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1 **Geographic range estimates and environmental requirements for the harpy**
2 **eagle derived from spatial models of current and past distribution**

3

4 **Running title: Geographic range estimates for the harpy eagle**

5

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26 **Abstract**

27 Understanding species-environment relationships is key to defining the spatial
28 structure of species distributions and develop effective conservation plans. However,
29 for many species this baseline information does not exist. With reliable presence
30 data, spatial models that predict geographical ranges and identify environmental
31 processes regulating distribution are a cost-effective and rapid method to achieve
32 this. Yet these spatial models are lacking for many rare and threatened species,
33 particularly in tropical regions. The harpy eagle (*Harpia harpyja*) is a Neotropical
34 forest raptor of conservation concern with a continental distribution across lowland
35 tropical forests in Central and South America. Currently the harpy eagle faces
36 threats from habitat loss and persecution and is categorised as Near-Threatened by
37 the International Union for the Conservation of Nature (IUCN). Within a point process
38 modelling (PPM) framework, we use presence-only occurrences with climatic and
39 topographical predictors to estimate current and past distributions and define
40 environmental requirements using Ecological Niche Factor Analysis. The current
41 PPM prediction had high calibration accuracy (Continuous Boyce Index = 0.838) and
42 was robust to null expectations (pROC ratio = 1.407). Three predictors contributed
43 96 % to the PPM prediction, with Climatic Moisture Index the most important (72.1
44 %), followed by minimum temperature of the warmest month (15.6 %) and Terrain
45 Roughness Index (8.3 %). Assessing distribution in environmental space confirmed
46 the same predictors explaining distribution, along with precipitation in the wettest
47 month. Our reclassified binary model estimated a current range size 11 % smaller
48 than the current IUCN range polygon. Paleoclimatic projections combined with the
49 current model predicted stable climatic refugia in the central Amazon, Guyana,
50 eastern Colombia, and Panama. We propose a data-driven geographical range to

51 complement the current IUCN range estimate, and that despite its continental
52 distribution this tropical forest raptor is highly specialized to specific environmental
53 requirements.

54

55 **Keywords:** *Harpia harpyja*, harpy eagle, Neotropical raptors, point process models,
56 geographic range size, Species Distribution Models

57

58 **Introduction**

59 Defining species distributions in geographical and environmental space is a
60 fundamental component of conservation management (Peterson *et al.* 2011). Yet
61 this information is lacking for many rare and threatened taxa in a rapidly changing
62 environment (Miller 2010; Lawler *et al.* 2011). Assessing geographic distribution and
63 environmental requirements of rare, poorly studied and cryptic species can be
64 problematic due to scarce occurrence data, resulting in limited information for
65 conservation managers to act upon (Pearce & Boyce 2006). For these under-
66 documented species this baseline spatial information is either inadequate, or non-
67 existent, especially in highly biodiverse tropical regions, often where organismal
68 biology is also poorly known (Rodríguez *et al.* 2007; Tobias *et al.* 2013; Wilson *et al.*
69 2016, Buechley *et al.* 2019). In response to this knowledge gap, spatial modelling
70 techniques have been developed to help direct conservation actions and implement
71 research programs.

72

73 Species Distribution Models (SDMs) can overcome deficiencies in information
74 regarding distribution by correlating the underlying environmental data at known
75 occurrences to predict the areas of highest environmental suitability (Scott *et al.*

76 2002; Elith & Leathwick 2009). On the other hand, ordination approaches define the
77 underlying environmental factors that explain the most suitable environmental
78 conditions for where a given species is found. Combining both SDMs and ordination
79 is an effective method to define the distributional and ecological constraints of a
80 given species (Chase & Leibold 2003; Soberón & Nakamura 2009; Peterson *et al.*
81 2011). These methods are particularly useful when using species occurrences
82 generated from biodiversity databases when modelling distributions for species in
83 remote, difficult to survey regions (Peterson 2001; Rhoden *et al.* 2017; Sutton &
84 Puschendorf 2018).

85

86 The Neotropics are well-known for high avian biodiversity. Yet many birds, including
87 raptors, face multiple threats across the area, largely driven by human activities such
88 as habitat loss, agricultural development and resource over-exploitation (Tobias *et*
89 *al.* 2013; Sarasola *et al.* 2018, McClure *et al.* 2018, Buechley *et al.* 2019). Due to the
90 difficulties of sampling across the extensive and complex terrain of the Neotropics,
91 applying SDMs using open-access distribution data can generate baseline
92 information on species distributions in a rapid and cost-effective manner (Cayuela *et*
93 *al.* 2009; La Sorte & Somveille 2020). The harpy eagle (*Harpia harpyja*) is a large
94 Neotropical raptor, with a broad yet shrinking range across Central and South
95 America from southern Mexico to northern Argentina (Ferguson-Lees & Christie
96 2005; Vargas González *et al.* 2006). Harpy eagles generally occur at low population
97 densities in lowland tropical forest (Vargas González & Vargas 2011) but are nearly
98 extinct in Brazil's Atlantic forest (Srbek-Araujo & Chiarello 2006; Meller & Guadagnin
99 2016) and in forest enclaves such as riparian forests in open savannahs (Silva *et al.*
100 2013).

101

102 With generally low population densities and a 3-year long breeding cycle, the harpy
103 eagle is considered a species of conservation concern due to continued habitat loss
104 and persecution (Vargas González *et al.* 2006; Miranda *et al.* 2019). Currently
105 categorised as 'Near-Threatened' by the International Union for the Conservation of
106 Nature (IUCN; Birdlife International 2017), local extirpations have occurred in most of
107 Central America, and the population status of the species across its continental
108 range is largely unknown (Vargas González *et al.* 2006). The current IUCN
109 geographic range for the harpy eagle estimates an Extent of Occurrence (EOO) of
110 17.6 million km² and an unknown Area of Occupancy (AOO, Birdlife International
111 2017). EOO measures the area within a minimum convex polygon (MCP) from all
112 known species occurrences, while AOO is a subset of the EOO where the species
113 actually occurs in occupied grid cells of 2x2 km, excluding vagrancy (Gaston & Fuller
114 2009; Brooks *et al.* 2019). Both measures are based solely on spatial locations and
115 not on underlying environmental information.

