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Multi-scale habitat overlap in two broad-ranged sympatric Neotropical forest eagles reveals shared environmental space and habitat use

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Quantifying resource partitioning between co-occurring species can provide insight into processes facilitating coexistence by closely related species, a fundamental question in ecology. We tested whether the habitat requirements of two closely related Neotropical forest eagles, the Crested Eagle *Morphnus guianensis* and Harpy Eagle *Harpia harpyja*, differ at fine and coarse resolutions across their shared geographical range. Using land-cover and topographical covariates, we quantified potential resource overlap first using higher resolution (30 arc-s, ~ 1-km^2 data) generalized linear models (GLMs), and secondly using coarser-grain (2.5 arc-min, ~ 4.5-km^2 data) environmental ordination to capture the potential effect of scale on habitat overlap. The distribution of both eagles was largely explained by canopy tree species richness and canopy structural complexity, with peak suitability of 60–80% evergreen forest cover. Both eagles were negatively associated with mosaic forest and cultivated areas. From the GLMs, habitat overlap was >93% in geographical space but was reduced to 73% when considering environmental space, a proxy for resource overlap. From ordination (principal component analysis), resource overlap was 67% in environmental space, with randomization tests supporting equivalent environmental space for both eagles. Our results suggest that at the continental scale, Crested and Harpy Eagles share identical environmental space when quantified at fine and broad scales, with little difference in distribution and habitat use. At the continental scale used here, both eagles can coexist, presumably with sufficient habitat heterogeneity for coexistence when they occur in close proximity. Therefore, further research is required at the local level to capture fully where coexistence at the local scale is facilitated more by fine-scale habitat selection, or difference in diet between two species with indistinguishable habitat use.

Keywords: environmental ordination, habitat use, *Harpia harpyja*, *Morphnus guianensis*, resource partitioning, resource selection functions.

The distribution of specific habitat resources is a major factor determining species range limits at both fine and broad spatial scales (Morrison *et al.* 2006). However, species interactions, which occur via resource use, are also important in determining animal distributions (MacArthur 1972, Cody 1974). Although support for habitat as a key factor limiting animal distributions is evident (Dorazio *et al.* 2015, Veech 2021), habitat resources alone cannot fully explain many species distributions (Thompson 2005, Anderson 2017), or where and how co-occurring species coexist when they

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have overlapping ranges (Diamond 1970, MacArthur 1972). Closely related species may exhibit completely overlapping distributions (MacArthur 1972) because species–habitat associations can be conserved over long evolutionary timescales, with closely related species likely to inhabit similar, though not always identical, environments (Wiens & Graham 2005). This may result in certain species coexisting through resource partitioning (Levins 1968, Cody 1974), where specific and subtle differences in resource and habitat requirements are encountered.

In Neotropical forests, raptors are among the least-studied bird groups due to their inherent rarity and large area requirements (Buechley *et al.* 2019). Compared with temperate regions, current knowledge on the environmental determinants of distribution for many Neotropical raptors is limited (McClure *et al.* 2018, Buechley *et al.* 2019). Among Neotropical forest raptors, the Crested Eagle *Morphnus guianensis* and Harpy Eagle *Harpia harpyja* have almost identical geographical ranges across Central and South America, occurring widely across lowland broadleaf rainforests (Gomes & Sanaiotti 2015, Miranda *et al.* 2019, Sutton *et al.* 2022). Both species occur at relatively low population densities, with the Harpy Eagle being on average ~ 1.3 times larger than the Crested Eagle (Ferguson-Lees & Christie 2005). The Crested Eagle is currently categorized as Near-Threatened on the International Union for the Conservation of Nature (IUCN) Red List (BirdLife International 2017), with no reliable population estimate currently for the species. The Harpy Eagle was recently relisted from Near-Threatened to Vulnerable (BirdLife International 2021), with an estimated population of 100 000–250 000 mature individuals.

Both eagles are monotypic and the only members of the subfamily Harpiinae in the Neotropics (Brown & Amadon 1968, Lerner & Mindell 2005). Generally, the Crested Eagle feeds on smaller and more diverse prey than the Harpy Eagle, mainly arboreal snakes, small primates, opossums and birds (Whitacre *et al.* 2012, Gomes *et al.* 2021), whereas Harpy Eagle diet largely comprises large arboreal mammals, primarily sloths and primates (Aguiar-Silva *et al.* 2014, Miranda 2015, Miranda *et al.* 2021). On a local scale, the two species may use differing forest canopy strata for breeding and hunting (Gomes *et al.* 2021), with Harpy Eagles nesting in canopy-emergent trees (Sanaiotti *et al.* 2015, Miranda *et al.* 2020) and Crested Eagles in canopy trees (Bierregaard Jr 1984, Whitacre *et al.* 2012). Observations of interspecific feeding of a fledged Harpy Eagle at its nest by a female Crested Eagle (Vargas González *et al.* 2006) and interactions at nest-sites between the two species (Aguiar-Silva *et al.* 2019) suggest that territorial behaviour can be relaxed when both eagles exist in close proximity.

Apart from localized observations reporting both Harpiinae eagles breeding within ~ 1 to 3 km of each other in similar habitats (Galetti *et al.* 1997, Muniz-Lopez *et al.* 2007, Sanaiotti *et al.* 2015), empirical evidence is lacking on how these two eagles coexist at a continental scale with highly overlapping geographical ranges. Both eagles were recorded in similar primary forest habitats from two landscape habitat selection studies, one in an 800-ha section of Amazonian Peru (Manu National Park; Robinson 1994), and the second along a 276-km stretch of the Xingu River in Amazonian Brazil (Sanaiotti *et al.* 2015). Harpy Eagles were observed more frequently than Crested Eagles, suggesting the Harpy Eagle may be the more abundant of the two species where both are present. From surveys along the Xingu River, Sanaiotti *et al.* (2015) concluded that territories of both eagle species overlapped, but this is contrary to earlier results from a 10 000-ha study area in French Guiana which suggested that territories of neither eagle species overlapped (Thiollay 1989).

At a local level, both eagles may partition food resources and prefer different micro-habitats. However, an unanswered question is whether these patterns scale up to a broader continental extent where both eagles may prefer differing habitat. Because both Harpiinae eagles co-occur within similar geographical ranges, the expectation in geographical space is for a high level of habitat overlap. However, given that habitat resources are rarely equally distributed across landscapes, geographical comparisons between sister species may over-represent the overlap in environmental requirements. Therefore, when assessed in environmental space, the assumption of high habitat overlap may be lower, indicating environmental niche partitioning (Pulliam 2000, Bleyhl *et al.* 2019). Even so, given that narrow niche breadth is viewed as optimal in the relatively stable and predictable environment of the tropics (Levins 1968), both eagles are expected to have specialized habitat requirements irrespective of the level of habitat resource overlap.

