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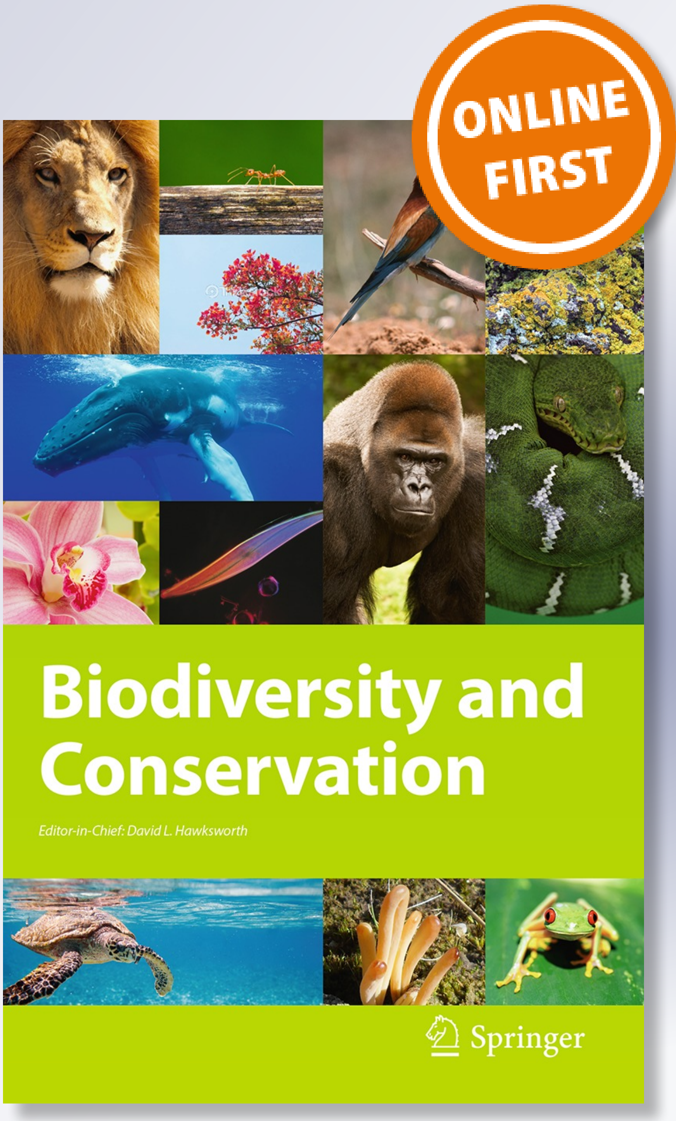

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ORIGINAL PAPER

Geographic patterns of species richness of diurnal raptors in Venezuela

Adrián Naveda-Rodríguez[1,2,3] · Keith L. Bildstein[2] · Félix Hernán Vargas[1]

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Abstract Knowledge of a species' geographic distribution is crucial to assessing its vulnerability. It is also important to know if protected areas provide effective protection for raptor species. Here, we examine the species richness (*S*) patterns, factors predicting *S* and the effectiveness of protected areas (EPA) in the conservation of diurnal raptors in Venezuela. We modeled geographic distributions (SDM) of 64 raptor species using ecological niche models. Nine climatic and seven landscape metrics were used as environmental predictors. SDM were stacked to examine *S* and predictors of *S* were investigated using regression models. This study evaluated *S* patterns in the 13 bioregions defined for Venezuela. A gap analysis was performed to evaluate the EPA in the conservation of raptor diversity. Forty species showed a continuous distribution, whereas as disjunct distributions were observed in 24 species. Species richness differed among bioregions; six pairwise compared bioregions did not show differences. Guyana Massif and the mountains of northern Venezuela had the highest species richness. Landscape features, specifically canopy height, land cover and terrain slope explained most of the species richness. Environmental heterogeneity affected the distribution of *S* and is therefore important in conservation planning for Neotropical raptors. Responses from environmental variables used to predict *S* were scale dependent; it is necessary to standardize methods/experimental design to study the biogeography of raptors. Priority-setting for the conservation of raptors

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✉ Adrián Naveda-Rodríguez
anaveda@wcs.org; adrian.naveda@gmail.com

[1] The Peregrine Fund, 5668 West Flying Hawk Lane, Boise, ID 83709, USA

[2] Acopian Center for Conservation Learning, Hawk Mountain Sanctuary, Orwigsburg, PA I17962, USA

[3] Present Address: Wildlife Conservation Society Ecuador, Av. Granados N40-53 y París, Quito, Ecuador

in Venezuela must consider restricted range species, even if they are not threatened. A new territorial ordering is urgent to improve the protection of this group of birds.