116

117 One of the main criticisms of using EOO is that it often includes unsuitable areas,
118 overestimating the true range, which is more likely to show a discontinuous pattern
119 of distribution (Jetz *et al.* 2007; Peterson *et al.* 2016; Breiner *et al.* 2017; Ramesh *et*
120 *al.* 2017). SDMs are useful as an alternative measure to complement IUCN
121 estimates, intermediate between EOO and AOO, especially for rare and under-
122 sampled species (Breiner *et al.* 2017). SDMs should not be viewed as surrogates for
123 IUCN criteria but can provide a basis for estimating AOO (Gaston & Fuller 2009;
124 Breiner *et al.* 2017; IUCN 2019), especially in the case for the harpy eagle where this
125 figure is unknown. Using the underlying environmental signature of the species as a

126 guide for model interpolation may produce a more realistic data-driven estimate of
127 distribution area (Peterson *et al.* 2016). Global range size is a key parameter for
128 assessing threat status and extinction risk, thus overestimating this figure could lead
129 to increasingly threatened species being missed (Ramesh *et al.* 2017). Predicting
130 areas with the highest environmental suitability can thus focus research effort and
131 update threatened species' conservation status (Bierregaard 1998).

132

133 Miranda *et al.* (2019) produced the first SDM for the harpy eagle, identifying its close
134 relationship to lowland tropical forest. We build on the strengths of this initial SDM,
135 first by incorporating extra presence-only occurrences with the Miranda *et al.* location
136 data, and second using an expanded set of environmental predictors. Additionally,
137 we project current predictions into two paleoclimatic scenarios and predict how past
138 distributions may influence present and future distribution. Long-term ecological
139 perspectives from paleoclimate models are important for comparing current
140 distribution to past fluctuations (Nogués-Bravo 2009; Fuller *et al.* 2011). Further,
141 having a long-term perspective of past distributions is critical to interpreting current
142 distribution and can point towards potential refugia expected from future changes in
143 range size (Fuller *et al.* 2011; Keppel *et al.* 2012). Understanding the species-
144 environment relationships regulating current and historical harpy eagle distribution
145 can therefore help direct conservation management by identifying the spatial extent
146 for the species.

147

148 Here, predictive spatial models are developed for the harpy eagle in geographical
149 space using a point process modelling (PPM) framework. Recently, PPMs have
150 been shown to be most effective for modelling distributions using presence-only

151 occurrences (Warton & Shepherd 2010; Renner *et al.* 2015). PPMs model the
152 intensity of occurrence points across a given area, thus under low spatial
153 dependence of occurrences the resulting outputs can be interpreted as either the
154 relative (Renner *et al.* 2015), or potential abundance of focal species (Phillips *et al.*
155 2017). An ecological profile is then developed using ordination with an Ecological
156 Niche Factor Analysis (ENFA) to best explain the environmental requirements of the
157 harpy eagle, compared to the background environmental conditions available.
158 Specifically, we aim to: **(1)** re-evaluate current harpy eagle distribution and establish
159 its ecological niche as a function of climatic and topographical predictors, **(2)** revise
160 the estimated current coarse-scale IUCN distributional area and provide
161 complementary range maps, and **(3)** predict past distributions from two paleoclimatic
162 time periods and combine with the current model to identify stable refugia.

163

164 **Materials and Methods**

165 **Harpy Eagle occurrence data**

166 Harpy eagle occurrences were sourced from the Global Raptor Impact Network
167 (GRIN, The Peregrine Fund 2018) a data information system for all raptor species.
168 For the harpy eagle, GRIN consists of occurrence data from the Global Biodiversity
169 Information Facility (GBIF 2019), which are mostly eBird records (89.88%, Sullivan *et al.*
170 *al.* 2009), combined with two additional datasets of nests and observations (Vargas
171 González & Vargas 2011; Miranda *et al.* 2019). Occurrence data were cleaned by
172 removing duplicate records, those with no geo-referenced location and for spatial
173 auto-correlation (see Appendix 1 in Supporting Information). To account for sampling
174 bias in occurrences, a 4 km spatial filter from each occurrence point was used to
175 minimise the effects of survey bias, using the ‘thin’ function in the R package spThin

176 (Aiello-Lammens *et al.* 2015). The 4 km thinning distance was selected as a proxy of
177 mean inter-nest distances based on breeding pairs in the Darien region of Panama
178 (Vargas González & Vargas 2011). We used 4 km as a minimum distance knowing
179 that inter-nest distances recorded across the harpy eagle range can vary (Piana
180 2007; Muñoz-López 2008). After data cleaning, a total of 1179 geo-referenced
181 records were compiled for inclusion in model calibration, generally within the current
182 range defined by the IUCN (Fig. S1, see Appendix 3 in Supporting Information;
183 Birdlife International 2017). Applying the 4 km spatial filter, resulted in 742
184 occurrence records for use in the calibration models. The resulting occurrence points
185 are thus best reported as locations in continuous space, providing the primary
186 motivation for using the PPM regression framework for subsequent spatial analysis
187 (Renner *et al.* 2015).