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Here, we use a multi-scale assessment across the entire environmental and geographical space available to both eagles to quantify habitat overlap and preference for specific conditions and resources. Previous studies have reported differences in habitat use at localized scales for the Crested and Harpy Eagle (Thiollay 1989, Robinson 1994, Sanaiotti *et al.* 2015) but how habitat differences potentially influence resource partitioning at broader continental scales is unknown. We used resource selection functions (RSFs) to determine the fine-grain habitat correlates of distribution in both geographical and environmental space across the entire shared range for both eagles. We then performed an environmental principal component analysis (PCA-env) to quantify the level of coarse-grain resource overlap solely in environmental space for comparison with the finer-scale RSFs. Given their almost identical distributions across lowland tropical forest, we first hypothesize that the range limits of both eagles would be restricted by similar habitat types at fine scales in both geographical and environmental space. Secondly, we hypothesize both eagles will share equivalent environmental space when tested at coarser scales. A finding of different habitat types would imply coexistence through habitat segregation, whereas failure to differentiate habitat types would imply the potential for coexistence through microhabitat and diet partitioning.

METHODS

Eagle occurrence data

We sourced Crested and Harpy Eagle point localities from the Global Raptor Impact Network (GRIN; McClure *et al.* 2021) consisting of occurrence data from previous distribution assessments for both the Crested Eagle (Gomes & Sanaiotti 2015) and Harpy Eagle (Vargas González & Vargas 2011, Miranda *et al.* 2019), which give precise point localities for nests and sightings. GRIN is an information system amalgamating multiple data sources from a global network of raptor researchers for the population monitoring and research of all raptor species. In addition, we downloaded presence-only data from the Global Biodiversity Information Facility (GBIF; Global Biodiversity Information Facility 2019a, 2019b), which were incorporated into our dataset. We cleaned occurrences by removing duplicate records, those with no geo-referenced location and with a resolution less than 1-km accuracy. Finally, a manual check for unlikely outliers was performed in the Quantum Geographic Information System software (v3.2.2; QGIS 2022). Only occurrences recorded from year 2000 onwards were included to match the habitat covariates temporally. We omitted eBird (Sullivan *et al.* 2009) occurrences from the GBIF datasets because eBird data are semi-structured presence/absence data that are more appropriately used with a data integration modelling approach (Johnston *et al.* 2021) were not possible for our analysis here, which relies on presence-only localities.

We quantified spatial overlap in the point occurrences using a point-proximity overlap metric (O; Cardillo & Warren 2016) to test whether both sets of occurrence points were distributed randomly and independent from each other. The point-proximity O metric tests for spatial overlap are based on the coaggregation in the point occurrences for each respective eagle species. The metric ranges from zero to one, with a value ~0.5 expected if the occurrence points of both species have a random and independent distribution. We compiled 509 Crested Eagle records and 913 Harpy Eagle records after data cleaning (Fig. 1). We applied a 1-km spatial filter between each occurrence point to reduce sampling bias using the 'geoThin' function in the R package enmSdm (Smith 2019). Using a 1-km filter approximately matches the resolution of the raster data (~ 1 km) and reduces the effect of biased sampling (Kramer-Schadt *et al.* 2013). Applying the 1-km spatial filter resulted in 412 occurrences for the Crested Eagle and 768 occurrences for the Harpy Eagle. Spatially filtered occurrences for both eagle species were distributed randomly and independently of each other (O = 0.443). Additionally, both sets of filtered occurrences presented a low level of spatial autocorrelation at the two shortest distances investigated when assessed with Mantel correlograms (Supporting Information Fig. S1) in the ecospat R package (Broennimann *et al.* 2023).

Habitat covariates

Current distribution maps show Crested and Harpy Eagles exist in similar geographical space (Fig. 1, Ferguson-Lees & Christie 2005), and thus our expectation was for their respective distributions to be limited by the same broad-scale habitat factors.

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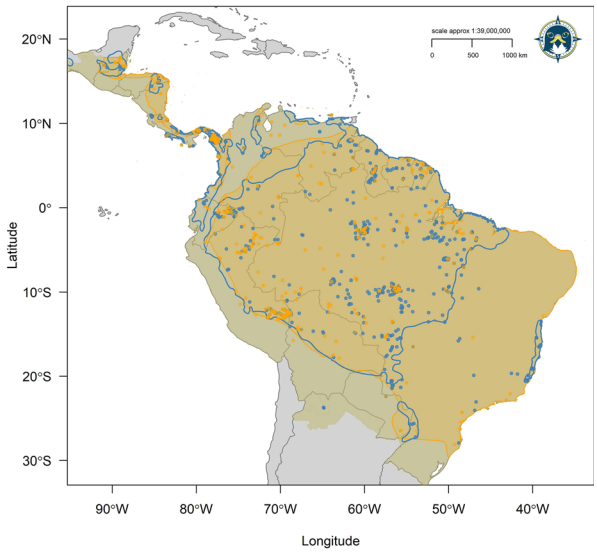

Figure 1. Distribution of Crested Eagle (orange points) and Harpy Eagle (blue points) occurrences across Central and South America sourced from the Global Raptor Impact Network data information system. Orange polygons show current IUCN range map for the Crested Eagle and blue polygons current IUCN range map for the Harpy Eagle. Pale green polygon shows the model accessible area used for each species derived from the ecoregions where each eagle is known to occur.

Potential covariates representing topography, canopy vegetation heterogeneity and landcover were downloaded from the ENVIREM (Title & Bemmels 2018) and EarthEnv (www.earthenv.org) databases. Biologically relevant covariates were selected *a prioiri* based on the key limiting habitat factors related theoretically and empirically to each species' distribution in lowland tropical forests (Vargas González *et al.* 2006, Whitacre *et al.* 2012, Sanaiotti *et al.* 2015, Miranda *et al.* 2019). We included a total of six continuous covariates (Table 1) in the RSF analyses at a spatial resolution of 30 arc-s (~ 1-km resolution). Raster layers were cropped using a delimited polygon consisting of all known ecoregions where each eagle is known to occur defining a biologically driven accessible area (Barve *et al.* 2011), further improving model predictive power by reducing the background area used for testing points used in model evaluation (Radosavljevic & Anderson 2014).

Heterogeneity is a biophysical similarity measure added as a variable to define canopy species richness (i.e. canopy structure, composition and diversity) derived from textural features of the

Table 1. Habitat covariates used in all spatial and modelling analyses for the Crested and Harpy Eagle.

Predictor	Source	Citation
Cultivated (%)	EarthEnv	Tuanmu and Jetz (2014)
Elevation (m)	EarthEnv	Amatulli *et al.* (2018)
Evergreen forest (%)	EarthEnv	Tuanmu and Jetz (2014)
Heterogeneity (0.0–1.0	EarthEnv	Tuanmu and Jetz (2015)
Mosaic forest (%)	EarthEnv	Tuanmu and Jetz (2014)
Terrain Roughness Index (TRI)	ENVIREM	Title and Bemmels (2018)

Enhanced Vegetation Index (EVI) between adjacent pixels, sourced from the Moderate Resolution Imaging Spectroradiometer (MODIS, https://modis.gsfc.nasa.gov/). We inverted the raster cell values in the original EarthEnv variable 'Homogeneity' (Tuanmu & Jetz 2015) to represent the spatial variability and arrangement of canopy species richness on a continuous scale which varied between zero (minimum heterogeneity, low species richness) and one (maximum heterogeneity, high species richness). The three measures of percentage landcover (Evergreen Forest, Mosaic Forest, Cultivated) are consensus products integrating GlobCover (v2.2), MODIS land-cover product (v051), GLC2000 (v1.1) and DISCover (v2) at 30 arc-s (~ 1-km) spatial resolution. Mosaic forest is derived from the EarthEnv variable 'Mixed trees' and represents a mosaic of forest, shrubland and woody savanna, with cultivated representing a mix of cropland, tree cover and managed vegetation. Full details on methodology and image processing can be found in Tuanmu and Jetz (2014) for the landcover layers, and Tuanmu and Jetz (2015) for the habitat heterogeneity texture measure.