Keywords Neotropic · Northern South America · Landscape heterogeneity · Cathartiformes · Acciptriformes · Falconiformes · Strict protected areas · Species richness

Introduction

Fundamental questions in conservation biogeography require overcoming the inadequate knowledge of the geographic distribution of species (Wallacean shortfall), to accurately evaluate threats to biodiversity in a changing world (Ladle and Whittaker 2011). Mapping species richness distribution is critical to design reserves for biodiversity conservation, decision making and natural resources management (Bini et al. 2006 and reference therein; Benito et al. 2013). Factors determining species richness patterns on Earth have been explained with more than a hundred hypotheses (Palmer 1994). Climate, productivity and landscape configuration have been identified as important factors in determining species richness (Field et al. 2008; Zhao and Fang 2006), nonetheless these factors are scale dependent (Field et al. 2008; Gaston and Blackburn 2000; Rahbek 2005). Although knowledge of geographic distribution and species richness patterns are important to evaluate vulnerability of birds of prey, no systematic studies have been conducted in Venezuela to allow accurate assessment of the conservation status, or facilitate the design and implementation of effective conservation strategies.

Birds of prey require large amounts of protected habitat for successful hunting and nesting (Newton 1979; Thiollay 1989; Whitacre 2012) and for avoiding human persecution, habitat destruction and therefore population declines. Natural protected areas of Venezuela cover around 16 % (148,871 km^2) of its territory; these areas, also known as strict protected areas, are represented by 43 National Parks, 21 Natural Monuments and seven Wildlife Refuges (Rodríguez and Rojas-Suárez 1998). Although protected areas help to conserve raptors and their prey, their effectiveness in conserving biodiversity in Venezuela has been poorly studied (Sanz 2007) although such an assessment has been previously suggested for the country (Naveda-Rodriguez and Strahl 2006; Sanz 2007).

There are 68 species of diurnal raptors in Venezuela distributed in four families of the orders Cathartiformes, Accipitriformes and Falconiformes (Ascanio et al. 2012; Hilty 2003). Similar to other tropical raptor species, these species are confronting threats such as habitat loss and destruction, environmental pollution and human persecution (Bierregaard 1998; Bildstein et al. 1998). As such conservation action is required to prevent species loss and population declines. In this study we performed biogeographic analysis and evaluation of conservation status by means of geographic distribution of diurnal raptors of Venezuela. We aim to describe the patterns of species richness, to determinate the environmental variables that shape species richness patterns and to assess the effectiveness of natural protected areas in the conservation of raptors species in Venezuela.

Methods

Study area

Venezuela is in northern South America, between latitudes 00°45′–15°40′ North and longitudes 59°45′–73°25′ West. Its total land mass occupies 916,445 km^2 and its maritime territory covers around 900,000 km^2. The country borders Colombia and Brazil in the south, Colombia in the west and Guyana in the east. The Dominican Republic, Netherlands Antilles, Puerto Rico and Virgin Island (US territory) lie to the north and Martinique and Guadalupe (French territory) and Trinidad and Tobago lie to the east (MARN 2000).

Delimitations of natural regions or bioregions of Venezuela vary according to the author and definition criteria. Nonetheless, there is a general consensus in recognizing at least nine spatial units with distinct environmental and geographical characteristics (PDVSA 1992; Linares 1998). In this work we included the 13 bioregions (Fig. 1) defined by Huber and Alarcón (1988). These include: Insular, Coastal, Central Coastal Range, Eastern Coastal Range, Orinoco Delta, Maracaibo Lake Basin, Llanos, Mountain Range of Mérida, Mountain Range of Perijá, Lara-Falcón Hill System, Guayana Massif, Foothills System of Guayana Massif and Amazonia.

