _c	OR10	CBI	pROC
A+B	12696.13	0.107	0.766	1.431
A+SR	12747.75	0.101	0.788	1.349
A	12803.06	0.101	0.715	1.288
B	12805.03	0.096	0.709	1.369

Note: Evaluation metrics are Continuous Boyce Index (CBI) and tested against null expectations using partial Receiver Operating Characteristic ratios (pROC). OR10 = 10% training presence omission rate threshold.

$\beta = 1$. Optimal selected models had robust discrimination ability with omission rates (OR10) at expected values of 0.10 (Table 3). The Abiotic+SpeciesRichness (A+SR) model had the highest model calibration performance (CBI = 0.788), but all models had good calibration accuracy between predicted environmental suitability and test occurrence points (range: CBI = 0.709–0.788). All models were robust against random expectations (range: pROC = 1.288–1.431). Visually, including prey distributions in both the Biotic (B) and Abiotic+Biotic (A+B) models constrained harpy eagle distribution (Figure 2), compared to using solely abiotic covariates. The Biotic (B) and Abiotic+Biotic (A+B) models captured more detail in defining areas of highest suitability and relative abundance for the harpy eagle (Figure 2). This was noticeable, especially across key areas of the harpy eagle range in Guyana, eastern Colombia, Panama and northern Peru and the central Amazon basin in Brazil.

3.3 | Predictor importance and responses

Climatic Moisture Index contributed the highest percentage to the Abiotic model prediction (76.0%), with three-toed sloth the highest contributor in both Biotic (82.3%) and Abiotic+Biotic (63.7%) models. Species richness was the most important predictor (63.7%) in the Abiotic+SpeciesRichness (A+SR) model, followed by Climatic Moisture Index (27.2%, Table S3). Covariate responses in the Abiotic model (Figure 3) showed a unimodal response to Climatic Moisture Index peaking at 0.4, with a positive response to minimum temperature for the warmest month peaking at suitable temperatures of 25°C. Harpy eagle occurrence had consistently high positive linear responses to predicted values of prey species occurrence in both the Biotic and Abiotic+Biotic models (Figures 4, 5), except for tree porcupine, which had a unimodal response at values between 0.6 and 0.8. Similar positive linear responses to high species richness were observed in both the Biotic (Figure 4) and Abiotic+SpeciesRichness models (Figure 6).

Model parameter estimates showed positive linear relationships with Climatic Moisture Index in all three models using Abiotic covariates, but negative quadratic relationships (Table 4), reflecting the unimodal response functions. Minimum temperature of the warmest month and Terrain Roughness Index beta coefficients

were penalized close to or at zero and showed weak linear and quadratic relationships when biotic covariates were included. Both sloth genera had positive quadratic relationships in the Biotic and Abiotic+Biotic models, with a stronger relationship stronger for the three-toed sloth in the Abiotic+Biotic model. Tree porcupine had the strongest linear and quadratic relationships in the Biotic model, but these responses were less pronounced in the Abiotic+Biotic model.

3.4 | Geographic overlap and correlation

In geographic space, pair-wise overlaps between the harpy eagle and its food resource distributions were highest with capuchin ($D = 0.871$) and howler monkey ($D = 0.855$), followed by tree porcupine ($D = 0.846$). Three-toed sloth ($D = 0.691$) and two-toed sloth ($D = 0.667$) both had similar, but lower overlap scores compared with the primate and porcupine genera. The most correlated areas of distribution were first along the Caribbean coast of Central America, extending into the Chocó region along the Pacific coast of Colombia (Figure 7). Second, a large but patchy area of high environmental suitability was predicted across Amazonia, extending from eastern Colombia, across the Guiana Shield and south into the northern Amazon of Brazil.