After selecting biologically relevant covariates, all six candidate variables were tested for multicollinearity using Variance Inflation Factor (VIF) analysis in the R package usdm (Naimi *et al.* 2014). VIF is based on the square of multiple correlation coefficients, regressing a single covariate against all other covariates. A stepwise elimination of highly correlated variables was used retaining covariates with a VIF threshold of < 5, considered suitable for multivariable correlation (Dormann *et al.* 2013). The remaining covariates were then checked for

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collinearity using Spearman's correlation coefficient with a threshold of $r_s = |0.7|$. All the selected covariates showed low collinearity and were therefore all included as predictors in model calibration (Supporting Information Table S1).

Resource selection functions

We calibrated RSFs for each species using logistic regression fitted as generalized linear models (GLMs) with a binomial cloglog link function in the ENMTools (Warren *et al.* 2019b) and stats R packages (R Core Team 2018). We used a complementary log–log (cloglog) function because this is an appropriate link function to use for asymmetrically distributed datasets, such as presence-background data used here (Matthiopoulos *et al.* 2020). Our RSFs followed geographical range first-order selection (Johnson 1980) using design I in a use-availability sampling protocol (Manly *et al.* 2002, Johnson *et al.* 2006, Thomas & Taylor 2006). GLMs were fitted with iteratively reweighted least squares to derive maximum likelihood estimates on model parameters, with no interaction terms. We fitted linear terms to all covariates and quadratic terms where we expected a quadratic effect with values of covariates to be highest at intermediate values and decrease at lower and higher values. All covariates were standardized with a mean of zero and a standard deviation of one.

Background-absence points were randomly sampled using 10 000 points suitable for regression-based modelling (Barbet-Massin *et al.* 2012) and weights assigned equally to both presence and background points. We tested calibration accuracy using the explained variance from each logistic model measured using the coefficient of determination, or McFadden's adjusted R^2 (R^2_{adj}, McFadden, 1974), which is an appropriate adjusted R^2 metric to use when using a cloglog link function in GLMs. We tested discrimination ability in environmental space, using a new implementation of the area under the curve (AUC) statistic (referred to here as AUC_{env}) calculated using the 'env.evaluate' function in the R package ENMTools (Warren *et al.* 2019b). AUC_{env} uses Latin hypercube sampling to estimate model fit in environmental space employing all possible environmental combinations, evaluating model performance between presence and background-absence points within the minima and maxima of the environmental predictors. An $AUC_{env} = 1.0$ indicates maximum predictive model performance, and an $AUC_{env} = 0.5$ no better than a random prediction.

Given the inherent spatial autocorrelation and environmental heterogeneity present in biodiversity inventory data (Legendre 1993), we used a Monte Carlo randomization to test for significance in the AUC evaluation metrics against null random expectations (Raes & ter Steege 2007). We set random null models to calculate 95% AUC confidence intervals (CIs) on a frequency histogram, randomly drawing points without replacement on 100 replicates using 20% test data under the same environmental parameters used in the best-fit models. With fitted 95% CI AUC values, model accuracy was assessed on being higher than expected by chance at $\alpha = 0.05$. Marginal response functions were used to assess habitat differences between both eagle species and biological realism of the fitted models (Guevara *et al.* 2018). Marginal responses show the response of an RSF to the habitat covariate with all other covariates held at their mean in the available environment. Last, we performed Global Moran's *I* tests on the GLMs using a spatial weights matrix with five *k*-nearest neighbours in the R package spdep (Pebesma & Bivand 2023) and fitted correlograms to test for spatial autocorrelation of the GLM residuals using the *correlog* function of the R package ncf (Bjornstad & Falck 2001). Note that in this case the Mantel correlation is the value relative to the overall mean autocorrelation among sites, not an average degree of autocorrelation between sites.

Resource overlap

Resource selection functions

We used Levin's standardized niche breadth *B2* (1968) to quantify the level of resource specialization by both eagles. We used the *B2* statistic for each GLM in geographical (gB2) and environmental (eB2) space given a vector of habitat suitability scores. Niche breadths were measured on a scale from 0 to 1, with zero indicating low niche breadth (habitat specialist) and 1 high niche breadth (habitat generalist; Krebs 1999). Second, we calculated pair-wise niche overlap metrics on each respective GLM in both geographical and environmental space to quantify similarity between models using Schoener's *D* (Schoener 1968,

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Warren *et al.* 2008). Schoener's *D* measures niche similarity between environmental conditions ranging from 0 (no overlap) to 1 (identical predictions). Niche breadth and overlap measures were calculated based on Monte Carlo integration using continuous predictions in the R package ENMTools (Warren *et al.* 2019a, 2019b).

PCA-env ordination

For the PCA-env, we included the same six covariates (Table 1) at a spatial resolution of 2.5 arc-min (~ 4.5-km resolution). All 30 arc-s (~ 1-km resolution) landcover layers were thus resampled to a spatial resolution of 2.5 arc-min using bilinear interpolation. We thinned occurrences using a 5-km spatial filter to match approximately the resolution of the raster data (~ 4.5-km). Applying the 5-km spatial filter resulted in 335 occurrences for the Crested Eagle and 586 occurrences for the Harpy Eagle. The 5-km filtered occurrences for both eagle species had a random and independent distribution (O = 0.519) compared with the unfiltered occurrences.

Ordination techniques such as principal component analysis (PCA) use direct comparisons of species-habitat relationships in environmental space, in contrast to predictive resource overlap analysis using RSFs. Using the PCA-env framework of Broennimann *et al.* (2012), we performed an environmental ordination using the R package humboldt (Brown & Carnaval 2019). We set the PCA-env method to calibrate a non-analogous environmental space using a minimum convex polygon around all spatially filtered occurrences on a 100 × 100 resolution grid, with a smoothed Gaussian kernel density function (bandwidth = 1) to account for spatial auto-correlation. We quantified niche overlap on the first two principal components using Schoener's *D* statistic. Using smoothed densities allows measured overlap to be independent of grid resolution, important for unbiased estimates of niche overlap using Schoener's *D* (Broennimann *et al.* 2012).

To test equivalency in shared environmental space, we first used a niche Equivalency Statistic to test for the difference ($\alpha = 0.05$) between the observed overlap scores and those under a null distribution hypothesis that the two distributions are equivalent (Warren *et al.* 2008). For the null distribution, presence points are randomly assigned to each species, and a PCA is built on these randomized data. This is repeated 100 times and a probability distribution is then estimated for niche overlap under the null hypothesis that both sets of species occurrences are randomly distributed in the environment. Secondly, to measure the ability of the Equivalence Statistic to detect differences in environmental space, we used a Background Statistic to test for the difference ($\alpha = 0.05$) if the observed occurrences of one species are more similar than expected by chance to the background occurrences of the other species ($n = 100$; Warren *et al.* 2008).