188

189 **Environmental predictors**

190 Thirty-seven bioclimatic and topographical predictors were obtained from the
191 WorldClim (v1.4, Hijmans *et al.* 2005) and ENVIREM (Title & Bemmels 2018)
192 databases. WorldClim variables ($n = 19$) are generated through interpolation of
193 average monthly weather station climate data from 1960-1990. The ENVIREM dataset
194 includes 16 climatic and two topographic variables to complement the WorldClim
195 dataset providing a wider range of potential variables from which to select model
196 predictors. Raster layers were cropped and masked to a delimited polygon
197 consisting of all known range countries (including the states of Formosa, Jujuy,
198 Misiones and Salta in northern Argentina, and the states of Chiapas, Oaxaca, and
199 Tabasco in southern Mexico), to extend into potential areas of marginal habitat on
200 the distribution edges. Reducing the accessible area to the known range improves

201 model predictive power by reducing the background area used for testing points
202 used in model evaluation (Barve *et al.* 2011; Radosavljevic & Anderson 2014).
203
204 For past predictions, three General Circulation Models (GCMs, Table 1) were used
205 from the Coupled Model Inter-comparison Project Phase 5 (CMIP5) and
206 Paleoclimate Modelling Inter-comparison Project Phase 3 (PMIP3) databases for two
207 paleoclimate scenarios in the Mid-Holocene (~6,000 cal yr BP) and Last Glacial
208 Maximum (~22,000 cal yr BP). Three GCMs were used to account for variation and
209 uncertainty in model predictions (Nogués-Bravo 2009), and a summed prediction
210 calculated from all models for both paleoclimate scenarios. Each summed paleo-
211 distribution was then stacked with the current distribution and overlaid to provide a
212 summed estimate of environmental stability (Peterson *et al.* 2017), using the
213 'stability' function in the R package 'sdStaf' (Atauchi 2018). Summed stability can
214 predict areas of stable refugia, where a species is predicted to be present
215 irrespective of time period (Carnaval *et al.* 2009). Geographic niche overlap from the
216 individual GCMs was tested using Schoener's *D* (Schoener 1968, Warren *et al.*
217 2008), which ranges between 0 (no overlap) to 1 (identical overlap). Paleoclimate
218 raster data were downloaded from the WorldClim (v1.4, Hijmans *et al.* 2005) and
219 ENVIREM (Title & Bemmels 2018) databases and masked to the current range
220 extent to predict areas of past climatic suitability compared to the current range.
221
222 Multicollinearity between environmental predictor variables can bias models by over-
223 representing the biological relevance of correlated variables (Franklin 2009; Phillips
224 *et al.* 2006). Before model construction, environmental cells containing occurrence
225 records from all 37 variables were tested for multicollinearity using Variance Inflation

226 Factor (VIF) analysis (Guisan *et al.* 2006; Hair *et al.* 2006) with the 'corSelect'
227 function in the R package fuzzySim (Barbosa 2015, 2018). A stepwise elimination of
228 highly correlated variables was used retaining predictors with a VIF threshold < 10
229 considered as suitable for multi-variable correlation (Dormann *et al.* 2013). The
230 remaining variables were then checked for collinearity using Spearman's Correlation
231 Coefficient with only variables $r_s \leq |0.7|$ retained for consideration as predictors. We
232 used solely climatic and topographical predictors as to our knowledge there are no
233 reliable estimates of landcover extent or anthropogenic impact extending back to the
234 two paleoclimate scenarios used here.

235

236 After removing highly correlated variables, eight climatic variables (isothermality;
237 maximum temperature warmest month; precipitation wettest month; precipitation
238 warmest quarter; Climatic Moisture Index (CMI); minimum temperature warmest
239 month, potential evapotranspiration (PET) driest quarter; PET wettest quarter), and
240 one topographic variable, Terrain Roughness Index (TRI), were included as
241 predictors at a spatial resolution of 2.5 arc-minutes (~4.5km resolution). Final
242 predictor selection was based on representing monthly and seasonal climatic trends,
243 extremes and limiting environmental factors strongly related theoretically and
244 empirically to species distributions (Stockwell 2006; Bradie & Leung 2017; Guevara
245 *et al.* 2018; see Appendix 1 in Supporting Information). For example, in tropical
246 forests rainfall regime and seasonality are predicted to have a strong effect on avian
247 survival, food availability, and reproductive effort (Stotz *et al.* 1996; Williams &
248 Middleton 2008). Therefore, predictors were selected based on seasonal and
249 monthly precipitation interacting with temperature, as potential limiting factors on
250 harpy eagle distribution (Williams & Middleton 2008; Busch *et al.* 2011).

251

252 **Species Distribution Models**

253 SDMs were fitted using a point process modelling (PPM) framework as a form of
254 infinitely-weighted logistic regression via penalized maximum likelihood (Fithian &
255 Hastie 2013), treating occurrences as points rather than grid cells in the R package
256 maxnet (Phillips *et al.* 2017) and maximum entropy software, MAXENT (v3.4.1).

257 Recent theoretical work has demonstrated the equivalence of MAXENT to an
258 inhomogeneous Poisson process (IPP; Fithian & Hastie 2013; Renner & Warton
259 2013; Renner *et al.* 2015), which is the most appropriate method for fitting presence-
260 only SDMs (Warton & Shepherd 2010). The complementary log-log (cloglog)
261 transform was selected as a continuous index of environmental suitability, with 0 =
262 low suitability and 1 = high suitability. Phillips *et al.* (2017) demonstrated the cloglog
263 transform is equivalent to an IPP and can be interpreted as a measure of relative
264 occurrence probability proportional to a species relative abundance.

265

266 We randomly selected 10,000 background absences recommended for regression-
267 based modelling (Barbet-Massin *et al.* 2012) and to sufficiently sample the
268 background calibration environment (Guevara *et al.* 2018). Convergent threshold
269 was set at 10^{-5} and iterations increased to 5000 from the default (500) allowing for
270 model convergence. Optimal-model selection was based on Akaike's Information
271 Criterion (Akaike 1974) corrected for small sample sizes (AIC_c; Hurvich & Tsai 1989),
272 to determine the most parsimonious model by tuning two key MAXENT parameters:
273 regularization multiplier and feature classes (Warren & Seifert 2011). Eighteen
274 candidate models of varying complexity were built by comparing a range of
275 regularization multipliers from 1 to 5 in 0.5 increments, and two feature classes

276 (Linear and Quadratic) in all possible combinations using the 'checkerboard2'
277 method of cross-validation (k -folds = 5) within the ENMeval package in R (Muscarella
278 *et al.* 2014). Response curves, parameter estimates, percent contribution,
279 permutation importance and a jack-knife test were used to measure variable
280 performance within the best-fit model (see Appendix 1 in Supporting Information).

