RESEARCH PAPER

Latitudinal effects of anthropogenic factors driving raptor species richness across the American continent

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Abstract

Aim: Geographic gradients in species richness have been traditionally attributed to variation in environmental conditions. However, untangling the importance of human activities in explaining spatial patterns in raptor species richness, still remains a challenge. We evaluated the relative importance of how human impacts and ecogeographical conditions shape the latitudinal patterns of resident ($n = 140$) and migratory ($n = 35$) raptor species richness in the American continent, and analysed whether these factors differ between the Nearctic and the Neotropical regions.

Location: American Continent.

Taxon: Raptor species.

Methods: We processed BirdLife distributional data for 175 raptor species distributed in America, and a set of three ecogeographical and three human impact variables at a spatial resolution of 96.5 × 96.5 km. We applied simple, multiple, simultaneous auto-regressive models and partial regression analyses to explore the associations between ecogeographical conditions and human impacts on raptor richness.

Results: At the continental scale and the Neotropical region, global forest structure is the main driver of richness patterns for all raptors combined, and for resident and migratory species alone. In the Nearctic region, human accessibility was the best explanatory variable to understand the spatial patterns of richness regardless of the raptor group analysed.

Main conclusions: Environmental features play a leading role in determining raptor species richness. However, the independent contribution of human activities emerges as an important factor in explaining richness patterns of migratory species at the continental scale and within the Neotropical region, whereas humans become particularly important in the Nearctic region for all raptors, residents and migratory species. We show for the first time how human-related factors influence raptor species richness.

KEYWORDS

anthropogenic biomes, bird of prey, ecogeographical conditions, forest structure, human accessibility, macroecology

1 | INTRODUCTION

In recent decades, human impacts such as climate change induced by humans, chemical pollution, overharvesting and land use change, have contributed to a massive loss of biodiversity worldwide (Butchart et al., 2010; Ceballos et al., 2015). Natural vegetation losses to farming, for instance, have increased exponentially and altered the size of populations and overall diversity of wild animal and plant communities on Earth (Heino et al., 2015; Steffen et al., 2015). Management oriented to mitigate these negative effects on biodiversity should be based on sound scientific knowledge related to abiotic, biotic and human-related factors that influence species distributions.

Top predators such as raptor birds promote the presence of high biodiversity through resource facilitation, maintenance of trophic cascades, and contributing to the breakdown of animal carcasses that may otherwise spread diseases. They also provide benefits to associated species through the limitation of mesopredator populations (Ralls & Ballou, 2004). Therefore, these organisms are essential for ecosystem stability, structure and function (Peisley, Saunders, Robinson, & Luck, 2017; Sergio et al., 2008). In addition, raptors include resident and migratory species and populations. The later migrate for food and reproduction purposes and some do not fully occupy their distributional range throughout the entire year, thus functioning as conservation surrogates for different geographic regions.

Species distributions and thus geographic patterns of species richness are influenced by many different factors. Latitude, position within continents, water availability, energy resulting from primary productivity and climate imposed by topography are ecogeographical drivers of distributional patterns for different taxonomic groups (e.g. Hawkins et al., 2003; Torres-Romero & Olalla-Tárraga, 2014). During the anthropocene, human activities have dramatically modified ecosystems. As result, organisms are affected through a variety of mechanisms that result in positive or negative effects on fitness and survival, and consequently on population size and persistence. Ultimately, this process affects overall patterns of distribution of species richness (Farwell & Marzluff, 2013; Wong & Candolin, 2015).

Regarding ecogeographical conditions, the most evident global-scale trend is the decrease in raptor richness from the equator towards the poles (Diniz-Filho, de Sant'Ana, de Souza, & Rangel, 2002). In addition, within the Nearctic region, landmass increases from the equator towards the pole, and the contrary happens within the Neotropical region. Therefore, the effect of oceans, which strongly influence continental climates, is very different between the Nearctic and the Neotropical regions (Chown, Sinclair, Leinaas, & Gaston, 2004). Exposure to sunlight throughout the year also varies between these two regions. Consequently, species richness differs significantly with higher values at the Neotropical region. More specific effects have also been documented at finer scales. Canopy height has been identified as a driver of raptor richness because it is often used by these organisms for breeding and as hunting perches (Nevada-Rodríguez, Bildstein, & Hernán-Vargas, 2016; Whitacre &