4 | DISCUSSION

Recent theoretical and empirical work has demonstrated the importance of including resource distributions in macro-scale species distribution models (SDMs, Araújo & Rozenfeld, 2014; Atauchi et al., 2018; Gherghel et al., 2018; Palacio & Girini, 2018). Our results show that incorporating the distribution of the harpy eagle's five main prey species at a continental scale improved its distribution estimates compared to using solely abiotic covariates. This result further counters the Eltonian Noise Hypothesis (Soberón & Nakamura, 2009), the assumption that biotic interactions are unimportant at broad spatial scales (Pearson & Dawson, 2003). Including food resources as individual prey species distribution rasters improved the predictive performance of the Abiotic model, but we acknowledge that this is also related to a higher number of parameters in the prey resource models. Moreover, using solely biotic covariates or combined as species richness still resulted in high-performing models, but the combination of Abiotic+SpeciesRichness (model A+SR) had highest calibration accuracy. Geographic overlap ranged from moderate to high between the harpy eagle and its main prey species, with highest environmental suitability for all species combined ranging across northern South America and Central America.

The spatial pattern of species' distributions is products of physiological constraints such as climate and topography, and interactions with other co-occurring species (MacArthur, 1972). It follows then that both abiotic and biotic factors combined should drive species distributions, and abiotic variables alone are unable to provide sufficient detail for distribution estimates at coarse scales