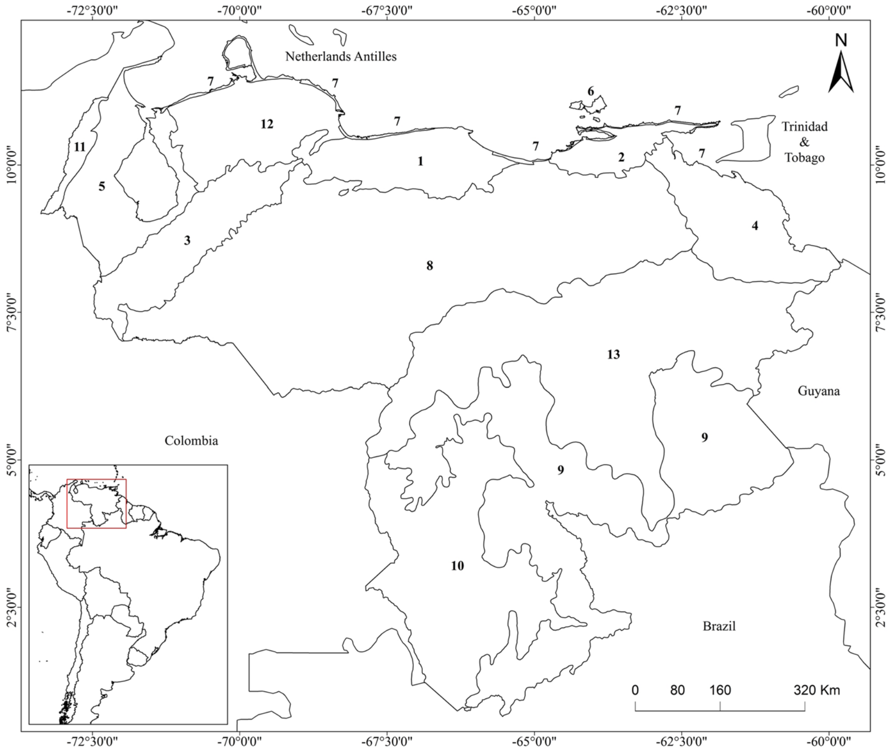

Fig. 1 Map of Venezuela showing the delimitation of the bioregions considered in this study, which are: *1* Central Coastal Range; *2* Eastern Coastal Range; *3* Mountain Range of Mérida; *4* Orinoco Delta; *5* Maracaibo Lake Basin; *6* Insular; *7* Coastal; *8* Llanos; *9* Guayana Massif; *10* Amazonia; *11* Mountain Range of Perijá; *12* Lara-Falcón Hill System; *13* Foothills System of Guayana Massif

Species data

We conducted the analyses on species of the orders Cathartiformes, Accipitriformes and Falconiformes, represented in Venezuela by 68 species of 35 genera distributed in four families (Ascanio et al. 2012). Presence records of the species were obtained from voucher specimens deposited in the Colección Ornitológica Phelps (COP), Colección de Vertebrados de la Universidad de Los Andes (CVULA), Museo de la Estación Biológica de Rancho Grande (EBRG), Museo de Biología de la Universidad del Zulia (MBLUZ), Museo de Biología de la Universidad Central de Venezuela (MBUCV), Museo de Ciencias Naturales de Caracas (MCNC), Museo de Ciencias Naturales de Guanare (MCNG) and Museo de Historia Natural La Salle (MHNLS). Additional records were obtained from eBird (Sullivan et al. 2009) and other pertinent literature. All gathered records were georeferenced, and taxonomically standardized following Remsen et al. (2013). This database which contained 9237 presence records was revised to reduce geographical and taxonomical bias resulting from input sources. The final edited database included 6,197 records of 64 species. Mississippi Kite (*Ictinia mississippiensis*), Hen Harrier (*Circus cyaneus*) and Buckley's Forest Falcon (*Micrastur buckleyi*) were not included in the analysis because recent or reliable presence records are lacking; Rufous-thighed Kite (*Harpagus diodon*) was excluded from the analysis since it is considered a vagrant species in Venezuela (Lees and Martin 2015).

Species geographic distribution

Species distributions were described by means of ecological niche modeling (Peterson 2001) using the maximum entropy method in the program MaxEnt 3.3.3 k (Phillips et al. 2006) to generate species distribution models (SDM). Twenty-six environmental predictors with spatial resolution of 1×1 km obtained from remote sensing data were used in MaxEnt. These included the 19 bioclimatic variables available in WorldClim 1.4 (Hijmans et al. 2005), digital elevation model (DEM) from shuttle radar topographic mission (Jarvis et al. 2008), slope and aspect derived from DEM, topographic roughness index calculated as the surface area ratio derived from DEM (Jenness 2013), Terra MODIS MOD44B (Townshend et al. 2011), Terra MODIS MCD12Q1 (NASA 2013), and ICESat/GLAS 3D Global Vegetation (Simard et al. 2011). In order to reduce collinearity we performed a Pearson's pairwise correlation test in SPSS 19.0 (IBM 2010) and removed one of the variables in each pair that had a pairwise correlation value higher than 0.8. The final variable set included 16 variables (Table S1). SDM were developed using MaxEnt default settings and cumulative output. Model accuracy was evaluated using Area Under the Curve (AUC) of Receiver Operator Characteristic. SDM with AUC values above 0.8 were considered indicative of good accuracy.

The models generated were reclassified into models of presence/absence (binary models) using MaxEnt's minimum training presence. Presence pixels of the binary models of each species were converted to polygons in ArcGIS 9.3 (ESRI 2008).