Burnham, 2012), but also because canopy height determines habitat type, and greater raptor richness correlates positively with diversity of habitats (Diniz-Filho et al., 2002; Piana & Marzden, 2014). Elevation also influences raptor abundance and richness. Within different regions, for instance, it has been reported that bird species richness decreases with increasing elevation (Rangel & Diniz-Filho, 2003; Wu et al., 2013). Although some bird species are unique to low elevations, others, including birds of prey are found across broad elevational gradients (Rahbek, 1997; Wu et al., 2013). It has been reported that for the Neotropical region, when area effects are controlled for, the highest diversity of raptors occurs at mid elevations between 500 and 1,500 masl (Rahbek, 1997). The Andean region, on the other hand, which holds a wide elevation range, harbours high values of raptor abundance and richness (Diniz-Filho et al., 2002), possibly due to the habitat heterogeneity associated with this gradient. Finally plant productive energy, usually quantified through indices such as NDVI or the leaf-area index, strongly correlates positively with richness of raptors and birds in general (Hobi et al., 2017; Rangel & Diniz-Filho, 2003), most likely because plant productivity provides energy that is available for food webs (Hawkins et al., 2003; Rahbek & Graves, 2001). Overall, 85% of all raptor species use forest habitats frequently, and 46% depend completely on forests (McClure et al., 2018; Trejo, Figueroa, Ricardo, & Alvarado, 2006).

Numerous studies have documented that modern human impacts strongly influence raptor populations (e.g. García-Fernández, Calvo, Martínez-López, María-Mojica, & Martínez, 2008). Sometimes, these effects are positive such as in some Falconiformes and Strigiformes, which adapt well to altered habitats (Bird, Varland, & Negro, 1996; Cardador, Carrete, & Mañosa, 2011). However, in the vast majority of cases the effects are negative; eagles, for instance, require large areas covered by high-quality habitat with sufficient food, nesting sites, refuges and water in order to maintain viable populations (Petty, 1998). Some of the most important types of modern human impacts that may influence raptor populations, and thus raptor species richness are human footprint, human accessibility and human biomes. Human footprint refers to the amount of human infrastructure, and it may influence raptor presence because raptors are highly sensitive to degradation in highly populated areas (Kettel, Gentle, Quinn, & Yarnell, 2018; Seress & Liker, 2015). In some cases, raptors are benefited by such infrastructure. Power poles and fences, for instance, may be used as hunting perches (D'Amico et al., 2018; Prather & Messmer, 2010). Tall buildings in cities are used as substrates by some raptor species, such as the Peregrine falcon (*Falco peregrinus*, Gahbauer et al., 2015). On the other hand, negative effects of human footprint on the majority of raptors include habitat loss, the electrocution of large raptors in power lines and collision with man-made objects (D'Amico et al., 2018; Kagan, 2016). In addition, roads facilitate accessibility for poachers and illegal wildlife traders to raptor habitat. These pressures may be enough to increase extinction risk significantly, especially in the case of species that are already vulnerable, as is the case of many raptors. Human footprint also includes polluted areas where raptors suffer from poisoning and other toxic effects. Human accessibility, which describes how "remote" an area

is, and human biomes such as forestry and agricultural fields, as well as urban areas could also affect raptor species. Though some raptors adapt well to urban areas and open fields that are typical of both agricultural and cattle grazing plots, the large proportion of diurnal raptor species, especially in tropical regions, have suffered dramatically from forest loss (Bildstein, 2006; Robinson, 1994; Thiollay, 1999). In fact, land use changes to human biomes have promoted significant declines in populations of many raptor species (Thiollay, 1999).

We propose that besides the ecogeographical component, landscape attributes and human impacts are also essential drivers of macroecological (e.g. continental or global scales) patterns of raptor richness distribution. Therefore, our objectives included assessing the relative influence of modern human impact and ecogeographical conditions on geographical patterns of raptor species richness in the American continent, and determining whether these factors differ between the Nearctic and the Neotropical regions. Our study differs from previous avian investigations at the continental and global scales (see. e.g. Blackburn & Gaston, 1996; Verschuyl, Hansen, McWethy, Sallabanks, & Hutto, 2008) because we focused exclusively on raptor richness distribution and because we considered the effects of both ecogeographical conditions and modern human impact simultaneously to increase accuracy in the assessment of direction of the effects. Regarding ecogeographical conditions, we anticipated that richness would increase from the poles towards the-equator, and that on average would be higher in the Neotropical than the Nearctic region. This pattern should be further modified such that richness would increase with increasing values of canopy height and productive energy (measured through the leaf-area index). We also expected that raptor richness would tend to be highest at the 500 to 1,500 masl range, and would decrease with increasing altitude (Figure 1). Regarding modern human impact, we hypothesized that raptor richness would increase with decreasing human footprint and accessibility and that it would be lower in human biomes (Figure 1). The direction of these trends should be similar between the Nearctic and the Neotropical regions, but the magnitude of the effects should differ between these regions because richness tends to be higher at the neotropics.