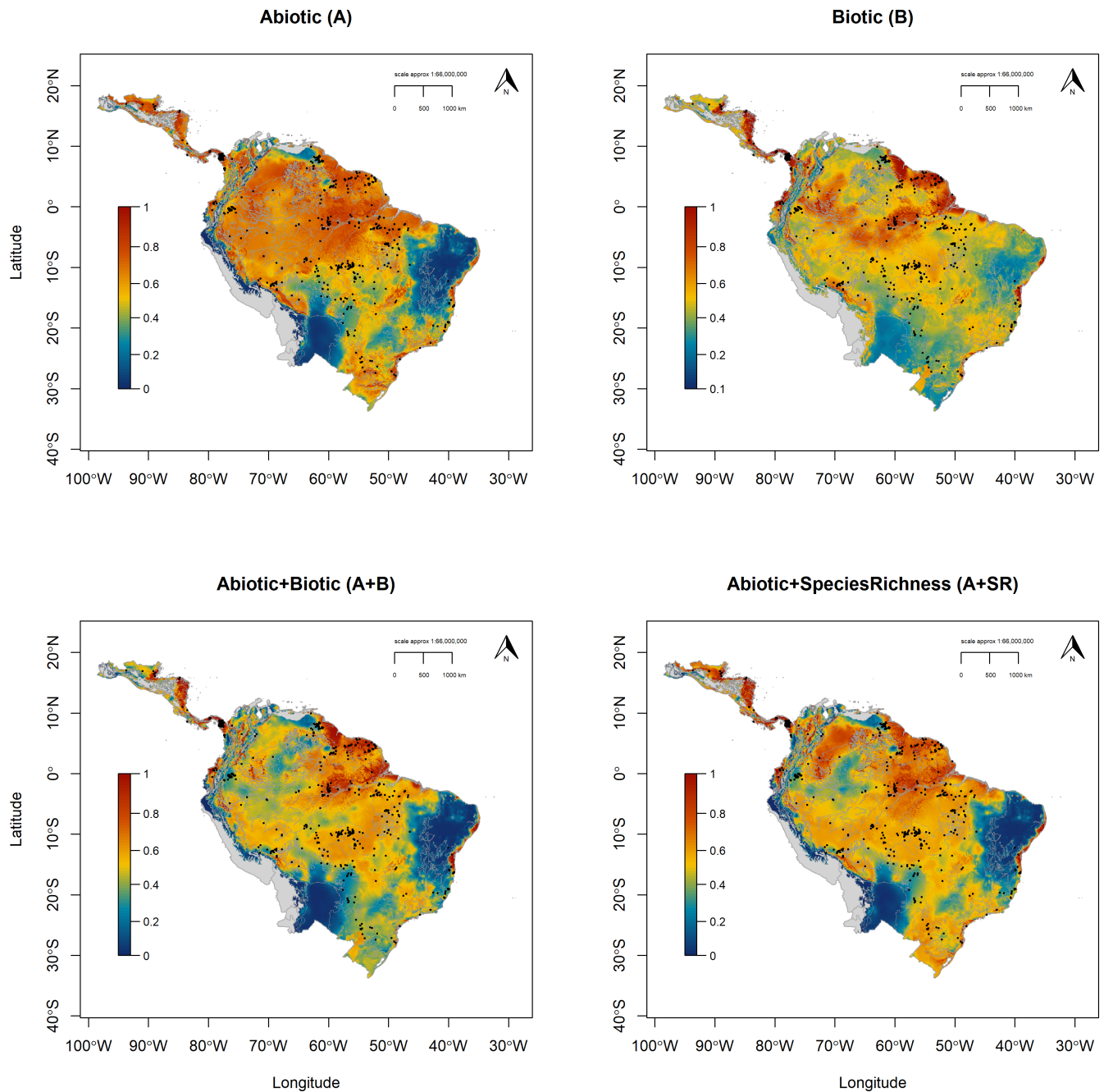


FIGURE 2 Predicted continuous distributions for the harpy eagle using abiotic and biotic covariates. Maps denote cloglog prediction with red areas (values closer to 1) having higher environmental suitability. Grey borders represent ecoregions, and black points define harpy eagle occurrences.

(Kass et al., 2019; Wisz et al., 2013). Our results support this conclusion by improving an abiotic model prediction with the inclusion of food resource distributions. Three-toed sloth was the most important biotic predictor in both the Biotic and Abiotic+Biotic (A+B) models (Table S3), consistent with this species being the principal prey for the harpy eagle across its range (Aguiar-Silva et al., 2014; Miranda, 2015, 2018). However, the importance of three-toed sloth distribution decreased when including abiotic factors, with Climatic Moisture Index the second most important predictor in the Abiotic+Biotic (A+B) model. This indicates that only a reduced

subset of climatic and biotic covariates are necessary to account for the major distributional constraints for the harpy eagle.

In the Abiotic+SpeciesRichness (A+SR) model, prey species richness was the most important predictor (63.7%), followed by Climatic Moisture Index (27.2%). Combined, these two covariates accounted for nearly 91% of model prediction, further supporting the inclusion of food resource species richness as a predictor in SDMs. Yet, when including species richness in the Biotic model, its importance was low, probably due to any predictive power lost amongst the other biotic noise from the individual food resource covariates. For SDMs,

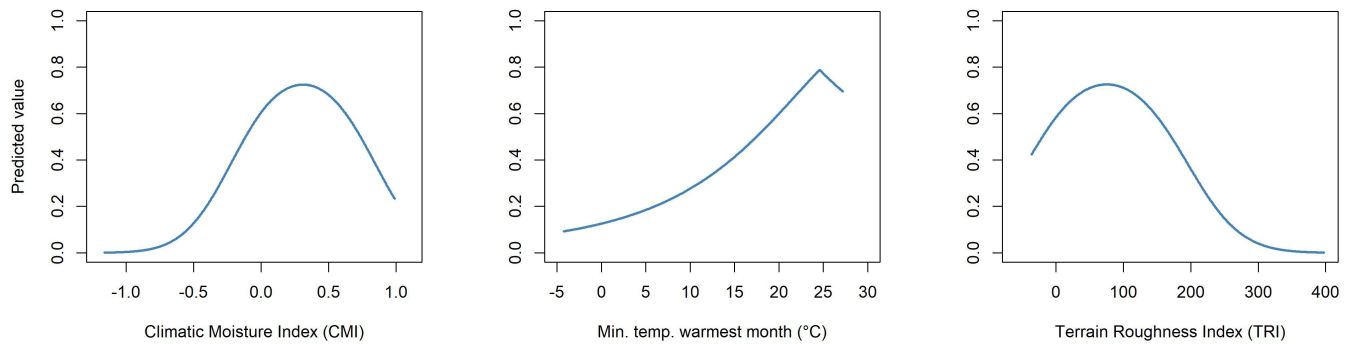


FIGURE 3 Response curves for covariates in the Abiotic distribution model for the harpy eagle. The response curves show the contribution to model prediction (y-axis) as a function of each continuous habitat covariate (x-axis). Maximum values in each response curve define the highest predicted relative 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.