Species richness patterns among bioregions

In order to obtain a species-richness grid (SRG), we stacked all the binary models generated in MaxEnt using ArcGIS 9.3 in which the digital number of each pixel represents the total species number in that pixel. Differences in species richness between biogeographic regions of Venezuela were evaluated with one-way ANOVA followed by a post hoc Dunnett's T3 test performed in SPSS 19.0. Additionally, we used the results of principal components analysis of the environmental variables (Table S1) from each bioregion, used in Naveda-Rodriguez (2013) to help explain variability in species richness among bioregions. A random stratified sampling was used to select 5 % of pixels of each bioregion. A total of 53,857 pixels were used in the analysis. Selected pixels were separated by three kilometers in order to avoid the spatial autocorrelation between two contiguous pixels (Legendre 1993).

Environmental variables predicting species richness

To determine the power of environmental variables to explain species richness patterns, we performed a forward stepwise regression in SPSS 19.0. One percent (10,741) pixels of the SRG and the same variables data set used in the SDM were employed in this analysis. Minimum distance between selected pixels was five kilometers. Significance values to enter and to leave the model were set at 0.05 and 0.10, respectively.

Gap analysis

A Gap analysis (Scott et al. 1993) was performed to evaluate the effectiveness of protected areas in habitat protection, using the digital cartography of national parks, natural monuments and wildlife refuges (Rodríguez et al. 2005), defined as strict protected areas (SPA) (Rodríguez and Rojas-Suárez 1998). Using ArcGIS 9.3, we intersected the SRG data set with SPA to estimate protected species richness.

Results

Species geographic distribution

Forty species showed continuous distributions, 25 species showed disjunct distributions. Values of AUC and number of presence records of each species are shown in Table 1. Thirty-seven (24 %) species showed a wide distribution within the country and were present in more than ten bioregions while seven (5 %) species had distributions restricted to one or two bioregions (Table 1). The 64 SDMs were accurate, mean AUC values averaged 0.91 with a range from 0.82 to 0.98.

Species richness patterns among bioregions

We found significant differences ($F_{12,\ 53,844} = 1561.1$, $p = 0$) in mean species richness between the 13 bioregions; nonetheless, the post hoc Dunnett's T3 test did not exhibit significant differences when comparing nine pairwise bioregions (Table S2). Lower values (<10) of species richness were recorded in the Coastal, Insular, southwest of Amazonia and south of Guayana Massif; the greatest species richness (>40) of diurnal raptors in Venezuela was found along the mountain ranges, northeast of Amazonia and north and east of Guyana Shield (Table 1).

Table 1 Distribution patterns of diurnal raptors in 13 bioregions of Venezuela

Species	#P	AUC	1	2	3	4	5	6	7	8	9	10	11	12	13	Total bioregion/Sp.
Cathartes aura	434	0.89	×	×	×	×	×	×	×	×	×	×	×	×	×	13
Cathartes burrovianus	82	0.92	×	×	×	×	×		×	×	×	×	×	×	×	12
Cathartes melambrotus	94	0.95				×					×	×			×	4
Coragyps atratus	578	0.91	×	×	×	×	×	×	×	×	×	×	×	×	×	13
Sarcoramphus papa	116	0.88	×		×	×	×		×	×	×	×	×	×	×	11
Vultur gryphus	6	0.98			×								×			2
Pandion haliaetus	160	0.92	×	×	×	×	×	×	×	×	×	×	×	×	×	13
Elanus leucurus	134	0.94	×	×	×	×	×			×	×	×	×	×	×	11
Gampsonyx swainsonii	148	0.9	×	×	×	×	×	×	×	×	×	×	×	×	×	13
Chondrohierax uncinatus	77	0.87	×	×	×	×	×		×	×	×	×	×	×	×	12
Leptodon cayanensis	63	0.86	×	×	×	×	×		×	×	×	×	×	×	×	12
Elanoides forficatus	126	0.93	×	×	×	×	×			×	×	×	×	×	×	11
Morphnus guianensis	21	0.96	×	×			×			×	×	×	×		×	8
Harpia harpyja	25	0.91				×					×	×	×		×	5
Spizaetus tyrannus	72	0.91	×	×	×	×	×			×	×	×	×	×	×	11
Spizaetus melanoleucus	31	0.94	×		×	×					×	×	×		×	7
Spizaetus ornatus	50	0.89	×	×	×	×	×			×	×	×	×	×	×	11
Spizaetus isidori	14	0.89	×		×								×			3
Busarellus nigricollis	95	0.93	×	×		×	×		×	×	×	×	×	×	×	11
Rostrhamus sociabilis	86	0.93	×	×	×	×	×	×	×	×	×	×	×	×	×	13
Helicolestes hamatus	12	0.96		×		×	×			×	×				×	6
Harpagus bidentatus	51	0.9	×	×	×	×	×				×	×	×	×	×	10
Ictinia plumbea	178	0.89	×	×	×	×	×		×	×	×	×	×	×	×	12
Circus buffoni	17	0.94	×	×	×	×	×	×	×	×	×	×		×	×	12
Accipiter poliogaster	8	0.94			×						×	×			×	4