2 | MATERIALS AND METHODS

2.1 | Species distribution data

In order to obtain raptor species richness information, we acquired geographic distribution maps from Birdlife International (http://www.birdlife.org, accessed November 2017). We used the following codes: extant, probably extant, and possibly extant and excluded introduced and extinct species from the analysis (see BirdLife distribution maps in http://datazone.birdlife.org/species/spcdistPOS for further details). The dataset consisted of 175 species out of which, 35 are migrants (see Appendix S1). Distribution ranges of all species were overlapped and combined to obtain a species richness map using ARCGIS 10.0. The same procedure was applied to the groups of residents and migrant species separately. This involved using a Behrmann equal-area grid
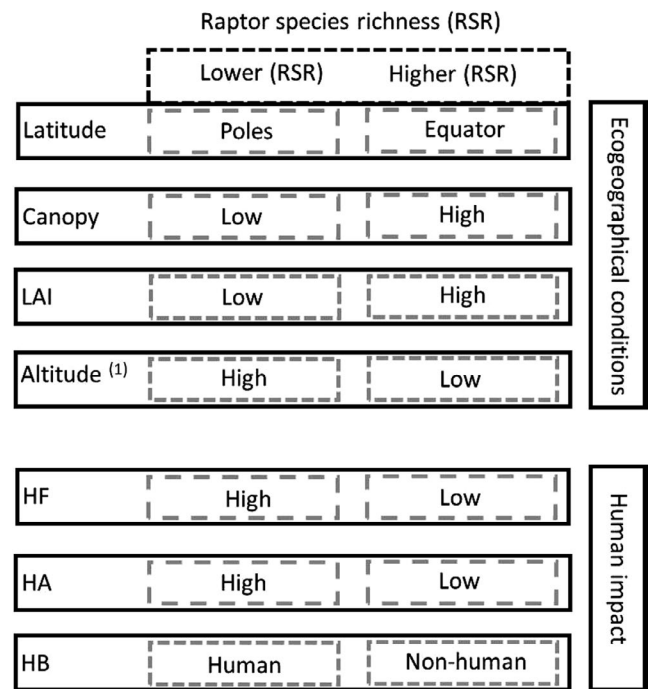
FIGURE 1 Graphical summary of predictions related to ecogeographical conditions and modern human impacts influencing raptor species richness at the American continent. Abbreviations: HA, human accessibility; HB, human biomes; HFP, human footprint; LAI, Leaf area index. [1] Expected optimal altitude is 500–1500 masl

with a cell size of 96.5 km × 96.5 km (approximately 1° at the equator). After excluding grid cells containing less than 50% of continental surface and those where species richness was zero, a total of 5,020 occupied cells were analysed, each of which was classified according to the zoogeographical regions defined by Cox (2001) to separate the Nearctic and Neotropical regions. The individual analyses by biogeographic region allowed us to account for differences in ecogeographical and human impact effects on species richness between these two large units (see introduction section).

2.2 | Environmental and human predictors of species richness

We assessed the effects of ecogeographical conditions and modern human impact on raptor richness. For this purpose, we considered three variables pertaining to ecogeographical conditions, and three related to human impact. Both sets of variables were selected based on their importance for defining distribution of biodiversity as reported by previous macroecological studies (Barros & Cintra, 2009; Hobi et al., 2017; Torres-Romero & Olalla-Tárraga, 2014). All variables were recalculated using a spatial grid of 1-degree. The predictors included in the study are described in detail below:

2.2.1 | Ecogeographical conditions

We evaluated effects of ecogeographical conditions on raptor richness based on the fact that certain landscapes may harbour higher

raptor richness (see introduction). To do this we integrated the following layers: (a) global forest structure (GFS) related to canopy height, a descriptor variable that includes proportions of different plant cover types with a 1km^2 resolution (Simard, Pinto, Fisher, & Baccini, 2011), (b) range in elevation as a measure of topography, which is often used as an estimator of habitat heterogeneity. This variable is calculated as the difference between maximum and minimum elevations using data from GTOPO30 with a resolution of 1 km^2 (available at http://www1.gsi.go.jp/geowww/globalmapgsi/gtopo30/gtopo30.html), and (c) leaf area index (LAI) as a measure of canopy foliage content. Values of LAI are strongly correlated with biophysical properties of the vegetation and with the importance of vegetation productivity (see. e.g. Hobi et al., 2017). We used LAI data sets for the period 2003–2014 with a spatial resolution of 1 km^2 (available at http://silvis.forest.wisc.edu/data/dhis/).

2.2.2 | Modern human impact

Anthropogenic impacts on raptor species were evaluated through "human footprint" (Venter et al., 2016)," human accessibility" (Nelson, 2008) and "human biomes" (Ellis, Klein Goldewijk, Siebert, Lightman, & Ramankutty, 2010). "Human footprint" integrates global records of human population density with different cumulative human pressures on the environment such as roads, nightlights, human land use and electrical power support infrastructure. This layer comes at the 1 km^2 resolution (Venter et al., 2016). "Human accessibility" includes the estimated travel time in hours via land or sea routes with a resolution of 30 arc seconds; this layer provides a measure of how isolated or "accessible" different parts of the world are from each other (Nelson, 2008). The "Human biomes" or "anthropogenic biomes" layer constitutes a measure of anthropogenic pressure in terms of land transformation and development of the terrestrial biosphere through sustained and direct human interactions with global ecosystems. It has a 5 arc minutes resolution (5' = 0.0833°) and considers activities such as agriculture, urbanization, forestry and other land uses (Ellis et al., 2010).