281

282 **Model evaluation**

283 Optimal model selection was evaluated using Area Under the Curve (AUC), and
284 omission rates. AUC is a non-parametric, threshold-independent measure with AUC
285 = 1.0 indicating maximum predictive performance, and AUC = 0.5 being no better
286 than a random prediction. AUC_{DIFF} ($AUC_{TRAIN} - AUC_{TEST}$) was used to quantify model
287 over-fitting (Muscarella *et al.* 2014), with a value close to zero indicating a low over-
288 fit model (Warren & Seifert 2011). AUC metrics were used as a measure of optimal
289 model selection, best suited to comparing a range of candidate models (Lobo *et al.*
290 2008; Jiménez-Valverde 2012). Omission rates are threshold-dependent metrics for
291 evaluating discriminatory ability and over-fitting at specified thresholds. Lower
292 omission rates show improved discrimination between suitable and unsuitable areas
293 (indicating higher performance), whilst overfitted models show higher omission rates
294 than expected by theory (Radosavljevic & Anderson 2014). Omission rates were
295 calculated based on two threshold rules: minimum training presence (MTP) and 10%
296 training presence (10TP). For low over-fit models the expectation in MTP is a value
297 close to zero and for 10TP a value close to 0.10.

298

299 Two further test metrics were used to evaluate the final best-fit model. First, model
300 accuracy was tested against random expectations using partial receiver operating

301 characteristic (pROC), which estimates model performance by giving precedence to
302 omission errors over commission errors (Peterson *et al.* 2008). Partial ROC ratios
303 range from 0 – 2 with 1 indicating a random model. Function parameters were set
304 with a 5% omission error rate, and 1000 bootstrap replicates on 50% test data to
305 determine significant ($\alpha = 0.05$) pROC ratios >1.0 in the R package ENMGadgets
306 (Barve & Barve, 2013). Second, Continuous Boyce Index (CBI, Hirzel *et al.* 2006)
307 was used to measure how much environmental suitability predictions differ from a
308 random distribution of observed presences (Boyce *et al.* 2002). CBI is consistent
309 with a Spearman correlation (r_s) with values ranging from -1 to +1. Positive values
310 indicate predictions consistent with observed presences, with values close to zero no
311 different than a random model. Negative values indicate areas with frequent
312 presences having low environmental suitability. Mean CBI evaluation was calculated
313 using five-fold cross-validation on 20% test data with a moving window for threshold-
314 independence and 101 defined bins in the R package enmSdm (Smith 2019).

315

316 **Reclassified binary prediction**

317 To calculate potential range size, the continuous current prediction was reclassified
318 to a binary (suitable/unsuitable) prediction to complement the current IUCN
319 geographic range polygon (BirdLife International 2017). Currently there is no
320 consensus on choosing binary thresholds and threshold selection can be an arbitrary
321 process (Liu *et al.* 2013; 2016). We selected 10% training presence (10TP), a
322 threshold that removes the lowest 10 % of predicted values accounting for any
323 uncertainty in the occurrence data (Pearson *et al.* 2007), and visually best fitted
324 current expert knowledge on harpy eagle distribution. We used the same 10TP
325 threshold for the paleoclimate predictions because this provided a more realistic

326 estimate for current range size to use for projecting into past climatic scenarios.
327 Finally, we calculated Extent of Occurrence (EOO) with a minimum convex polygon
328 around all our occurrence points (excluding the ocean) following IUCN guidelines
329 (IUCN 2019). General model development and spatial analysis were performed in R
330 (v3.5.1; R Core Team, 2018) using the *dismo* (Hijmans *et al.* 2017), *raster* (Hijmans
331 2017), *rgdal* (Bivand *et al.* 2019), *rgeos* (Bivand & Rundle 2019) and *sp* (Bivand *et*
332 *al.* 2013) packages.

333

334 **Environmental ordination**

335 To determine species-environment relationships in environmental space, the
336 underlying environmental data at occurrence points were extracted using the three
337 most important predictors from their contribution to model prediction. A random
338 sample of 100,000 background points were extracted to represent the background
339 environment, with occurrence data and environmental space defined using a
340 minimum convex polygon. Ecological Niche Factor Analysis (ENFA, Hirzel *et al.*
341 2002; Basille *et al.* 2008) was calculated using all unfiltered occurrence points ($n =$
342 1179), against the background environmental data. ENFA directly measures
343 environmental conditions at the presence points, thus spatial auto-correlation in
344 occurrence data is not considered a serious issue (Basille *et al.* 2008). Including as
345 many presence points as possible is therefore advisable in ENFA to obtain accurate
346 measures of occupied environmental space (Hirzel *et al.* 2001).

347

348 ENFA is a multivariate, factorial analysis extracting two measures of a species
349 realized niche along two axes. The first axis metric, marginality (M), measures the
350 position of the species ecological niche, and its departure relative to the available

351 environment. A value of $M > 1$ indicates that the niche deviates more relative to the
352 reference environmental background and has specific environmental preferences
353 compared to the available environment. The second axis metric, specialization (S), is
354 an indication of niche breadth size relative to the environmental background, with a
355 value of $S > 1$ indicating higher niche specialization (narrower niche breadth). A high
356 specialization value indicates a high reliance on the environmental conditions that
357 mainly explain that specific dimension. ENFA was calculated in the R package
358 CENFA (Rinnan 2018), using a corrected calculation on the coefficient matrix for
359 specialization and weighting all cells by the number of observations (Rinnan &
360 Lawler 2019). Predictors were rescaled thus the resulting ENFA can be interpreted
361 similar to a PCA with eigenvalues and loadings represented along the first axis of
362 marginality and the following secondary orthogonal axes of specialization (Basille *et*
363 *al.* 2008).