Table 1 continued

Species	#P	AUC	1	2	3	4	5	6	7	8	9	10	11	12	13	Total bioregion/Sp.
Accipiter superciliosus	28	0.95	×		×					×	×	×			×	6
Accipiter collaris	6	0.97			×								×			2
Accipiter striatus	63	0.96	×	×	×		×				×	×	×	×	×	9
Accipiter bicolor	38	0.84	×		×		×		×	×	×	×	×	×	×	10
Geranospiza caerulescens	89	0.91	×	×	×	×	×		×	×	×	×	×	×	×	12
Buteogallus schistaceus	7	0.98									×	×			×	3
Buteogallus anthracinus	72	0.89	×	×	×	×	×		×	×			×	×		9
Buteogallus aequinoctialis	24	0.98		×		×										2
Buteogallus meridionalis	152	0.93	×	×	×	×	×		×	×	×	×	×	×	×	12
Buteogallus urubitinga	125	0.88	×	×	×	×	×		×	×	×	×	×	×	×	12
Buteogallus solitarius	12	0.9	×	×	×						×		×		×	6
Rupornis magnirostris	468	0.86	×	×	×	×	×		×	×	×	×	×	×	×	12
Parabuteo unicinctus	44	0.94	×	×	×	×	×	×	×	×		×	×	×	×	12
Parabuteo leucorrhous	18	0.9			×								×			2
Geranoaetus albicaudatus	124	0.88	×	×	×	×	×	×	×	×	×	×	×	×	×	13
Geranoaetus melanoleucus	23	0.95			×											1
Pseudastur albicollis	59	0.92	×	×	×	×	×		×	×	×	×	×	×	×	12
Leucopternis melanops	17	0.94									×	×			×	3
Buteo nitidus	132	0.93	×	×	×	×	×		×	×	×	×	×	×	×	12
Buteo platypterus	142	0.95	×	×	×				×		×	×	×	×	×	9
Buteo albigula	7	0.93			×											1
Buteo brachyurus	80	0.93	×	×	×	×	×		×	×	×	×	×	×	×	12
Buteo swainsoni	13	0.96			×											1
Buteo albonotatus	58	0.88	×	×	×	×	×		×	×	×	×	×	×	×	12
Herpetotheres cachinnans	125	0.9	×	×	×	×	×	×	×	×	×	×	×	×	×	13

Table 1 continued

Species	#P	AUC	1	2	3	4	5	6	7	8	9	10	11	12	13	Total bioregion/Sp.
Micrastur ruficollis	67	0.91	×		×		×				×	×	×		×	7
Micrastur gilvicollis	17	0.93									×	×			×	3
Micrastur mirandollei	12	0.89									×	×			×	3
Micrastur semitorquatus	41	0.88	×	×	×	×	×		×	×	×	×	×	×	×	12
Caracara cheriway	248	0.9	×	×	×	×	×	×	×	×	×	×	×	×	×	13
Ibycter americanus	76	0.91			×	×	×			×	×	×	×	×	×	9
Daptrius ater	64	0.93		×	×	×	×			×	×	×	×		×	9
Milvago chimachima	355	0.89	×	×	×	×	×	×	×	×	×	×	×	×	×	13
Falco sparverius	350	0.9	×	×	×	×	×	×	×	×	×	×	×	×	×	13
Falco columbarius	54	0.95	×	×	×	×	×	×		×	×		×	×	×	11
Falco rufigularis	144	0.9	×	×	×	×	×		×	×	×	×	×	×	×	12
Falco deiroleucus	12	0.83									×	×			×	3
Falco femoralis	105	0.9	×	×	×	×	×	×		×	×	×	×	×	×	12
Falco peregrinus	41	0.93	×	×	×	×	×	×		×	×	×	×	×	×	12
Total species/bioregion			46	43	53	44	44	15	31	42	54	52	50	41	55	

Number of species presence records (#P), accuracy of species distribution models (AUC) and distribution of 64 species of diurnal raptors in Venezuela. Bioregions *1* Central Coastal Range, *2* Eastern Coastal Range, *3* Mountain range of Mérida, *4* Orinoco Delta, *5* Maracaibo Lake Basin, *6* Insular, *7* Coastal, *8* Llanos, *9* Guayana Massif, *10* Amazonia, *11* Mountain Range of Perijá, *12* Lara-Falcon Hill System, *13* Foothills System of Guayana Massif. Species present in ≥10 bioregions were considered as widely distributed and those present in ≤2 as restricted-ranged species

Environmental variables predicting species richness

The stepwise regression model incorporating 13 of 16 variables explained 45 % of the variation in species richness (Table S3). Forest canopy height (forhei), land cover (land), annual mean temperature (bio_1) and slope emerged as the most important predictors of species richness.