2.3 | Statistical analyses

We used the data pertaining to species richness in combination with ecogeographical conditions and modern human impact to assess the effects of these predictors on raptor species richness at the American continent and within the Nearctic and the Neotropical biogeographical regions applying the following statistical analyses. Initially, Pearson product-moment correlations (PPMC) were used to explore associations between richness and the predictor variables considering predictors separately (i.e. without taking into account the simultaneous effects of other variables). To control for spatial autocorrelation in PPMC, modified *t*-tests were used (Dutilleul, Clifford, Richardson, & Hemon, 1993) to calculate the unbiased estimates of significance for each correlation coefficient (results provided in Appendix S2). Secondly, relationships between predictor variables and species richness were investigated through

non-spatial ordinary least squares (OLS) models combined with partial regression analysis techniques. However, given the number of variables in our models, we calculated variance inflation factors (VIF) to detect the potential presence of collinearity in our models; VIF of <10 indicate that collinearity is not a major concern (Olalla-Tárraga, Diniz-Fiho, Bastos, & Rodríguez, 2009). We then generated multiple alternative competing models with different combinations of relevant predictor variables by using OLS models, and characterized their relative model support using the Akaike's information criterion (AIC) as well as Akaike differences (ΔAIC). As a rule of thumb we selected the best-supported models (ΔAIC ≤2) following the recommendations of Burnham and Anderson (2002). It is considered that models with such ΔAIC values have substantial support and should receive consideration in making statistical inferences. For each model, we also obtained Akaike weighting factors (*wi*) to evaluate strength of evidence and relative support to each model. We further obtained coefficients of determination (R^2) for the OLS models to evaluate their overall explanatory power. We then used standardized regression coefficients to assess the relative importance of each predictor in regression models. This second analysis allowed us to evaluate the effect of each predictor considering the simultaneous effect of other independent variables, and comparing models representing alternative combinations of such variables. Thirdly, in order to investigate the simultaneous effects of predictors, we followed Bini et al. (2009) recommendations and compared standardized regression