The background test corrects for the environmental heterogeneity inherent in environmental data underlying occurrence data, assuming that all species are choosing environments at random throughout their respective geographical ranges (Warren *et al.* 2008). If distributions are not equivalent, a statistically significant difference allows rejection of the null hypothesis of niche equivalency between the two distributions, regardless of the significance of the Background Statistic. A non-significant Equivalence Statistic and significant Background Statistic supports the hypothesis of equivalent shared environmental space. If both statistics are non-significant, this implies niche equivalency could be the result of shared identical environmental space, with limited power for the Equivalency Statistic to detect any significant differences (Brown & Carnaval 2019). Importantly, the Background Statistic assesses the power of the equivalency test by asking whether two distribution models are equivalent based on the matching environments available. It does not provide any evidence that niches are not equivalent. General model development and geospatial analysis were performed in R (v3.5.1; R Core Team 2018) using the dismo (Hijmans *et al.* 2017), raster (Hijmans 2017), rgdal (Bivand *et al.* 2019), rgeos (Bivand & Rundel 2019) and sp (Bivand *et al.* 2013) packages.

RESULTS

Resource selection functions

Both GLMs had high discrimination ability (Crested Eagle: $AUC_{env} = 0.991$, Harpy Eagle = $AUC_{env} = 0.985$), with randomization tests robust against null expectations ($P < 0.01$; Supporting Information Fig. S1). GLM residuals

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showed global spatial autocorrelation in both species (Crested Eagle: Moran's $I = 0.28$, $P < 0.001$; Harpy Eagle: Moran's $I = 0.42$, $P < 0.001$), and the correlograms showed small deviations from the mean values at distances <60 km (Supporting Information Fig. S2). This was confirmed by the Monte Carlo resampling tests (Supporting Information Fig. S3). On the other hand, the model's residuals were generally small and negative, with the largest, positive values concentrated in areas of frequent occurrences (Figs S4 and S5). For the Crested Eagle, six covariates had significant terms (Table 2), with the full model able to explain 88% of the variability in environmental space ($R^2_{adj} = 0.88$). For the Harpy Eagle, seven covariates had significant terms (Table 2), with the full model able to explain 86% of the variability in environmental space ($R^2_{adj} = 0.86$). Both eagles were more likely to be positively associated with high habitat heterogeneity (i.e. canopy species richness) and evergreen forest, but negatively associated with elevation, mosaic forest cover (comprising forest and woody savanna) and cultivated areas.

Overall, responses in distribution to habitat were consistent for the Crested and Harpy Eagle, with similar responses to canopy species richness and topography, and restricted tolerances for higher elevations and terrain roughness (Fig. 2). Both eagles were positively associated with areas of high heterogeneity, indicating similar preference for highly species-rich canopy vegetation. Responses to the three landcover covariates were similar, with each eagle species having high peak suitability between 60% and 80% evergreen forest cover, but with the Harpy Eagle occurring in 75–80% forest cover, greater than the Crested Eagle. Both eagles had steep negative responses to mosaic forest cover. For cultivated areas, both eagles had fairly broad tolerances but with highest suitability in areas with < 20% cultivation cover (Fig. 2).

Table 2. GLM terms derived from maximum likelihood estimates obtained from each respective species model. Covariates are ranked by the value of regression coefficient estimates.

Predictor	Estimate	Lower CI	Higher CI	*z*	*P*
Crested Eagle					
Intercept	−1.07	−1.27	−0.86	−10.20	<0.001
Mosaic Forest	−67.10	−96.30	−37.90	−4.50	<0.001
Heterogeneity	52.38	37.06	67.71	6.70	<0.001
Evergreen Forest	35.17	3.54	66.81	2.18	0.030
Cultivated	−29.27	−55.11	−3.43	−2.22	0.030
Elevation	−26.61	−50.26	−2.95	−2.20	0.030
Evergreen Forest[a]	−25.14	−38.88	−11.39	−3.58	<0.001
Terrain Roughness Index[a]	−22.68	−50.82	5.45	−1.58	0.114
Cultivated[a]	−7.91	−29.54	13.73	−0.72	0.474
Terrain Roughness Index	−2.44	−24.05	19.16	−0.22	0.825
Harpy Eagle					
Intercept	−1.05	−1.20	−0.89	−13.20	<0.001
Evergreen Forest	59.89	33.33	86.46	4.42	<0.001
Elevation	−49.65	−71.55	−27.75	−4.44	<0.001
Heterogeneity	42.79	32.02	53.56	7.79	<0.001
Cultivated	−37.09	−62.05	−12.13	−2.91	0.010
Mosaic Forest	−34.65	−56.54	−12.76	−3.10	0.010
Evergreen Forest[a]	−27.18	−37.90	−16.46	−4.97	<0.001
Cultivated[a]	−19.08	−39.89	1.73	−1.80	0.072
Terrain Roughness Index[a]	−18.18	−33.91	−2.45	−2.27	0.023
Terrain Roughness Index	9.17	−8.12	26.46	1.04	0.298

[a]Indicates quadratic model terms.

Environmental overlap

From the GLMs, both eagles had similar niche breadth across geographical space, with Crested Eagle niche breadth marginally greater (gB2 = 0.698) than the Harpy Eagle (gB2 = 0.689). In environmental space, niche breadth was markedly reduced for the Crested Eagle (eB2 = 0.038) and Harpy Eagle (eB2 = 0.037), meaning that both eagles have similar specialized habitat requirements.

Resource overlap across geographical space from the GLMs was high ($D = 0.933$) but was reduced across environmental space ($D = 0.727$). Measuring overlap in environmental space using the coarser-grain PCA-env resulted in moderate overlap ($D = 0.670$; Fig. 3), with both eagles sharing equivalent environmental space supported from the combination of a non-significant Equivalency Statistic ($P = 0.218$) and significant Background Statistics (both tests: $P = 0.01$; Fig. S3). Both eagles occupied more similar environmental space than expected by chance, with both eagles occurring across almost identical environmental space (Figs 4 and 5).