Gap analysis

The size and numbers of SPA varied among bioregions. Altogether the SPA cover 149,910 km^2, or 16.3 % of Venezuela; SPA cover a disproportionate percentage of bioregion areas (Table 2). The Foothills System of the Guyana Massif (the richest bioregion holding 56 species) is covered by SPA in only 0.9 % of its extent without SPA in the northeast where the species hotspot of the region and the country is located. Nonetheless, the Guyana Massif with 55 species is covered by SPA in 52.9 % of its extent. The area of protection in the mountain ranges averaged 22.9 %. The remaining bioregion accounts for 1.6–26.5 % of area protected.

Discussion

Species geographic distribution

This study provides information on 64 species with confirmed presence records, which represent 95 and 70 % of diurnal raptors of Venezuela and South America, respectively. The presence of Mississippi Kite and Buckleýs Forest Falcon is considered hypothetical as there are no confirmed records of these species in the country. The presence of Hen Harrier is known from only one museum record (COP 65,704) from 1903 from the Mountain Range of Mérida (Hilty 2003); it is considered a vagrant species.

Table 2 Coverage of strict protected area (SPA) in Bioregions of Venezuela

Bioregion	No. species	Area (km^2)	SPA (km^2) (%)
Insular	15	810	213 (26.2)
Coastal	31	5061	966 (19.1)
Lara-Falcon Hill System	41	44,836	731 (1.6)
Llanos	42	250,600	12,831 (5.1)
Eastern Coastal Range	43	14,070	1734 (12.3)
Orinoco Delta	44	44,623	3182 (7.1)
Maracaibo Lake Basin	44	39,164	2297 (5.9)
Central Coastal Range	46	36,194	4827 (13.3)
Mountain Range of Perijá	50	6321	2447 (38.7)
Mountain Range of Merida	53	40,626	11,009 (27.1)
Amazonia	52	100,833	20,635 (20.5)
Guyana Massif	54	165,475	87,491 (52.9)
Foothills of Guayana Massif	55	171,469	1546 (0.9)

Species richness pattern among bioregions

The distribution of species richness of diurnal raptors in Venezuela is similar to other vertebrates within the country, with highest richnesses in the mountain ranges and the Guayana Massif, and lower richnesses in the Coast and Insular regions (Aguilera et al. 2003). The species richness derived from modeling is consistent with species numbers reported by Thiollay (1996), Alvarez et al. (1996) and Jensen et al. (2005) in the central Mountain Range of Mérida, Imataca and southern Llanos, respectively, indicating a good performance of the models. As a functional group, diurnal and nocturnal (Strigiformes) raptors share an analogous pattern of distribution in species richness among bioregions of Venezuela (Naveda-Rodríguez and Torres 2015), suggesting a possible response to the same environmental variables driving species richness which could be interpreted as a convergence in patterns and processes among these two distinct taxonomic groups (Carnicer and Díaz-Delgado 2008).

We attribute the differences in species richness among bioregions to the environmental heterogeneity. At regional scale of analysis, different biomes would be represented with their own levels of species richness, therefore the highest levels of species richness occur in highly heterogeneous biomes (Rahbek 1997). Although, at a larger scale, landscape heterogeneity did not affect species richness of carnivore birds in North America (Carnicer and Díaz-Delgado 2008), Rahbek and Graves (2001) found it to be an important predictor of birds species richness in South America. Environmental heterogeneity has been described as a determinant of species diversity of Neotropical raptors at both coarse and fine-scale resolution (Jullien and Thiollay 1996; Anderson 2001; Diniz-Filho et al. 2002). The highest values of raptors species richness occurred in the mountainous regions of Venezuela (harboring 50 land cover classes, sensu Huber and Alarcón 1988) which was expected as this pattern of mountains harboring large number of species has been documented (Lomolino 2001; Rahbek and Graves 2001; Ruggiero and Hawkins 2008; Davies et al. 2008). This pattern is associated with climatic and topographic features gradients, hilly and mountainous areas are more rugged than flat areas, favoring the amplitude of climatic conditions that drives vegetation diversity, which then has strong influence on animal diversity (see Ruggiero and Hawkins 2008). Lower values of species richness in the Coastal and Insular bioregions are explained by the homogeneity of these flat regions with no more than six land cover classes (sensu Huber and Alarcón 1988). On the other hand, lower values of species richness were not expected in the southwest of Amazonia and south of Guyana Massif. We attribute this result to the lack of records from these areas used during the modeling process which yielded the non-representation of environmental variables in the models' training data.