coefficients between OLS models and simultaneous autoregressive (SAR) models to assess possible rank shifts. This is because spatial autocorrelation in OLS can present a serious type I error problem (see Legendre & Legendre, 1998) (results provided in Appendix S3). The use of SAR models reduces spatial autocorrelation under a variety of spatial pattern scenarios (Kissling & Carl, 2008), and thus, allows controlling for these effects. We conducted SAR modelling combining the data for all raptor species as well as separate analyses for two groups of species, residents and migrants alone. Finally, we conducted partial regression analyses on species richness as the response variable and using two sets of predictor variables (i.e. ecogeographical conditions and modern human impact). This analysis allowed us to explore the independent contributions of ecogeographical conditions versus modern human impact in more detail and to better explain the variation in raptor richness. Again, spatial autocorrelation may inflate the type I error rate in correlative analyses (see Legendre & Legendre, 1998). To control this bias in our models, spatial filters were used to address spatial dependence and to minimize the autocorrelation in the residuals of the final model (Griffith & Peres-Neto, 2006). The selected filters were included as predictors in the partial regression model to explore the independent contributions of predictive variables in greater detail and thus, explaining variation in species richness (see Legendre & Legendre, 1998 for a detailed description of this variation partitioning method). All statistical analyses were conducted in R 3.4.0 (R Development Core Team, 2012), using the "spdep" (Bivand et al., 2009) and "Spatial Analysis in Macroecology" (SAM 4.0: Rangel, Diniz-Filho, & Bini, 2010) packages.
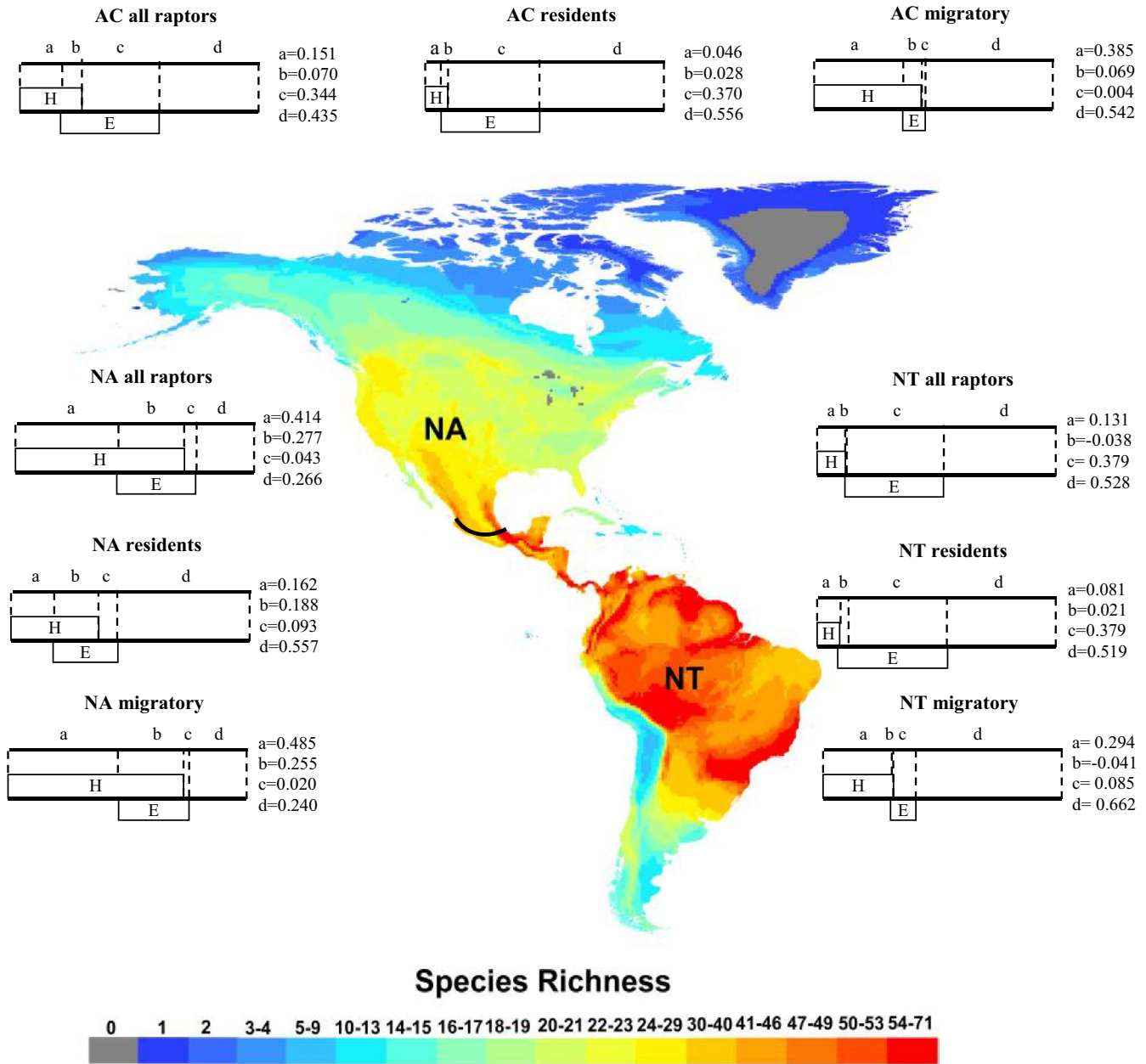
FIGURE 2 Richness patterns of raptor species in the American continent obtained by overlaying species ranges from Birdlife (2017) on a 0.5° × 0.5° grid cell system. Abbreviations are: AC, American Continent; NA, Nearctic; NT, Neotropic. Results of partial regression analyses in the American continent and biogeographical realm levels, using species richness as response variable and modern human impact (H) and ecogeographical conditions (E) as explanatory variables are shown. In each case, (a) represents the independent contribution of modern human impact, (b) shows the variation shared between modern human impact and ecogeographical conditions, (c) the independent contribution of ecogeographical conditions, and (d) is the unexplained variance