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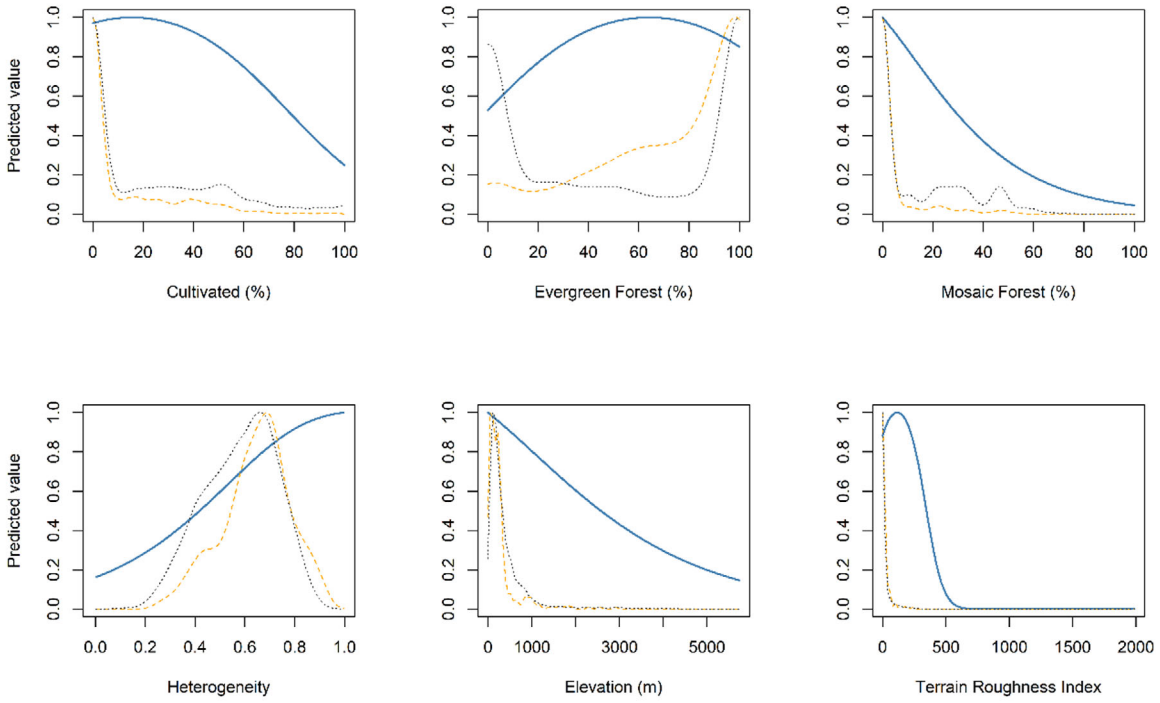
Crested Eagle



Harpy Eagle

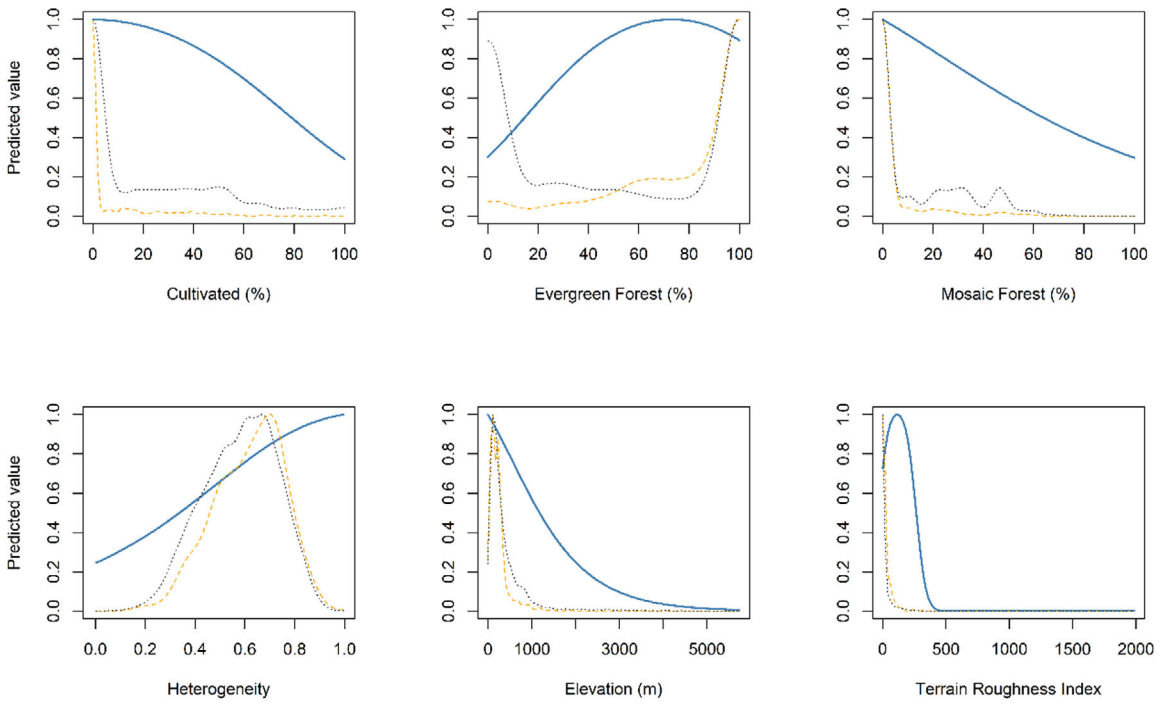


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Figure 2. Marginal responses for each respective species model from all continuous GLM covariates. Blue lines indicate environmental suitability, orange dashed line presence locations, and grey dotted line background locations. The curves show the 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.