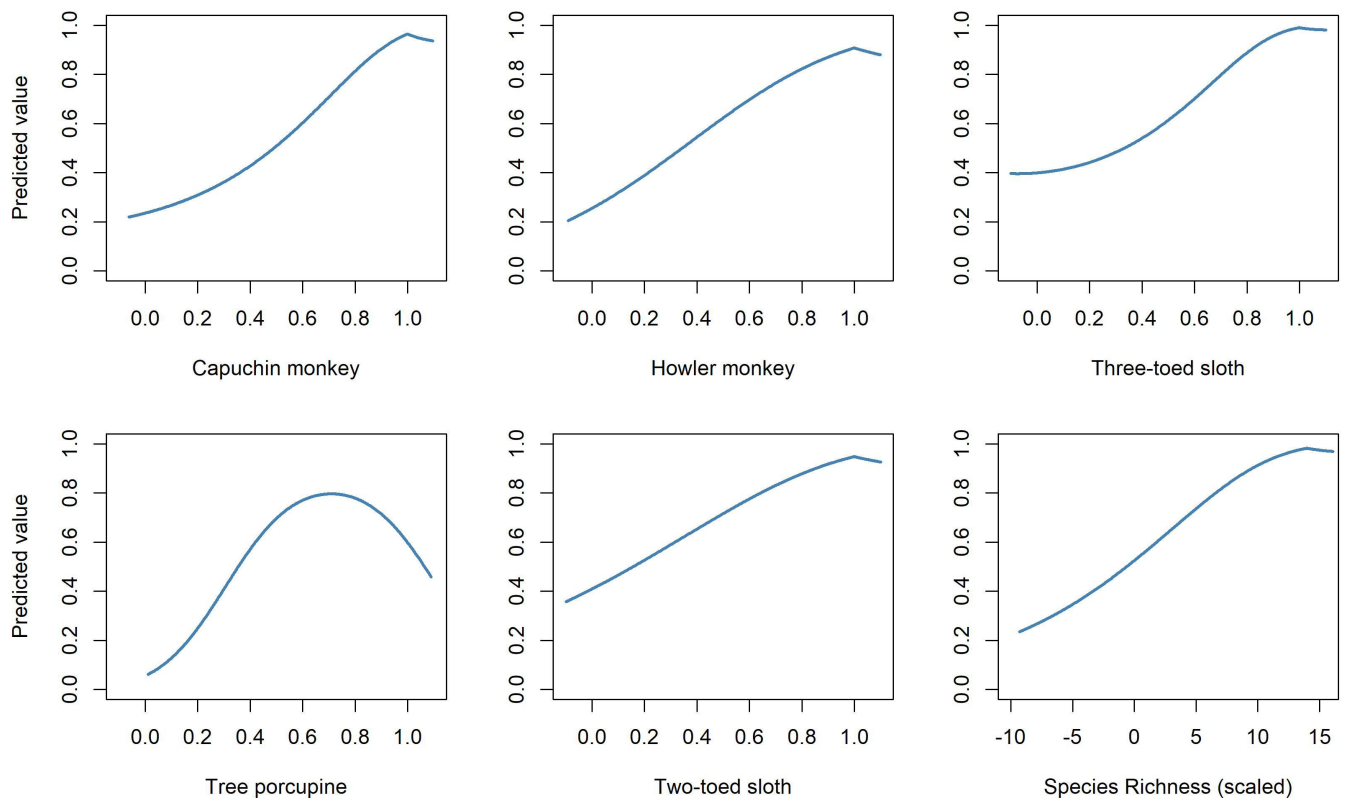


FIGURE 4 Response curves for covariates in the Biotic distribution model for the harpy eagle. The response curves show the contribution to model prediction (y-axis) as a function of each continuous habitat covariate (x-axis). Maximum values in each response curve define the highest predicted relative 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.

food resource distributions should thus be included as single covariates where predator–prey interactions are well established, and occurrence data are available. However, if occurrence data for single prey species are lacking (as is often the case), then combining all known food resource species into a single species richness predictor is a valid method (Kass et al., 2019), confirmed by our highest performing model (A + SR) including species richness as a predictor.