3 | RESULTS

3.1 | Latitudinal gradients of species richness

Bird of prey species richness increases from the poles towards the equator (Figure 2). In addition, within the Neotropical region, which holds higher raptor richness than the Nearctic region, the highest number of species occurred at elevations between 270 and 1,400 masl. Higher species richness, was registered in areas

of high topographic relief including the eastern and western mountain ranges in Mexico ("Sierra Madre Oriental" and "Sierra Madre Occidental"), Belize, Guatemala, Panama, the Brazilian highlands, the Guinea Plateau, the Amazon basin, the oriental slope of the Andes of Colombia, Peru and Bolivia (Figure 2). At the continental scale, based on our best multiple regression models for all raptors combined and for resident species, GFS was the most important predictor of raptor species richness, while LAI yielded secondary importance. Migrants, on the other hand, are more sensitive to

modern human impacts. Indeed, human accessibility (HA) and anthropogenic biomes (AB) were the first and second most important predictors of migratory raptor species richness. The trend directions for these two variables were opposite (Table 1). The relationship between (GFS), (LAI), (HA), (AB) and species richness patterns was further supported by Pearson-product moment correlations; these variables showed the most significant correlations with richness patterns for all raptors combined as well as for resident and migrant species alone (results provided in Appendix S2).

Within the Nearctic region, standardized regression coefficients indicated that HA negatively affects raptor richness. This last variable along with AB were the most important predictors of richness for all raptors combined, and for migrants and residents separately, while LAI and range in elevation were identified as of secondary importance with positive signs (Table 1). According to the simple regression models, HA and AB were the most important variables associated with richness patterns of all groups of raptor species (results provided in Appendix S2).

Results of standardized coefficient models for the Neotropical region identified GFS as the strongest predictor of raptor richness, while HA and AB were the second and third most important predictors for all raptors combined and for residents and migratory species separately. Range in elevation also contributed to raptor richness, but to a lesser extent with a negative sign for all raptors combined and for migratory species (Table 1). PPMC coefficients also revealed a significant association of (GFS), (HA) and (AB), and species richness for all raptors combined, as well as for residents and migratory species separately (results provided in Appendix S2).

Based on coefficients of determination (R^2), our models explained proportions of variance for the American continent in species richness ranging between 47%–73% for all raptors, 44%–48% for residents, and 33%–76% for migratory species, and received strong support as shown by wi values (Table 1). The inclusion of SAR models did not alter the sign or rank of standardized regression coefficients obtained using non-spatial OLS models and yielded quantitatively similar results for the relative importance of each predictor (Table 1). Therefore, the interpretation is not affected by the method employed (results provided in Appendix S3).

Partial regressions allowed us to explore the independent contribution of ecogeographical conditions and modern human impact variables in greater detail. These analyses confirmed the important role of ecogeographical conditions in predicting richness patterns for all raptors and for resident species in the American continent, representing 34% and 37% of variance in richness, respectively. Within the Neotropical region, ecogeographical conditions accounted for 37% of variance in richness for all raptors combined and for residents alone. However, the independent contribution of human impact increases their relative importance for migratory species in the American continent and within the Neotropical region with 38% and 29% of contribution to variance, respectively. For the Nearctic region, human variables strongly contributed to explaining richness patterns in the three status categories of top predators (e.g. all raptors accounting for 41% of variance, residents accounting for

16% of variance, and migratory species accounting for 48% of variance) (Figure 2).

4 | DISCUSSION

Our results are consistent with the original hypotheses based on previously reported high values of species richness around the equator which decrease towards the poles within the American continent (Blackburn & Gaston, 1996). We also confirmed that richness would decrease with elevation and that it would be highest approximately within the 500–1500 masl altitudinal range. The effects of the remaining variables that we investigated are significant and deserve further and more detailed discussion. Until now, the potential effect of modern human impact on bird of prey species richness at the continental scale had not been analysed. The simultaneous effects of human impact and ecogeographical conditions on raptor species richness are complex because responses vary among species due to evolutionary and ecological histories (Barnagaud et al., 2014; Violle & Jiang, 2009) and because influencing factors may have effects on different directions and at different rates simultaneously. Our results are consistent with previous reports indicating that human activities affect vertebrate diversity (Ceballos et al., 2015). Within the Nearctic region, for instance, raptors are highly responsive to modern human impacts. In this region, lower species richness correlates with higher human accessibility, and higher richness takes place in anthropogenic biomes. However, socioeconomic pressures have resulted in intense land use transformations, species invasions and soil erosion, and likely cause negative impacts on predator populations, possibly leading to extinction (Ellis et al., 2013). Land use changes frequently contribute significantly to species extinction, as in the case of the Guadalupe caracara (Bildstein, 2006). On the other hand, variation in habitat heterogeneity strongly influences the distribution of migratory species.

Within the Neotropical region, on the other hand, higher raptor richness was associated to natural, forested environments. Therefore, raptors within this biogeographic region are sensitive to deforestation. Even local forest loss due to human activities may disrupt the short and medium-term resilience of biodiversity, causing dramatic changes in species distributions and increasing extinction probabilities (Alroy, 2017). Previous studies have demonstrated the importance of the structure characteristic of pristine forests for the maintenance of flora and fauna (Gibson et al., 2011). In consistency with our results, it has been found that biodiversity values are substantially lower in all types of degraded forest habitats (reviewed in Gibson et al., 2011). For example, forest structure can affect the occurrence and abundance of owl species in the Amazon forest (Barros & Cintra, 2009). Thus, undisturbed tropical forests are truly unique, safeguard biodiversity, and must be preserved to provide refuges for animal and plant species. On the other hand, Torres-Romero and Olalla-Tárraga (2014) recently found that human impact is an important predictor of mammal richness patterns, such that zones that are most accessible to humans often have lower mammal species richness. These results

TABLE 1 Multiple-regression models explaining continental and regional patterns of raptor species richness including groups of residents and migratory species in America