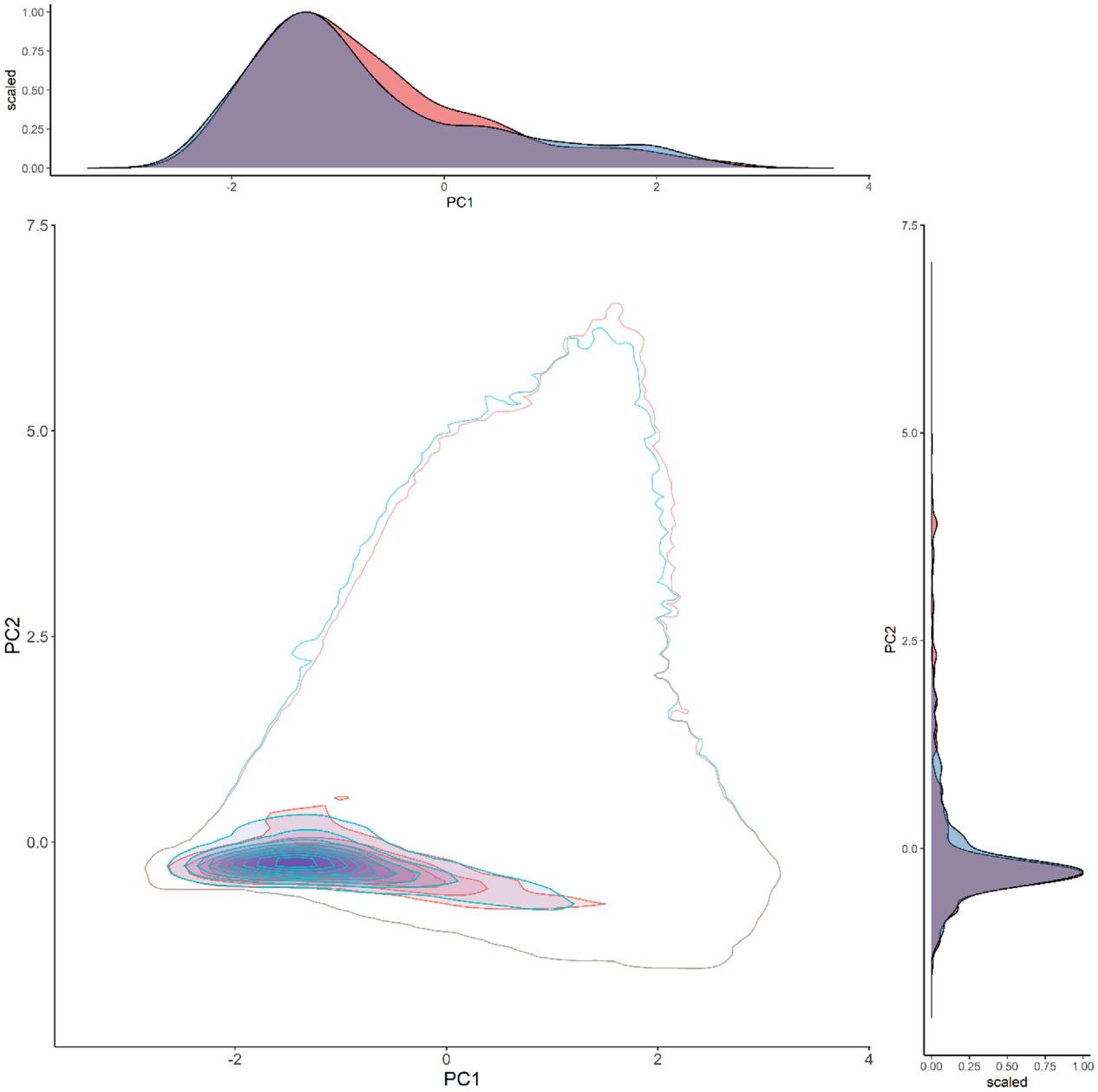

Figure 3. Environmental overlap (purple) for the Crested Eagle (red) and Harpy Eagle (blue) across environmental space from two principal components. Total variance explained by the two principal components = 73.3% (PC1 = 45.75%, PC2 = 27.55%). Filled isopleths are kernel densities from 1 to 100%. Empty kernel density isopleths represent the 1% density isopleth of the environment.

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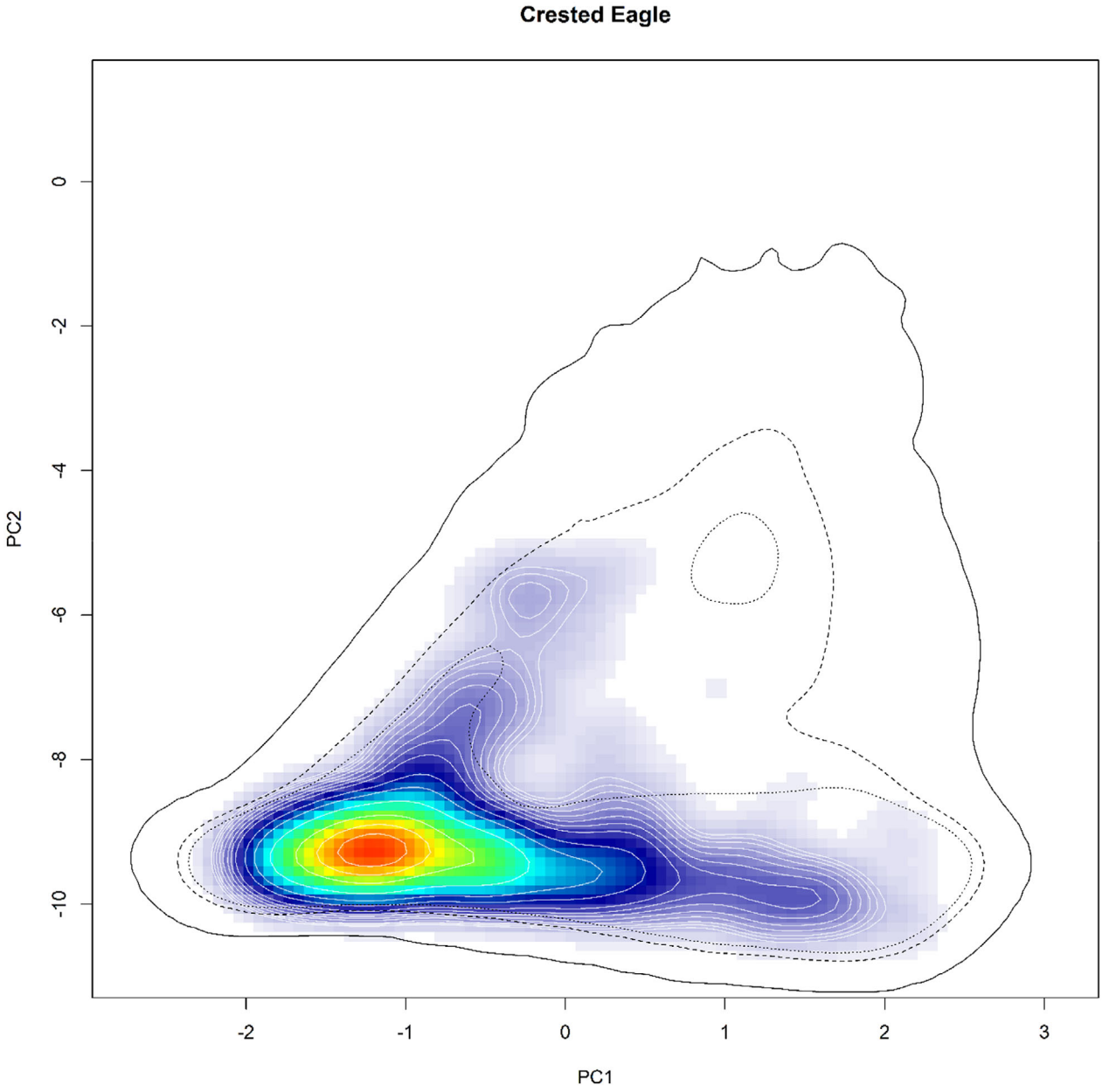

Figure 4. Distribution in environmental space for the Crested Eagle across two principal components. Red areas indicate highest environmental suitability. Filled kernel density isopleths characterize kernel density values from 0.4 (blue) to 0.99 (red). Black isopleth lines define kernel density of the corresponding environment, with black solid line = 0.1, black hashed line = 0.5 and black dotted line = 0.75.