Our results confirm the importance of sloth distribution as one of the main drivers for harpy eagle distribution. There were high positive responses between harpy eagle distribution and

three-toed sloth occurrence and with the highest per cent contributions to the Biotic model prediction. Indeed, in some parts of their range harpy eagles have narrow diets comprised of 80–95% sloths (Miranda et al., 2020), in central and eastern Amazonia (Aguilar-Silva et al., 2014; Galetti & de Carvalho Jr, 2000) and north-east Ecuador (Muñiz-López, 2008). However, the harpy eagle is not so specialized on a diet of three-toed sloths as to be absent from areas where sloths are not present. It seems likely that in the southern and eastern parts of the harpy eagle range primates and porcupines are the key prey species, replacing sloths as the primary food source

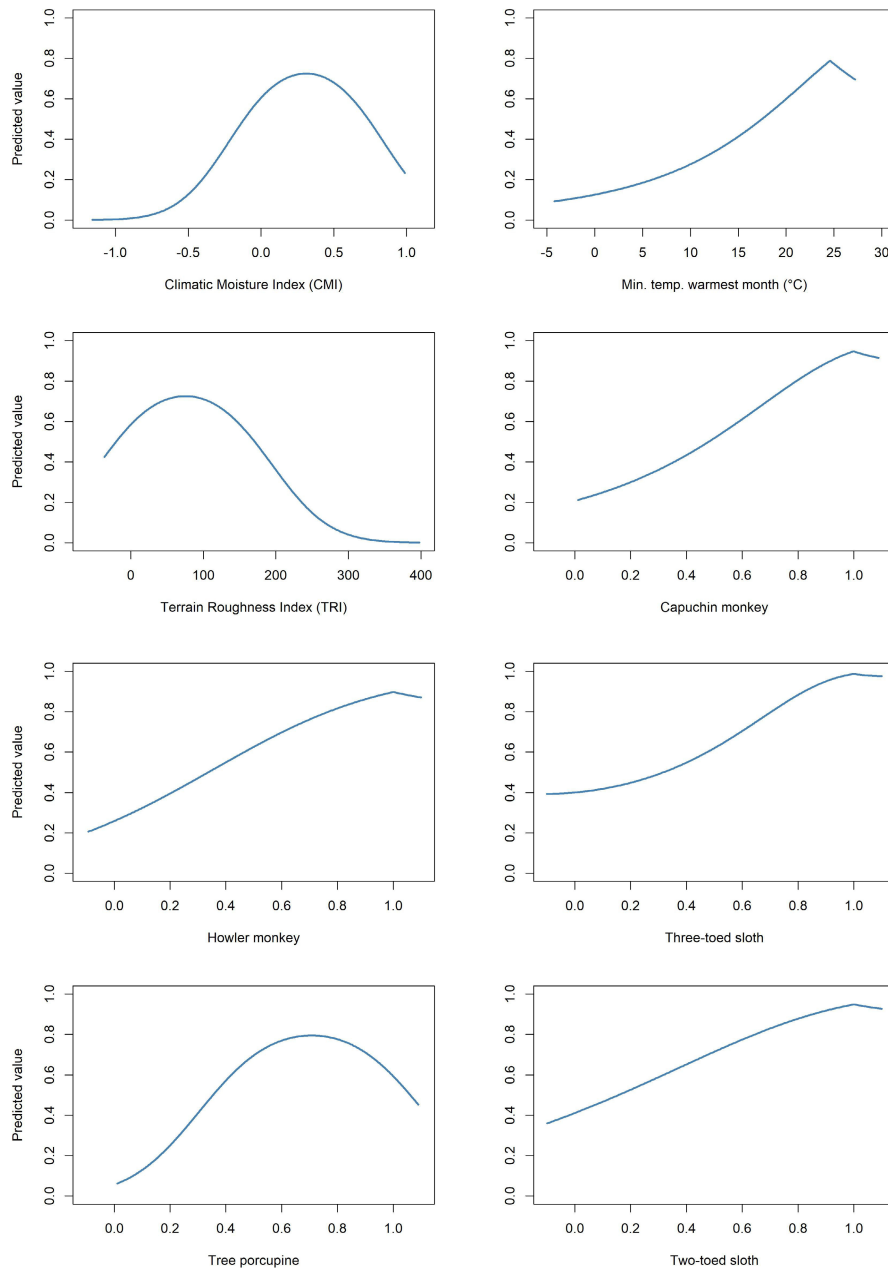


FIGURE 5 Response curves for covariates in the A + B distribution model for the harpy eagle. The response curves show the contribution to model prediction (y-axis) as a function of each continuous habitat covariate (x-axis). Maximum values in each response curve define the highest predicted relative 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.