Region	Assemblage level	Model #	Predictor in model (standardized regression coefficients)						ΔAIC	AIC	wi	R²
			HFP	AB	HA	LAI	RE	GFS				
American continent	All raptors	1	**0.126 (0.069)**	**0.151 (0.102)**	**−0.204 (−0.075)**	**0.212 (0.107)**	0.014 (0.047)	**0.451 (0.309)**	0	39149.576	0.506	0.565
		2	**0.124 (0.061)**	**0.155 (0.116)**	**−0.203 (−0.078)**	**0.211 (0.105)**		**0.450 (0.311)**	0.045	39149.621	0.494	0.565
	Residents	1	**0.129 (0.038)**	0.046 (0.056)	**−0.088 (−0.011)**	**0.238 (0.086)**		**0.451 (0.303)**	0	40157.148	0.667	0.443
		2	**0.131 (0.040)**	0.044 (0.050)	**−0.088 (−0.013)**	**0.239 (0.050)**	0.007 (0.029)	**0.451 (0.302)**	1.596	40158.745	0.301	0.444
	Migratory	1		**0.353 (0.226)**	**−0.384 (−0.306)**	−0.070 (−0.012)	0.023 (0.067)	**0.034 (0.035)**	0	28362.830	0.519	0.458
		2	0.020 (0.096)	**0.353 (0.180)**	**−0.384 (−0.290)**	−0.071 (−0.009)	0.023 (0.075)	**0.034 (0.043)**	1.980	28364.809	0.193	0.458
Nearctic	All raptors	1	**0.096 (0.104)**	**0.371 (0.204)**	**−0.451 (−0.286)**	**0.155 (0.099)**	**0.129 (0.156)**	0.018 (0.094)	0	17042.098	0.533	0.734
	Residents	1	**0.082 (0.058)**	**0.259 (0.195)**	**−0.238 (−0.198)**	**0.214 (0.154)**	**0.172 (0.158)**	**0.112 (0.178)**	0	13723.095	1	0.443
	Migratory	1	**0.092 (0.118)**	**0.387 (0.175)**	**−0.511 (−0.284)**	**0.104 (0.055)**	**0.089 (0.142)**	**0.035 (0.037)**	0	14757.769	1	0.760
Neotropic	All raptors	1	**0.087 (0.142)**	**0.263 (0.177)**	**−0.184 (−0.203)**		**−0.143 (−0.033)**	**0.795 (0.621)**	0	16628.541	0.687	0.471
		2	**0.088 (0.139)**	**0.264 (0.174)**	**−0.187 (−0.195)**	0.013 (0.036)	**−0.142 (−0.034)**	**0.790 (0.635)**	1.584	16630.125	0.311	0.472
	Residents	1	0.018 (0.104)	**0.241 (0.189)**	**−0.172 (−0.209)**		**−0.179 (−0.052)**	**0.776 (0.601)**	0	16279.324	0.486	0.480
		2		**0.233 (0.149)**	**−0.166 (−0.182)**		**−0.179 (−0.045)**	**0.778 (0.611)**	1.374	16280.698	0.244	0.480
	Migratory	1	**0.374 (0.264)**	**0.244 (0.204)**	**−0.171 (−0.183)**	**0.080 (0.051)**	**0.127 (0.064)**	**0.335 (0.259)**	0	9918.649	0.995	0.338

Note: Standardized regression coefficients of the six predictors are provided by non-spatial ordinary least-squares (OLS) models and (in parentheses) for spatial models generated with simultaneous autoregressive (SAR) model techniques (see materials and methods). We report OLS models ranked from best to worst fits (e.g. according to increasing AIC) and selected only the best models (e.g. ΔAIC < 2). Coefficients of determination (R²) and Akaike weights (wi) for each predictor in the models are also given. Significant values are highlighted in bold.

Abbreviations: ΔAIC, Akaike differences; AB, anthropogenic biomes; AIC, Akaike's information criterion; GFS, global forest structure; HA, human accessibility; HFP, human footprint; LAI, leaf area index; RE, range in elevation.

are consistent with our findings at the continental scale and in the Nearctic region, and for migratory species in the Neotropical region as well. Therefore, if the current trends of rapid land use change within the neotropical region continue (FAO, 2016), many raptors associated to neotropical forests may become extinct, and the distribution ranges of many others will likely decrease. Consequently, the areas harbouring high raptor species richness in Mexico, Central America and in South America (Figure 2) could decrease.

On the other hand, the contribution of ecogeographical and human conditions not considered in this study to the observed patterns may not be negligible. These variables that are difficult to measure at the scale of the current study may indeed influence to some extent the recorded pattern of distribution of richness across latitudinal gradients. Specifically, raptor species richness is likely influenced by availability of prey or nesting habitat (Love & Bird, 2000; Marti, Poole, & Bevier, 2005). Responses of raptor species to these variables may contribute to some of the variation inherent of the observed trends. Despite the shared variance between ecogeographical and human impact variables in explaining bird of prey species richness, and the potential effect of other biotic and abiotic variables that could have influenced the observed patterns, our partial regression analyses revealed the independent contribution of both predictor types. The findings that both ecogeographical factors and human impacts influence raptor species richness in the Nearctic region is similar to the effect on resident species in the neotropics, and is consistent with the notion that these habitat characteristics are crucial components of bird niches (Pianka, 1974).