Huber and Alarcón (1988) defined the bioregions of Venezuela based on floristic, edaphic and climatic traits, recognizing four regions with similar characteristics: the Central Coastal Range and Eastern Coastal range are considered subregions of the major Coastal Range, the same is observed with Mountain Range of Mérida and Mountain Range of Perijá which are subregions of the Venezuelan Andes. These subregions are separated by the Unare depression and Táchira depression in the Coastal Range and the Venezuelan Andes, respectively (Meier 2011; Schargel 2011) and therefore, species richness is not expected to be different among subregions. The principal component analysis of the environmental variables used in this study (Table S1) did not exhibit differences among the regions: Coastal Ranges and Foothills System of Guayana Massif; Insular and Coastal; and Orinoco Delta and Foothills System of Guayana Massif (Naveda-Rodríguez 2013). The similarities of environmental conditions among these regions, would explain the similarity in mean number of species among these bioregions. Moreover, Coastal Ranges, the Orinoco Delta, as well as Maracaibo Lake Basin and Lara Falcon Hill System show partial similarity in respect to the environmental variables values. The dissimilarities between these pair-compared bioregions are defined by the mountainous areas of Sierra de San Luis in Lara-Falcon Hill Systems and Coastal Range.

Environmental variables predicting species richness

In Venezuela, diurnal raptors species richness was linked to three landscape features (forest canopy height, land cover type and slope) and one climatic variable (mean annual temperature). Forest canopy height and land cover types were the best environmental predictors of raptor species richness. This is consistent with the hypothesis of environmental heterogeneity, which asserts that the greater the heterogeneity the greater the species richness (Houston 1979). This has been found to be an important predictor of raptor species richness at coarse spatial scales (Bellocq and Gómez-Insausti 2005; Diniz-Filho et al. 2002; Meynard et al. 2004). At fine-scale resolution, habitat heterogeneity is an important predictor of bird species richness (Böning-Gaese 1997; Anderson 2001; Lee et al. 2004; Koh et al. 2006). In Honduras, Anderson (2001) found a positive correlation between diurnal raptor species richness and habitat heterogeneity when studying this relationship at very fine-scale resolution (1:50,000).

Forest canopy is a regularly measured variable in studies of birds of prey, specifically in habitat sampling studies (Bednarz 2007; Tapia et al. 2007) because many raptors are highly dependent of forest canopy for perching, hunting and breeding. In open areas such the Venezuelan Llanos, Mader (1981) found 13 species of hawk nests, all the nests were located at different canopy heights. In the Foothills of Guayana Massif, Alvarez et al. (1996) recorded diurnal raptors perching and hunting in tree branches at the top of the canopy forest. Thiollay (1993) found low number of raptor species in open areas with few or no trees, while species number increased in forested areas and woodlots. Canopy height was found to be an important variable when describing nest-site habitat in woodland hawks in the Central Appalachians in North America (Titus and Mosher 1981). Researchers of the Maya Project observed most breeding and hunting of Neotropical raptors in the forest canopy, and forest canopy height was a determinant feature of nesting habitat (Whitacre and Burnham 2012).

Land cover classes represent spatial heterogeneity at any scale in a landscape (Pickett and Cadenasso 1995). This is associated with an increase in resource availability for an organism (e.g. food, nesting sites) therefore, a positive relation of raptors species richness to land cover types was expected. This pattern was also observed in other areas. Ellis et al. (1990) and Carrete et al. (2009) found the richest communities of raptors in mixed habitats throughout South America. Besides forest canopy, terrain slope plays an important role determining the presence of birds of prey. For example, terrain updrafts influence raptor migration pathways (Brandes and Ombalski 2004). Furthermore, slope gradients influence vegetation patterns and define hilly and mountainous regions which also effect species richness. Some raptors species have habitat preferences in stepper terrain. Tapia et al. (2004) and López-López et al. (2006) found this topographic feature as an important predictor of presence when modeling the distribution of birds of prey in Spain.

Other variables are used as measures of landscape heterogeneity (vegetation structure, Ott 2007; topographic roughness, Ruggiero and Hawkins 2008 and references therein), but they have been used alone, and depending on the scale and extent of analysis, they did not necessarily describe spatial heterogeneity. Rather than using one variable, this study used seven variables; one corresponding to land cover type, two related to vegetation structure and four to ground description, (which is more informative on landscape heterogeneity) and considered landscape features. From here, one variable of each group was identified the most important predictor of species richness. Altogether, the three landscape variables selected in the regression model constitute 73 % of the total variability explained (45 %). This supports our previous assumption on landscape heterogeneity and diurnal raptor richness in Venezuela.

Although elevation seems to have no effect on the overall raptor species richness in Venezuela, Thiollay (1996) and Meynard et al. (2004) found a negative effect of this variable on the species richness of birds of prey in northern and southern South America, respectively; we attribute this inconsistency to differences in the methodological approach, the geographical extent of the analysis, and the scale of analysis.