(Miranda, 2015). Thus, our models are able to capture the spatial variation in predator–prey distribution across a continental tropical forest system by using a range of key prey genera and not relying solely on a single biotic predictor.

Using response curves to interpret model outputs is a useful though underused aspect of model evaluation in many SDMs (Guevara et al., 2018; Kass et al., 2019). Here, modelled partial responses for the three-toed and two-toed sloth were strongly positive in both the Biotic and Abiotic+Biotic (A + B) models, peaking at 1.0 as expected (Figures 4, 5). Capuchin and howler monkey followed similar positive linear responses, peaking between 0.9 and 1.0. Tree porcupine had unimodal responses in both the Biotic and Abiotic+Biotic models peaking at 0.7, suggesting this prey type is less important for driving harpy eagle range limits. This consistency in model response functions suggests a strong

reliance on all prey types for the distribution of the harpy eagle and adds further weight to conservation programmes that take a wider landscape approach to conserving all elements of this tropical forest predator–prey system.

Pair-wise geographic overlaps supported strong relationships in distribution between the harpy eagle and its main food resources. High overlaps with most of its main prey suggest that harpy eagle distribution is largely dependent on where its main food resources exist. Both primate prey genera (capuchin and howler monkey) had higher overlap values than the other main prey species. This could be partly explained by both primate genera having similar broad distributions across the Neotropics to the harpy eagle; thus, overlap values would be expected to be high. Conversely, overlaps for both sloth genera were lower, even though in many areas of the harpy eagle range sloths are often the primary food resource. However,

FIGURE 6 Response curves for covariates in the A + SR distribution model for the harpy eagle. 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.

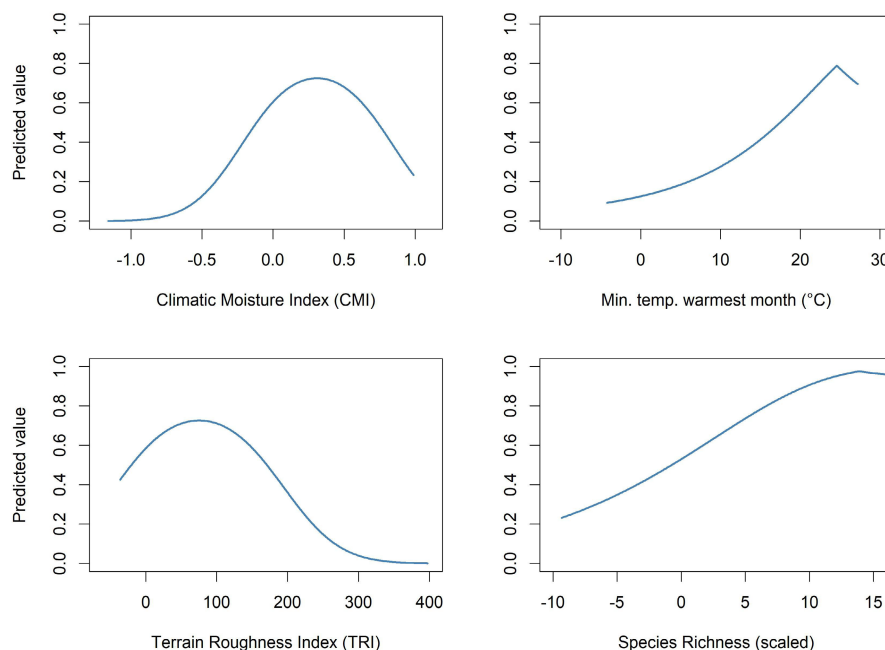


TABLE 4 Linear and quadratic (with superscript 2) parameter estimates for each optimal model derived from penalized logistic regression beta coefficients.