DISCUSSION

Previous localized studies on the co-occurrence of Crested and Harpy Eagles have produced contrasting results on the level of shared environmental space (Thiollay 1989, Sanaiotti *et al.* 2015). Here, we used a continental perspective to attempt to identify environmental differences between these two eagles, knowing that factors affecting distribution in certain areas may not be generalizable to other regions within their shared range. Our predictive GLMs identified

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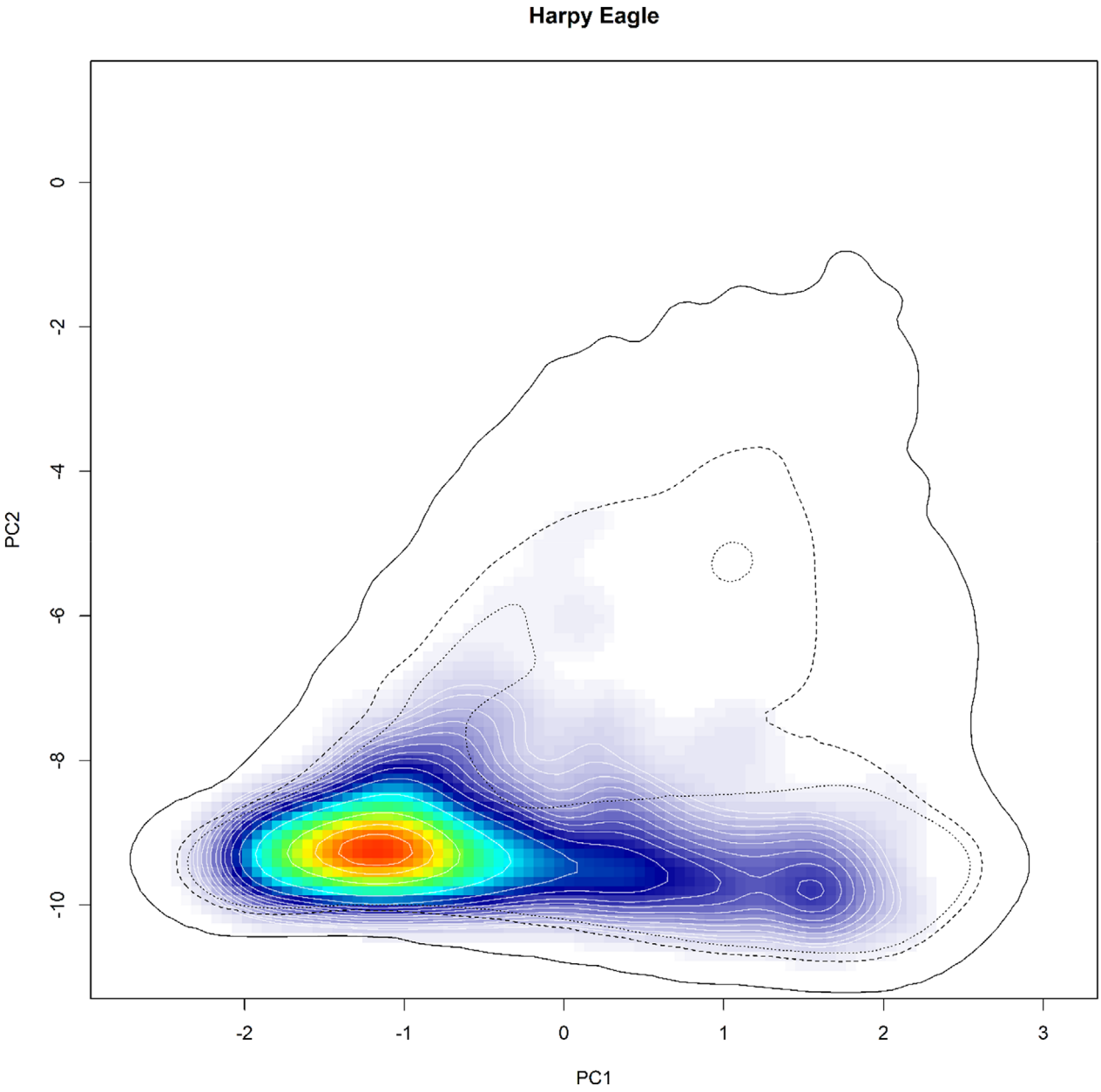

Figure 5. Distribution in environmental space for the Harpy Eagle across two principal components. Red areas indicate highest environmental suitability. Filled kernel density isopleths characterize kernel density values from 0.4 (blue) to 0.99 (red). Black isopleth lines define kernel density of the corresponding environment, with black solid line = 0.1, black hashed line = 0.5 and black dotted line = 0.75.

narrow environmental niche breadths for both eagles, despite broad niche breadth measured in geographical space. Habitat overlap in geographical space was high using GLMs, with a modest reduction in niche overlap when assessed in environmental space using GLMs and PCA-env. Both eagles shared identical environmental niches from randomization tests, with little difference in distribution across environmental space. Thus, at the continental scale the two species can coexist, presumably if there is sufficient habitat heterogeneity for both eagles to coincide when they occur in close proximity (see Tilman 2004).

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Environmental differences

All species are expected to be non-randomly distributed in environmental space and to occur within an optimal range of conditions (Hirzel *et al.* 2002). For both the Crested and Harpy Eagle, six and seven primary limiting factors, respectively, were sufficient to explain their distributions from the GLMs. Both distributions were positively associated with high canopy heterogeneity, indicating a preference for areas of highly species-rich canopy vegetation and structural complexity. High species richness and structural diversity of canopy trees may offer greater diversity of prey species (Tews *et al.* 2004, Stein *et al.* 2014) and provide attack conditions to the dietary generalist Crested Eagle. Harpy Eagles, in contrast, are more specialized in diet (Aguiar-Silva *et al.* 2014) and hunting strategy (Touchton *et al.* 2002) and may benefit from a simpler forest structure where prey detection and ambush favours the larger and presumably less agile specialist. This reliance on species-rich canopies, and thus indirectly prey species richness, supports previous calls for prioritizing protection of areas of high habitat heterogeneity (Sutton *et al.* 2022) and focusing conservation action on areas of high prey species richness (Sutton *et al.* 2023).

Both eagles were most likely to be associated with areas of abundant evergreen forest cover peaking between 60% and 80% (see Fig. 2), with only minor differences in their respective negative responses to mosaic forest cover. Further, both eagles had a broad tolerance of cultivated landcover, though highest suitability occurred in areas of < 20% cultivated landcover, similar to the findings of Miranda *et al.* (2021) for Harpy Eagle. This suggests that both eagles may struggle to adapt to habitat highly fragmented by cultivation, particularly the Harpy Eagle, which does not switch to terrestrial prey in cultivated areas, resulting in a lack of food provisioning for nestlings (Miranda et al. 2021). Likewise, the Crested Eagle may be reliant on mature forest, possibly associated with their stronger reliance on a diet of arboreal snakes and cavity-nesting arboreal birds and mammals (Whitacre *et al.* 2012, Gomes *et al.* 2021). Even so, this does not consider how this may affect breeding performance, with Harpy Eagles having lower breeding success in fragmented habitats (Miranda *et al.* 2021).

Resource overlap

Measuring the level of habitat overlap in both geographical and environmental dimensions further revealed how both eagles respond to habitat conditions at different spatial resolutions with different biological consequences. Measuring overlap in geographical space is relevant only for models solely estimating distribution. In contrast, measuring habitat overlap in environmental space will often reveal the underlying processes determining the occupation of those spaces (Warren *et al.* 2019a). Our results suggest differences between geographical and environmental space, highlighting the importance of measuring habitat overlap across geographical and environmental dimensions. Further, altering the spatial resolution had little effect on the general pattern of high habitat overlap. Importantly, both eagles had narrow niche breadth in environmental space when compared with geographical space, suggesting habitat specialization, which may facilitate geographical co-occurrence as previously reported (Sanaiotti *et al.* 2015). This follows the general trend for both eagles being generally reliant on highly speciose tropical forest (Whitacre *et al.* 2012, Vargas González *et al.* 2014, Miranda *et al.* 2019, Sutton *et al.* 2022).