364

365 **Results**

366 **Species Distribution Models**

367 The best-fit model ($\Delta AIC_c = 0.0$) had feature classes Linear and Quadratic with a
368 regularization multiplier of $\beta = 1$. AUC metrics showed moderate predictive
369 performance ($AUC_{TRAIN} = 0.698$, $AUC_{TEST} = 0.692$), with minimal overfitting (AUC_{DIFF}
370 $= 0.06$) and high discrimination ability with omission rates close to expected values
371 ($MTP = 0.003$, $10TP = 0.11$). Testing the model against random expectations
372 resulted in robust mean pROC ratios (pROC = 1.407, $SD \pm 0.057$, range = 1.235-
373 1.577), with high calibration accuracy between predicted environmental suitability
374 and test occurrence points (Mean CBI = 0.838). The continuous best-fit model
375 defined the spatial complexity in distribution for the harpy eagle, and identified an

376 area of highest abiotic suitability across Amazonia (Fig. 1), with patchier distribution
377 across southern Brazil and north into Central America (Fig. S3, see Appendix 3).
378 Reclassifying the continuous prediction using the 10TP threshold (0.415; Fig. 2)
379 gave an estimate for geographic range size of 9,844,399 km². Based on our
380 occurrence data we estimated an EOO of 13,050,940 km².

381

382 **Environmental predictors**

383 From parameter estimates, the harpy eagle was more likely to be associated with
384 CMI and minimum temperature of the warmest month (Table 2). Overall, three
385 predictors contributed 96 % to model prediction. Climatic Moisture Index (CMI)
386 contributed the highest percentage (72.1 %, Table 3), with minimum temperature in
387 the warmest month (15.6 %) and Terrain Roughness Index (TRI, 8.3 %) the next two
388 highest contributions (Table 3). CMI had the highest regularized training gain,
389 followed by precipitation in the wettest month and minimum temperature in the
390 warmest month (Fig. S4, see Appendix 3). CMI had the highest gain when used in
391 isolation, so had the most useful information on suitable environmental conditions
392 when used alone. CMI decreased the gain the most when omitted and could best
393 explain the environmental requirements of the harpy eagle not present in the other
394 predictors.

395

396 From the response curves there was a positive response to CMI peaking at ~0.4,
397 with highest suitability for the minimum temperature of the warmest month increasing
398 rapidly after 10°C, peaking at 25°C (Fig. 3). Precipitation in the wettest month
399 peaked at 90 mm/month, before levelling off up to 100 mm, with highest suitability for
400 precipitation in the warmest quarter at 200 mm. Isothermality peaked at 9-10 %,

401 reflecting the constant temperatures harpy eagles need in lowland tropical forests.
402 PET in the driest quarter had highest suitability at 100 mm/month, but with highest
403 suitability for PET in the wettest quarter at 50 mm/month indicating a preference for
404 climates with greener vegetation. TRI peaked at 100 indicating high preference, as
405 expected, for lowland flat areas with low terrain complexity.

406

407 **Environmental ordination**

408 Within selected axes of environmental space harpy eagle occurrences were
409 clustered within a Climatic Moisture Index ranging between -0.5 and 0.7 (Fig. 4a).
410 Harpy eagle occurrences showed a lower limit for minimum temperature with no
411 location points below 10.5 °C in the warmest month. Most occurrences were
412 clustered around or above 20 °C (Fig. 4a), linked to the harpy eagle's preference for
413 generally flat, lowland areas with low terrain complexity (Fig. 4b). Harpy eagle
414 environmental space did not deviate substantially from the average background
415 environment available, with the ENFA marginality factor slightly below the available
416 background environment ($M = 0.99$; Fig. 5, red circle). However, the harpy eagle is
417 restricted to a particular environmental space relative to the reference environmental
418 background with a narrow environmental niche breadth indicating highly specialized
419 environmental requirements ($S = 1.431$). Five significant ENFA factors explained
420 80.75 % of the total variance in niche structure, with the first specialization axis
421 (Spec1) explaining 28.81 % of this total (Table 4). CMI and precipitation in the
422 wettest month were the two highest coefficients on the marginality axis, with
423 minimum temperature in the warmest month the highest on the specialization axis.

424

425 **Paleo-distributions**

426 All individual paleoclimate GCMs predicted similar paleo-distributions with high
427 geographical niche overlap (Table S1, see Appendix 2 in Supplementary
428 Information; Figs. S5-S6, see Appendix 3). From the mean projections, hindcasting
429 the current prediction to the LGM defined a large area of high suitability across
430 northern-central South America. A further strip of high suitability extended from
431 present-day Panama, south along the Pacific slope west of the Andes into the
432 present-day Chocó region and west Ecuador (Fig. S7, top left). In the Mid-Holocene
433 high suitability areas increased, extending north into Central America, across
434 Amazonia and east in present-day Brazil (Fig. S7, top right). During the LGM mean
435 range size was 17 % smaller (Fig. S7, bottom left; Table S2, see Appendix 2),
436 compared to the current 10TP geographic range size (9,844,399 km²). In the Mid-
437 Holocene, range size had increased from the LGM, but was still 6 % smaller than the
438 current 10TP range size estimate (Table S2, see Appendix 2; Fig. S7, bottom right).
439 Areas of highest stable refugia were identified in the central Amazon basin north into
440 Guyana, south-east Colombia and Panama (Fig. 6), consistent with these areas
441 having continuous high suitability since the LGM.