Predictor	Abiotic	Biotic	A + B	A + SR
Climatic Moisture Index	2.055		0.955	1.108
Min. temp. warmest month	0.013		0.049	0.022
Terrain Roughness Index	0.022		-0.001	
Climatic Moisture Index ²	-3.691		-6.481	-6.643
Min. temp. warmest month ²	0.000			
Terrain Roughness Index ²	0.000		0.000	0.000
Tree porcupine		7.434	4.186	
Three-toed sloth			-2.039	
Two-toed sloth		-3.540	-1.649	
Howler monkey		0.905	-1.038	
Capuchin monkey		0.203	0.734	
Tree porcupine ²		-6.679	-3.042	
Three-toed sloth ²		2.697	4.537	
Two-toed sloth ²		2.413	1.544	
Howler monkey ²		0.965		
Capuchin monkey ²		0.902	0.476	
Species richness ²		0.001		0.013

both sloth genera have more restricted ranges than both the primate genera; thus, overlap values would be expected to be lower.

The correlation model predicted the most common areas of distribution across Amazonia, the Guiana Shield, and the Caribbean coast of Central America. Given the high reliance that harpy eagle distribution has with its main food resources, we recommend conserving extensive tropical lowland forest habitat and prioritizing research in these key regions. Further, due to its reliance on lowland tropical forests the harpy eagle may act as a surrogate example, enabling greater understanding of how the range limits of an apex predator may point to how other tropical forest biota are predicted to respond to a changing climate (Urban et al., 2017). Our results

show predictive models can identify those areas of highest environmental suitability, and where the main coincidence of the taxa in this predator-prey system is concentrated. This then leads into where preventative conservation action would have the most benefit—not reactive conservation but proactive planning. The overall picture is of highest climate stability and food resources in northern Amazonia and the Guiana shield, along with eastern and western Colombia, extending into eastern Panama. Thus, conservation efforts for the harpy eagle need extending beyond current programmes to focus on these regions, some of which have seen little conservation action.

The biotic interaction hypothesis states that species interactions are the main driver for species distribution in the

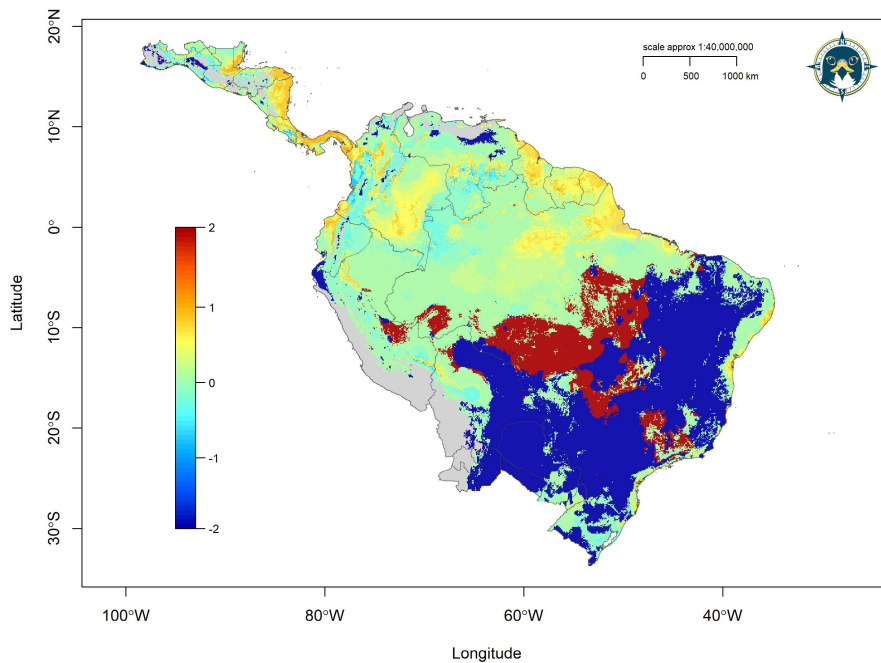


FIGURE 7 Predicted distribution correlation for the harpy eagle given the distribution of its five main prey species. Values close to -2 suggest absence, -1 to 0 can be interpreted as colonizable areas, 0 to 1 defines areas of highest suitability (prey availability) and values of 2 (dark red patches) show the most unsuitable (low prey availability) areas. Grey borders represent national borders and state boundaries for Argentina, Brazil and Mexico.