Residents and migratory birds of prey were affected differently. Modern human factors (e.g. anthropogenic biomes and human accessibility) seem to constitute suitable habitat for migratory raptors in the American continent. Indeed, some raptors such as the American Kestrel, Red-tailed hawk, Swainson's Hawk, Northern Harrier and White-tailed Kite (*Falco sparverius*, *Buteo jamaicensis*, *B. swainsoni*, *Circus cyaneus*) search for food in agricultural fields during migration (Bobowski, Rolland, & Risch, 2014; Preston, 1990; Tinajero, Barragán, & Chapa-Vargas, 2017). Furthermore, some raptors such as the Peregrine falcon (*Falco peregrinus*) and the Osprey (*Pandion haliaetus*) use artificial structures (e.g. buildings and power towers) as nesting and roosting substrates (Müller, Ignatieva, Nilon, Werner, & Zipperer, 2013). Some other species that adapt well to human settlements include the Black Vulture, Turkey Vulture, Cooper's Hawk, Sharp-shinned Hawk, Mississippi Kite, Red-tailed Hawk and Barn Owl, (*Coragyps atratus*, *Cathartes aura*, *Accipiter cooperii*, *A. striatus*, *Ictinia mississippiensis*, *Buteo jamaicensis* and *Tyto alba*) (Bird et al., 1996; Rullman & Marzluff, 2014). Open habitats created by humans are frequently occupied by some raptor species (Tinajero et al., 2017), because increased visibility facilitates foraging (Bird et al., 1996). Similarly, power line towers and fences are used by some raptors as perches (Bird et al., 1996; Bobowski et al., 2014), because these substrates are ideal for some foraging strategies and hunting. In fact, prey for some raptor species may be available within human settlements and in human-modified habitats such as agricultural fields and pasturelands throughout the year, resulting in higher biomass of potential prey (Preston, 1990). These resources may not be as abundant within the original distribution of some raptor species. Therefore, those modified habitats have the potential of allowing some migratory raptors to remain in or near these sites with high food availability. These habitats may also be used as breeding territories throughout the winter (Powers, 1996).

From the conservation perspective, our results suggest that preservation of forested areas with dense, tall canopies would promote the conservation of resident raptors such as northern goshawks, red-shouldered hawks, and barred owls among other species in the Nearctic region (Bosakowski & Smith, 1997). In the Neotropics, these actions would benefit some highly specialized resident raptors such as those from the genera *Leptodon*, *Buteogallus*, *Accipiter*, *Leucopternis*, *Harpia*, *Spizaetus*, *Megasccops*, *Pulsatrix*, *Glaucidium*, *Strix* and *Micrastur*, as these organisms are associated to mature forest (Robinson, 1994; Thiollay, 1999). On the other hand, some migratory species and many other raptors that benefit from open areas where high visibility facilitates hunting may suffer less from anthropogenic impacts such as land use changes. However, even in the case of these species, nesting substrates (e.g., woodpecker holes in trees that are used both by diurnal and nocturnal raptors), cover, large territories and the presence of specific prey are necessary (Eduardo, Carvalho, & Marini, 2007; Robinson, 1994; Thiollay, 1999). Moreover, the potential effect of chemical pollution may be detrimental within these areas (Butchart et al., 2010).

Our study shows that the ecogeographical conditions measured through forest structure components at the continental scale and within the Nearctic region are good predictors of richness of all-raptor species combined and residents alone. Although forested areas in the American continent as well as in other biogeographical regions are rapidly decreasing due to urban growth and expansion of the agricultural frontier, migratory raptor richness seems to be high in urban landscapes. This type of habitat may provide food and sufficient nesting substrates for species that are adaptable to human impacts (Rullman & Marzluff, 2014). We also detected that high raptor richness occurs in areas that are less accessible to humans. This type of habitat is suitable for many raptor species because it is not highly fragmented and provides higher forest structure, and it is where hunting pressures are lower.

Finally, our findings may be useful in predicting the loss of species and changes in species distribution resulting from climate change. In terms of latitude, it has been predicted that many avian species extinctions will be uncommon (Peterson et al., 2002), but species will likely shift their distribution ranges away from the equator (Peterson et al., 2002; Thomas & Lennon, 1999). In addition, species distribution ranges are expected to shift to higher altitudes (Tingley, Monahan, Beisinger, & Moritz, 2009). Therefore, it is expected that species richness will decrease around the equator and in low elevations, especially in the Neotropical region, and species richness may increase moderately in higher latitudes and

altitudes. Consequently, range distribution of high species richness may become fragmented as many species may become restricted to higher altitudes. In combination to these changes, the dynamics of interspecific relations may change, thus promoting further changes in species distributions and further species extinctions. However, it is currently difficult to make more specific predictions related to these potential changes.

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SUPPORTING INFORMATION

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

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