442

443 **Discussion**

444 More than half of all global raptor species have declining populations, and there is a
445 significant knowledge gap on the extent of their distribution and ecological
446 requirements (McClure *et al.* 2018). In particular, accurate distribution estimates are
447 lacking for many tropical forest raptors (Sarasola *et al.* 2018; Buechley *et al.* 2019).
448 We provide an analytical framework for applying predictive spatial models to address
449 these fundamental issues to a tropical forest raptor. More broadly, we propose this
450 analytical framework as an efficient and cost-effective approach to tackling this

451 problem across all taxa. Using a PPM regression framework is now viewed as one of
452 the most effective methods to determine species distributions and relative
453 abundance (Aarts *et al.* 2012; Renner *et al.* 2015; Isaac *et al.* 2019), as supported by
454 our results. Using climatic and topographical predictors resulted in high model
455 predictive performance, defining in more detail the spatial and environmental
456 requirements for the harpy eagle across its geographical range. However, we
457 recognise that including predictors such as landcover and human impact, which are
458 changing rapidly, would improve predictions. These, however, will be analysed and
459 presented elsewhere.

460

461 **Spatial requirements**

462 How species are distributed in geographical and environmental space is fundamental
463 to conservation planning (Loiselle *et al.* 2003; Pearce & Boyce 2006). Yet accurate
464 and reliable spatial information, such as geographic range size and environmental
465 constraints, are often lacking in many tropical biodiversity assessments (Cayuela *et al.*
466 *et al.* 2009; Tobias *et al.* 2013), and specifically for Neotropical raptors (Sarasola *et al.*
467 2018). Using a PPM framework enables the predictions given here to be interpreted
468 as areas of relative abundance (Renner *et al.* 2015; Philips *et al.* 2017) under the
469 assumption that historical habitat is still intact. Building on a previous SDM (Miranda
470 *et al.* 2019), our continuous prediction adds further spatial detail showing a
471 discontinuous distribution. This is likely a consequence of patchy environments,
472 resulting in spatial heterogeneity in harpy eagle distribution. Miranda *et al.* (2019)
473 used both climatic and vegetation predictors, and there is a close visual
474 correspondence between their predictions and both our continuous and binary
475 models. This suggests that at the continental scale biologically relevant climatic and

476 topographical predictors alone can accurately predict the distribution for the harpy
477 eagle.

478

479 Our models refine previous coarse estimates of harpy eagle distribution (Ferguson-
480 Lees & Christie 2005; Birdlife International 2017), providing an empirically-derived
481 range size to complement the species' current IUCN status. Our binary threshold
482 polygon estimate of geographic range size (Fig. 2; 9,844,399 km²), was 11 %
483 smaller than the current IUCN polygon (11,064,295 km²), and our estimated EOO
484 (13,050,940 km²) was 25.9 % less than the current IUCN EOO (17,600,000 km²).
485 Based on these figures we recommend reviewing the IUCN distributional area for the
486 harpy eagle, which can over-estimate avian geographic range sizes (Jetz *et al.* 2008;
487 Peterson *et al.* 2016; Ramesh *et al.* 2017). Specifically, the removal of semi-arid
488 areas (such as the Caatinga in eastern Brazil) from across the IUCN range would
489 show a more realistic geographic distribution. The Caatinga area had low predicted
490 suitability, no current or historical occurrence records, and was not predicted suitable
491 for the harpy eagle including during the last glacial maximum (LGM). Similarly, the
492 Cerrado (in central Brazil) was not predicted as suitable for the harpy eagle either
493 during the LGM, and all recent records for the species show no evidence of breeding
494 in the area. Although early naturalists reported breeding harpy eagles in this region
495 (Sick & Barruel 1984), there is no evidence of a functional population and the area
496 should be removed from the IUCN range polygon (and any present range
497 projections) following IUCN guidelines for not including areas where the species
498 does not exist (IUCN 2019).

499

500 **Species-Environment relationships**

501 The continuous model highlighted distinct areas of high environmental suitability
502 (Fig. 1), with the binary model closely matching the primary vegetation types for
503 recognized harpy eagle habitat (lowland tropical broadleaf forest, Beck *et al.* 2018).
504 Thus, in the Chocó biogeographic region of north-west Ecuador and south-west
505 Colombia west of the Andes, the current model defined areas of high environmental
506 suitability, which correlate with new records of harpy eagles in the Pacific slope
507 region (Muñiz-López 2005; Muñiz-López *et al.* 2007; Zuluaga *et al.* 2018). However,
508 due to continued habitat loss in this area and across the species range, climatically
509 suitable areas predicted for some regions may over-represent suitability where there
510 is no longer harpy eagle forest habitat. Our models also defined previously
511 unrecognized areas of high environmental suitability in south-east Colombia,
512 northern Guyana, and along the east Andean slope of Peru and Bolivia. All these
513 regions may hold viable populations of harpy eagles, with further research and
514 continued surveys in these areas recommended where possible.

515

516 Environmental suitability predicted for the harpy eagle largely correlates with habitat
517 selection studies from Amazonian Peru (Robinson 1994). Here, highest frequency of
518 harpy eagle sightings were recorded in mature flood plain forest, with high nesting
519 densities below 300 m elevation in lowland humid forest in Darien, Panama (Vargas
520 González & Vargas 2011), analogous to the environmental suitability predictions
521 here. Due to the rarity and large home range sizes of harpy eagles, Thiollay (1989)
522 was not able to provide population density estimates from French Guiana, but
523 suggested harpy eagles are rare but widespread throughout the largely tropical
524 lowland forest in the region, consistent with our results. Although largely thought to
525 be extirpated from much of Central America, our models identify areas of high

526 suitability for harpy eagles along the Caribbean slopes of Costa Rica, Honduras,
527 Nicaragua and Panama (Fig. S3), which should be prioritised for continued surveys
528 and habitat protection.

529

530 Using the combined analytical approach enabled a further development of the spatial
531 modelling process by unravelling the preferred environmental space and ecological
532 conditions where harpy eagle abundance should be at its highest (VanDerWal *et al.*
533 2009; Osorio-Olvera *et al.* 2019). Climatic Moisture Index (CMI) was the most
534 important environmental variable defining harpy eagle distribution, with a preferred
535 CMI = ~ 0.4 (Fig. 3), along with the highest model gain when used solely in a jack-
536 knife test, demonstrating its importance to account for harpy eagle distribution. This
537 indicates a preference for wet, moist environments, correlating with lowland tropical
538 forest across Central and South America (Willmott & Feddema 1992; Beck *et al.*
539 2018), and suggests that CMI may be a useful surrogate predictor for habitat in
540 tropical areas. Aligned with CMI and lowland tropical forest distribution was the
541 positive response to higher minimum temperatures in the warmest month (Fig. 3).
542 Harpy eagle environmental suitability was highest in areas with a minimum
543 temperature of $\sim 24^{\circ}\text{C}$, reflected in the stable temperature conditions found across
544 lowland tropical forests.