Using ordination to measure species–habitat relationships directly at a coarser grain showed a similarly moderate to high habitat overlap to the fine-grain GLMs. Randomization tests showed no support for differing spatial niches, demonstrating that both eagles generally inhabit similar environmental spaces within the same geographical range. This concurs with the theory of niche conservatism, where there is an expectation for greater niche equivalence between pairs of sister-species (Wiens & Graham 2005, Warren *et al.* 2008). Niches can be conserved over long evolutionary timescales, with sister-species likely to inhabit similar, though not identical, environments (Wiens & Graham 2005). Given a multi-locus phylogeny that concluded high genetic similarity (~ 91%) between these two eagle species (Lerner & Mindell 2005), the moderate to high geographical and environmental overlap and equivalent niches supporting niche conservatism was expected. Indeed, because of this high genetic similarity, Barrowclough *et al.* (2014) suggested lumping *Harpia* and *Morphnus* together with the Papuan Eagle (*Harpyopsis novaeguineae*) into a single genus, *Harpia*.

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Our results show no support for competition restricting geographical range limits between either species, regarding vegetation heterogeneity, topography and landcover. In contrast, resource partitioning may be driven by specific diet preferences at a local scale, which are undetectable at the continental scale used here (though see Sutton *et al.* 2023). Therefore, future research should focus on habitat use at finer scales, for example testing for differences in nesting elevation, or characteristics of nest tree selection (e.g. size, structure, epiphyte cover). Harpy Eagles generally nest below 350 m asl (Vargas González & Vargas 2011, Vargas González *et al.* 2020), but Crested Eagles are known to have a wider elevational tolerance (Gomes & Sanaiotti 2015).

We recognize there are potential limitations to our approach if spatially biased occurrences (e.g. from community science data) occurred across the large geographical area of study (Beck *et al.* 2014). To address the possibility of biased sampling, we followed established methods for subsampling our occurrence datasets using spatial filters that matched the resolution of our environmental covariate rasters. This procedure still resulted in low spatial autocorrelation of individual observations at short distances (Figs S1 and S2), and larger positive model residuals in areas with more occurrences (Figs S4 and S5). Whereas the former may simply corroborate Tobler's first law of geography (Tobler, 1970), the latter reveals that the model downweights true presences in a sea of hypothesized pseudoabsences. Thus, if anything, the model underestimates the probability of detection in suitable habitat.

Many different factors can produce spatial autocorrelation (Dormann *et al.* 2007) but its presence cannot be uniquely ascribed to biased sampling. At any rate, if positional uncertainty of records were responsible for the observed autocorrelation, this has been shown to exert a negligible effect on model output (Gábor *et al.* 2023). Furthermore, spatial autocorrelation contributes the least to variation in model performance (Thibaud *et al.* 2014), in our opinion lowering the concern for its relevance as evidence of biased sampling in our study. If imperfect detection is an issue when using presence-only data, a more reliable observation method would be required to model species' distributions (Kéry *et al.* 2010). Using, for example, existing opportunistic records from community science data to infer absences in a semi-structured observation process accounting for spatial biases would probably improve model predictions (Gorleri *et al.* 2021, Johnston *et al.* 2021).

Of course, while it would be ideal to have reliable absence data, reality trumps expectations because suitable habitat is not always occupied (e.g. Hanski & Ovaskainen 2000) and animals may stray into unsuitable habitat. Moreover, coarse-grained presence–absence points on a map, no matter how reliable, cannot possibly account for the fine-grained demographic detail that may be responsible for spatial patterning (e.g. Ferrer *et al.* 2015). In the absence of large-scale systematic sampling across the vast ranges for both eagles, using readily available data is a first step in assessing habitat use for species distributed across remote and hard to survey regions (Sutton *et al.* 2021, 2022). Thus, we view our results here not as the ultimate answer but as a baseline from which to further develop hypotheses on the factors influencing range dynamics for both these eagles.

Determining overlap in habitat use between pairs of potentially competing species has long been a focus in ecology (Levins 1968, MacArthur 1972). Using logistic regression and ordination has been effective here for identifying overlap in both distribution and aspects of the habitat that can determine the nature and abundance of available resources between these two tropical forest raptors. Both the Crested and Harpy Eagle occupy equivalent environmental space within similar geographical ranges and show a high (and not significantly different) level of habitat overlap. Because both eagles share the same environmental space, coexistence is probably driven by the availability of each eagle's specific food resources. Habitat preference may be driven by where the most favourable food resources are distributed, but this assertion would need testing at local scales within their shared range. Our results highlight the importance of measuring geographical and environmental overlap using multiple grain resolutions to gain a broad understanding of the processes determining distribution for coexisting species with similar geographical ranges. Smaller, individual-scale studies of resource partitioning are necessary further to clarify the determinants of their coexistence.

We thank all individuals and organizations who contributed occurrence data to the Global Raptor Impact Network (GRIN) information system. We thank the

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AUTHOR CONTRIBUTIONS

Luke J. Sutton: Conceptualization; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **David L. Anderson:** Data curation; writing – review and editing. **Miguel Franco:** Conceptualization; formal analysis; investigation; methodology; supervision; writing – review and editing. **Felipe Bittioli R. Gomes:** Data curation; writing – review and editing. **Christopher J. W. McClure:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; supervision; writing – review and editing. **Everton B. P. Miranda:** Data curation; writing – review and editing. **Hernán Vargas:** Data curation; writing – review and editing. **Jose Vargas Gonzalez:** Data curation; writing – review and editing. **Robert Puschendorf:** Conceptualization; formal analysis; investigation; methodology; supervision; writing – review and editing.

ETHICAL NOTE

No animals were used directly in this research.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

Data Availability Statement

GRIN is an information system amalgamating multiple data sources from community science and a global network of raptor researchers, which we are unable to share publicly because of nest-site confidentiality. Data requests for the Crested Eagle locations can be made directly to Gomes and Sanaiotti (2015) and for the Harpy Eagle nest locations directly to Vargas González and Vargas (2011). Harpy Eagle occurrences from Miranda *et al.* (2019) can be downloaded from https://journals.plos.org/plosone/article?id=10.1371/journal.pone.0216323.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Multi-collinearity test using stepwise elimination Variance Inflation Factor (VIF) analysis for the GLMs.

Figure S1. Mantel correlograms showing level of spatial autocorrelation between the filtered Crested (a) and Harpy Eagle (b) occurrences and six habitat covariates using 50 distance classes (km) every 20 km over 999 permutations.

Figure S2. Mantel correlograms showing level of spatial autocorrelation from the model residuals for the Crested Eagle GLM (a) and Harpy Eagle GLM (b).

Figure S3. Monte-Carlo randomization test based on 100 random null models to test significance against the best-fit model for the Crested Eagle (a) and Harpy Eagle (b) in environmental space.

Figure S4. Geographical representation of GLM residuals from the Crested Eagle model.

Figure S5. Geographical representation of GLM residuals from the Harpy Eagle model.

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