Mean annual temperature (bio_1, MAT) has been show to influence raptor species richness in southern South America. In Argentina, species richness increases with temperature (Bellocq and Gómez-Insausti 2005), while in Chile this relationship was negative (Meynard et al. 2004). In Venezuela, bio_1 is not correlated more strongly with species richness, explaining 9.8 % of the variability of the dependent variable. Rahbek and Graves (2001) identified MAT in only one of 10 regression models developed to explain bird species richness in South America, but it was not an important variable. We found that the inconsistences in variable responses are an artifact of experimental design (e.g. scale, geographic extent of analysis).

Macroecological studies determining environmental factors predicting species richness have been developed at different spatial scales and geographic extent, with most studies performed at scales of lower resolution and large geographic extent (>0.5° or >50 km minimum mapping unit, e.g. Cueto and Lopez de Casenave 1999; Rahbek and Graves 2001; Diniz-Filho et al. 2002; Meynard et al. 2004; Bellocq and Gómez-Insausti 2005; Ruggiero and Hawkins 2008; Ramirez and Telleria 2003; Rios-Muñoz and Navarro-Sigüenza 2012) and very few fine-scale (<0.04165° or <5 km minimum mapping unit, e.g. Böning-Gaese 1997; Lee et al. 2004; Koh et al. 2006, this study) studies. This is worth highlighting because richness patterns and environmental variable responses vary according to the scale and geographic extent, affecting conclusions on the drivers of patterns and processes and therefore decisions in conservation planning. As in other areas of South America, raptor diversity is influenced by environmental heterogeneity; however, this has been described primarily at coarse-scale resolution. Because there is a strong influence of spatial scales in variable responses, macroecologists need to standardize methods that allow for higher resolution results, including a precise definition of variables measuring environmental heterogeneity. For instance, cartographic scales for the analysis of macroecological patterns and processes could be predefined, so that biogeographers would recognize the minimum mapping scale required for studies of varying spatial extent.

Gap analysis

Our analysis leads us to confirm that the establishment of strict protected area (SPA) was not a planned activity in Venezuela. Although it is an act covered in the Forest Law and Wildlife Protection Law (República de Venezuela 1970; República Bolivariana de Venezuela 2013) the main reason for the creation of National Parks and Natural Monuments was the protection of soils and water. The richest region located south of the Orinoco River (Foothills of Guayana Massif) is the least protected—in fact it is protected in only 0.9 % of its extent. The Rio Grande area (in Imataca) holds around 42 species of diurnal raptors (Alvarez et al. 1996) and more than 40 Harpy Eagle (*Harpia harpyja*) nests (Alvarez-Cordero 1996), but this natural heritage is not protected. Instead of a SPA here, a forest reserve with serious problems of illegal logging and mining has been established.

Fortunately, the montane regions of northern Venezuela have a different situation. These mountains represent 10 % of the national territory and 20 % of their extent is protected. In spite of this, areas with high values of species richness (>41) are best represented—by chance—in the SPA system. Mountains of northern Venezuela, specifically the Coastal Range of Mérida and Central and Eastern Coastal Ranges retain the greatest number of protected areas in contrast with other bioregions of the country; but these large numbers of SPA are not well connected. A priority for bird conservation at landscape scale is the maintenance of connectivity between protected areas (Tobias et al. 2013).

Rodríguez et al. (2004) suggested that northern Venezuela should receive priority conservation attention because a number of threatened bird species inhabit the region; moreover, his analysis is skewed to species listed as threatened, excluding an important number of unthreatened but rare species. Although species rareness is often controversial due to relationships of abundance and distribution, Van Auken (1997) considers a species to be rare if it has a limited distribution. This is the case of Rufous Crab-Hawk (*Buteogallus schistaceus*), Black-Faced Hawk (*Leucopternis melanops*), Lined Forest-Falcon (*Micrastur gilvicollis*), Slaty-backed Forest-Falcon (*Micrastur mirandollei*) and Orange-breasted Falcon (*Falco deiroleucus*), with distribution restricted to the south of Venezuela.

On the other hand, areas with 31–40 species are barely covered by an SPA. The distribution of areas with that number of species matches the distribution of tropical dry forest. This ecosystem is mainly distributed in the Llanos and is considered the most threatened ecosystem in Venezuela (Fajardo et al. 2005). Only 5 % of the Llanos (Venezuela's largest bioregion) are protected, and its largest SPA provides protection for less than 50 % of diurnal raptor species in Venezuela.

Moving forward raptor conservation in Venezuela needs to be planned more methodically. Criteria used to create a natural protected area must go beyond water or soil conservation. In the same context, a new territorial ordering is urgent to improve the protection of birds of prey. Priorities for species conservation must be guided by multiple, not only threatened species or endemism; species rareness and commonness as well as a complementarity analysis will provide better results when proposing priority geographical areas for conservation.

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Compliance with ethical standards

Conflict of Interest The authors declare that they have no conflict of interest.

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