relatively stable climates of the tropics (Louthan et al., 2015; MacArthur, 1972). Our results in general support this, though abiotic processes are clearly important, with Climatic Moisture Index (CMI) still the key abiotic predictor in the Abiotic (A + B) and Abiotic+SpeciesRichness (A + SR) models. Because CMI is closely correlated with the primary vegetation types in Neotropical forests (Beck et al., 2018), it seems likely that CMI is acting as a proxy for lowland tropical forest, which by definition is the key vegetation type for all species distributions in this tropical forest system. Thus, both specific food resources and habitat type are likely the main drivers on harpy eagle distribution, which hardly seems unexpected. A useful next step would be to include direct habitat variables, competitor distributions and human impacts, along with food resources, to provide a broader perspective on the main influences determining harpy eagle distribution (Joint-SDMs, Pollock et al., 2014).

Consistent with previous smaller scale regional studies (e.g. Aragón et al., 2018; Gherghel et al., 2018; Hof et al., 2012), our results support not only including food resources in SDMs but also that including the main food resource distributions for apex predators is important at continental scales. Further, our results dispute the Eltonian Noise Hypothesis, similar to conclusions from landscape to regional scale studies (Atauchi et al., 2018; de Araújo et al., 2014). However, it is recognized that increases in predictive power were relatively slight and the Abiotic SDM still had high predictive accuracy. Including resource distributions has much practical value for advancing SDM predictions across a range of applications in space (spread of invasive species) and time (climate change range shifts). As demonstrated here, predictions were improved when applied to basic model interpolation; thus, not including resource distributions may result in poorer model transferability when extrapolating in

space and time. However, we recognize limitations with interpreting model outputs, with the prey model for two-toed sloth overpredicting in northern Central America, beyond the species' known northern range limits (McCarthy et al., 1999), which will have subsequent impacts on harpy eagle range predictions.

We recognize the potential limitations in our modelling approach for selecting a varying number of environmental covariates a priori for each harpy eagle SDM even though this is an established and biologically driven method for variable selection (Fourcade et al., 2017). The inconsistent model structure and number of parameters could lead to overfitting, with a potential solution to generate randomly permuted variables (Niittynen & Luoto, 2018). However, in this case all four harpy eagle models had 10% omission rates at or near to the recommended OR10 value (0.10), demonstrating low overfitting in all models, including the A + B model with the highest number of parameters. Thus, selecting biologically plausible variables based on current knowledge was effective in this case rather than relying on random generation of covariates. In addition, we acknowledge the limitations of using community science data, which often does not sample over the entire extent of a species range (Beck et al., 2014). This lack of occurrence coverage has implications for producing accurate and realistic models, reflected in regional variation in prey availability. However, as shown here, the point process model framework using penalized logistic regression produces reliable and useful predictions for species range limits in the absence of detailed distributional information for tropical forest species.

We show how incorporating food resource distributions improves model predictive power and circumscribes the spatial complexity in harpy eagle distribution. Adding food resource distributions revealed the crucial role of predator-prey interactions in harpy eagle distribution. Given the wide variation in food type

taken by the harpy eagle across its range (Aguiar-Silva et al., 2014; Miranda, 2018), maintaining these prey resources should also be a priority in conservation programmes for the harpy eagle. Conserving habitat for the key arboreal mammal prey populations along with one of their main predators as a complete tropical forest system seems a viable approach given the reliance on harpy eagle presence with their main food resource distributions. We encourage practitioners to incorporate known biotic interactions into SDMs, but modellers should recognize that understanding the complex interactions inherent in natural systems is a challenge (Aragón et al., 2018). Whilst we demonstrate that using resource distributions improves model predictions at macro-scales, this needs further testing across multiple taxa and ecosystems to determine whether this finding is consistent elsewhere.

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CONFLICTS OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

The data and results that support the findings of this study are openly available on the data repository Dryad DOI: [10.5061/dryad.76hnr7szs](https://doi.org/10.5061/dryad.76hnr7szs). R code to run the analyses is available on Github: <https://github.com/lsutton74/HAEA-BioticSDM>

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BIOSKETCH

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SUPPORTING INFORMATION

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