545

546 Assessing harpy eagle distribution in environmental space revealed similar patterns
547 of environmental tolerances to the geographical models (Figs. 4 & 5), with CMI
548 having the highest positive correlation with harpy eagle occurrence. However,
549 precipitation in the wettest month was also highly correlated with harpy eagle
550 occurrence (Table 4), following the general observation for tropical regions that

551 seasonal rainfall patterns are the main limiting factor for primary productivity and
552 therefore species distributions (Schloss *et al.* 1999; Williams & Middleton 2008). The
553 ENFA confirmed the specialized environmental requirements for the harpy eagle,
554 strongly linked to CMI and precipitation, which are likely operating as useful
555 surrogate predictors of lowland tropical forest habitat. Importantly, minimum
556 temperature of the warmest month (MTWM) had a high negative coefficient value on
557 the specialization axis (Table 4). This indicates that MTWM is a key climatic predictor
558 restricting harpy eagle distribution, linked to harpy eagle preference for lower
559 elevations (Piana 2007; Muñiz-López 2008; Vargas González & Vargas 2011).
560 Harpy eagle nests are rarely found above an altitude of 300m (Vargas González &
561 Vargas 2011), and as temperature and elevation are closely correlated it seems
562 likely the harpy eagle is negatively responding to lower temperatures at higher
563 elevations restricting breeding distribution.

564

565 **Paleo-distributions**

566 The two paleoclimate predictions given here place current harpy eagle distribution in
567 context. During the LGM, highest suitability was centred on northern and western
568 Amazonia and present-day Panama. This follows current evidence that suggests
569 during the LGM much of Amazonia was forested (Mayle *et al.* 2004), contrary to the
570 rainforest refugia hypothesis (Haffer 1969). However, forest structure was likely quite
571 different from the present-day, due to lower temperatures, rainfall and atmospheric
572 CO₂ (Mayle *et al.* 2004), resulting in mixed-forest communities. Climate
573 reconstructions from Amazonia during the LGM show that temperatures were 5°C
574 cooler than today (Guilderson *et al.* 1994; Stute *et al.* 1995), and that rainfall was
575 spatially highly variable, as it is in the present-day. Thus, dry forest-savannahs may

576 have dominated the region of central and southern Amazonia during the LGM, which
577 may explain the low environmental suitability for the harpy eagle in this region from
578 the LGM paleo-climate model.

579

580 During the Mid-Holocene the continuous prediction was similar to the current model
581 with expansion of high suitability across Amazonia and north into Central America
582 (Fig. S7, top right, Appendix 3). This may be explained by the correlation of these
583 areas with expansion of deciduous broadleaf forest in the region during the Mid-
584 Holocene, ultimately related to changing precipitation levels (Mayle *et al.* 2004). The
585 increase in distributional area size during this period correlates with a population
586 expansion identified from genetics from 60,000 cal yr BP, well before the LGM, and
587 subsequently through the Mid-Holocene (Lerner *et al.* 2009). The population
588 expansion prior to the LGM occurred with climatic changes in Amazonia, leading to a
589 reduction of tropical forest (Mayle *et al.* 2004), followed by expansion of forest
590 through the LGM and Mid-Holocene up to pre-Industrial times. Thus, harpy eagle
591 distribution area is strongly associated with changing climatic conditions (and
592 therefore vegetation), which suggests a potential reduction in range size under future
593 drier climate change conditions predicted across much of Central and South America
594 (da Costa *et al.* 2010). However, our stable refugia prediction identified key areas of
595 stable conditions since the LGM where a suitable climatic envelope for the harpy
596 eagle is likely to persist into the future (Fig. 6). We recommend these areas be
597 prioritized for conservation and research, holding some encouragement for the future
598 survival of the species as long as habitat can be maintained.

599

600 Explaining the observed distribution and ecological constraints of an organism by
601 reference to its environmental requirements is one of the central goals in ecology
602 (Krebs 2009). Species at high trophic-levels with slow life histories are often at
603 increased risk of extinction (Purvis *et al.* 2000). Therefore, understanding the
604 environmental processes regulating distribution of apex predators is an especially
605 pressing conservation need. By refining previous range estimates using relevant
606 abiotic variables (including those that may act as vegetation surrogates), our models
607 define the ecological processes shaping both current and past harpy eagle
608 distribution. However, future distribution models should include variables such as
609 biotic interactions, landcover and human impacts at broad and fine scales to improve
610 current predictions, and project into future climate change scenarios. With recent
611 work demonstrating strong relationships between suitability predictions from SDMs
612 and species abundance (Weber *et al.* 2017, Osorio-Olvera *et al.* 2020), we
613 confirmed the suitability of spatial point process models to deliver cost-effective and
614 reliable first estimates of relative abundance for species conservation management.
615 Having accurate distributional data on the current ranges of tropical birds and raptors
616 has long been a priority in the Neotropics (Snow 1985; Bierregaard 1998). Using a
617 range of spatial modelling methods, we were able to establish a baseline of
618 ecological constraints for the harpy eagle that may help to better plan its
619 conservation across its vast continental distribution.

620

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630

631 **Authors' Contributions**

632 L.J.S., M.F., C.J.W.M., & R.P. conceived the ideas and designed methodology;
633 D.L.A, E.B.P.M., F.H.V. & J.J.V.G collected data; L.J.S. analysed the data; L.J.S. led
634 the writing of the manuscript. All authors contributed critically to the drafts and gave
635 final approval for publication.

636

637 **Conflict of Interest**

638 The authors have no conflicts of interest to declare.

639

640 **Data Accessibility Statement**

641 The data that support the findings of this study are openly available on the data
642 repository *Dryad*: <https://doi.org/10.5061/dryad.9cnp5hqgn>

643

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1013

1014 **Tables**

1015 **Table 1.** General Circulation Models (GCMs) from the Coupled Model Inter-comparison Project Phase
 1016 5 (CMIP5) and Paleoclimate Modelling Inter-comparison Project Phase 3 (PMIP3) databases used to
 1017 predict past distributions for the harpy eagle to two paleoclimate scenarios in the Mid-Holocene
 1018 (~6,000 cal yr BP) and Last Glacial Maximum (~22,000 cal yr BP).

1019

GCM	Acronym	Citation
Community Climate System Model, v4	CCSM4	Gent <i>et al.</i> 2011
Model for Interdisciplinary Research on Climate – Earth System Model	MIROC-ESM	Watanabe <i>et al.</i> 2011
Max Planck Institute for Meteorology – Earth System Model - Paleo	MPI-ESM-P	Giorgetta <i>et al.</i> 2013

1020

1021

1022 **Table 2.** Parameter estimates derived from beta-coefficients for the harpy eagle distribution model fitted
 1023 using Linear and Quadratic feature classes.

1024

Predictor	Linear	Quadratic
Climatic Moisture Index	1.38	-3.62
Minimum temperature warmest month	0.13	*
Maximum temperature warmest month	0.05	*
PET driest quarter	0.03	0.00
Precipitation wettest month	0.02	*
Terrain Roughness Index	0.02	0.00
Precipitation warmest quarter	0.00	*
Isothermality ²	*	-0.01
PET wettest quarter ²	*	0.00

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1031 **Table 3.** Percent contribution and permutation importance for variables used as environmental
 1032 predictors in the current distribution model for the harpy eagle. All values are %.

1033

Predictor	Percent contribution	Permutation importance
Climatic Moisture Index ¹	72.1	43.1
Minimum temperature warmest month	15.6	22.8
Terrain Roughness Index ²	8.3	12.4
PET driest quarter	3.0	9.8
PET wettest quarter	0.5	5.2
Isothermality ³	0.2	5.2
Precipitation wettest month	0.2	5.2
Precipitation warmest quarter	0.0	0.7
Maximum temperature warmest month	0.0	0.4

1034

1035

¹ Ratio of annual precipitation to annual evapotranspiration

1036

² Variation in local terrain around a central pixel

1037

³ Mean diurnal temperature range/temperature annual range*100.

1038

1039

1040 **Table 4.** Variance explained by the five most significant factors (Marg. = marginality; Spec =
 1041 Specialization) in an Ecological Niche Factor Analysis (ENFA) for suitable harpy eagle environment
 1042 space. Coefficient values for the nine environmental predictors are ordered according to the highest
 1043 coefficient values in the marginality factor.

1044

ENFA axis	Marg	Spec1	Spec2	Spec3	Spec4
Variance explained (%)	14.05	28.81	13.82	12.51	11.56

Predictor	Marg	Spec1	Spec2	Spec3	Spec4
Climatic Moisture Index	0.56	0.24	-0.08	-0.24	0.26
Precipitation wettest month	0.47	0.04	0.00	-0.05	-0.04
Min. temp. warmest month	0.36	-0.72	-0.30	-0.28	-0.27
Isothermality	0.28	0.12	0.03	0.08	0.33
PET wettest quarter	-0.26	-0.35	-0.31	-0.40	0.20
Precipitation warmest quarter	0.25	-0.07	0.01	0.15	-0.15
PET driest quarter	0.23	-0.39	-0.49	-0.19	-0.56
Max. temp. warmest month	0.21	0.31	0.73	0.77	0.57
Terrain Roughness Index	-0.12	-0.17	-0.18	0.23	0.21

1045

1046

1047 **Figure legends**

1048

1049 **Figure 1.** Predicted current distribution for the harpy eagle with values closer to 1 having highest
1050 environmental suitability. Grey borders represent national borders and internal state boundaries for
1051 Argentina, Brazil, and Mexico. Black points define harpy eagle occurrences.

1052

1053 **Figure 2.** Reclassified binary range prediction for the harpy eagle using 10% training presence (10TP
1054 = 0.415) threshold. Khaki area is the suitable environmental space above the 10TP threshold, white
1055 areas not suitable. Red polygons define current IUCN range for the harpy eagle. Grey borders
1056 represent national borders and internal state boundaries for Argentina, Brazil, and Mexico. Blue points
1057 define harpy eagle occurrences.

1058

1059 **Figure 3.** Response curves for predictors used in the current distribution model for the harpy eagle.

1060

1061 **Figure 4.** Distribution of harpy eagle occurrences in selected pairs of environmental variables. Grey
1062 points are random background environmental points, red points are harpy eagle occurrences. Black
1063 hashed line defines the minimum convex polygon of harpy eagle occurrences.

1064

1065 **Figure 5.** Ecological Niche Factor Analysis (ENFA) for suitable harpy eagle environment space
1066 (khaki) within the available background environment (grey) shown across the marginality (x) and
1067 specialization (y) axes. Arrow length indicates the magnitude with which each variable accounts for
1068 the variance on each of the two axes. Red circle indicates niche position (median marginality) relative
1069 to the average background environment (the plot origin).

1070

1071 **Figure 6.** Predicted climate stability for the harpy eagle summed from the current, Last Glacial
1072 Maximum (LGM, ~22,000 years ago) and Mid-Holocene (~6,000 years ago) predictions. Values of -2
1073 indicate species absence, -1 to 0 shows colonizable areas, 0 to 1 defines areas of highest stability
1074 and values of 2 (dark red patches) show the most unstable areas. Map defines summed prediction
1075 masked to current geographic extent and geo-political boundaries.