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Bird Diversity Patterns in the Nuclear Central American Highlands: A Conservation Priority in the Northern Neotropics

Luis Enrique Sánchez-Ramos[1,2], Alejandro Gordillo-Martínez[1], Claudia R. Gutiérrez-Arellano[1,3], Tania Kobelkowsky-Vidrio[1], César A. Ríos-Muñoz[1,4], and Adolfo G. Navarro-Sigüenza[1]

Abstract

The Nuclear Central American Highlands (NCAH) is a mountainous region located within a complex transition zone. Here, we analyzed the distribution patterns of 282 species of resident land birds of the NCAH. We gathered a database with records of presence of species, from which we generated realized ecological niche models using the Genetic Algorithm for Rule Set Production. These ecological niche models were used to obtain maps of each species' potential distribution and generated species richness maps that were also compared to the map of protected areas. In addition, the maps were overlaid with a 0.25° diameter hexagonal grid to generate a presence–absence matrix to create regionalizations through (a) a Parsimony Analysis of Endemism and (b) a phenogram. Results show contrasting patterns of distribution between total species richness and endemic species richness. The regionalizations show groups influenced by slope and altitude. Species composition is mainly Mesoamerican and Neotropical species. Our results offer a new view of the regional understanding of bird diversity patterns and biogeographical processes that have shaped regional richness, like the effects of the Great American Biotic Interchange that are visible in the species composition of the NCAH. We believe that these maps of both species richness and regionalization can serve as useful tools for conservation biologists and authorities in implementing strategies for the protection of natural areas in the NCAH.

Keywords

areas of endemism, Central America, avifauna, species richness, biological representativeness

Introduction

Nuclear Central America is a region located between the Isthmus of Tehuantepec and the Nicaragua Depression characterized by a combination of coastal plains and montane systems with high plateaus (Husley & López-Fernández, 2011; McKay, 2008; Vinson & Brineman, 1963). It is located in a complex transition zone that shows intermediate biological characters between North and South America, as a result of its complex geological and evolutionary history (Halffter, 1976; Sánchez-Osés & Pérez-Hernández, 2005). The region is also key for understanding the set of biogeographic events known as the Great American Biotic Interchange (GABI; Webb, 2006; Weir, Bermingham, & Schuter, 2009; Woodburne, 2010), which involved

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a series of migrations of taxa between North and South America, due to the closure of the Panama bridge and the impact of Quaternary glaciations (Woodburne, 2010). These events gave rise to the present biota of Central America (e.g., Husley & López-Fernández, 2011; Webb, 2006; Weir et al., 2009). As a result, the region is an important center of diversity and endemism for many taxa (e.g., Castoe et al., 2009; Halffter, 1978; Husley & López-Fernández, 2011; Rovito et al., 2012; Savage, 1966; Schuster & Cano, 2005; Stattersfield, Crosby, Long, & Wege, 1998).

Bird faunas of the region are also a product of those very complex historical factors, including geophysical events, migrations, invasions, speciation events, and regional extinctions (Gaston, 2000; Weir et al., 2009; Woodburne, 2010). Overall, the avifauna of Nuclear Central America is distributed in three main regions: the Atlantic slope, the Pacific slope, and the Highlands (Álvarez del Toro, 1964, 1971; T. R. Howell, 2010; Jolón-Morales, 2005; Komar, 1998). The montane systems of the region, known as the Nuclear Central American Highlands (NCAH), are often considered a biogeographical unit given the general distribution of several components of its fauna (e.g., Halffter, 1978; Morrone, 2001; Olson et al., 2001; Savage, 1966). Previous works have documented the species richness and overall distribution of birds in selected areas of the region, most of them supported by specimen records in scientific collections worldwide, like those for Chiapas (Álvarez del Toro, 1964, 1971; González-García, 1993), Guatemala (Eisermann & Avendaño, 2018; Jolón-Morales, 2005; Land, 1962, 1970), Honduras (Stone, 1932), El Salvador (Dickey & van Rossem, 1938; Komar, 1998), Nicaragua (T. R. Howell, 2010), northern Central America (Peterson, Escalona-Segura, & Griffith, 1998), and Central America as a whole (T. R. Howell, 1969; Salvin & Godman, 1879–1904). However, there is an information gap in occurrence records (specimens and observations) during the last three decades of the 20th century that has been largely attributed to regional sociopolitical conflicts that prevented field expeditions from traveling to these sites (e.g., local wars, Peterson et al., 1998). Currently, the problems persist in several areas, now related to drug trafficking (McSweeney et al., 2014) and high rates of deforestation (Redo, Grau, Aide, & Clark, 2012).

Peterson et al. (1998) also suggested that more scientific activity is needed in three major areas: inventory, systematics, and biogeographical analyses. The application of a synthetic approach to address questions regarding biogeographic and ecological patterns of bird diversity might be particularly useful for the region. Over the last few decades, this approach has been developed based on the identification of areas of endemism (areas where there is a substantial congruence in the distribution of several endemic species, Noguera-Urbano, 2017) and the analysis of relationships among them (Morrone, 2014). In particular, two methods have been recently used to identify biogeographic patterns: Parsimony Analysis of Endemicity (PAE) and the Cluster Analysis. PAE classifies areas according to the most parsimonious solution using shared species (Cracraft, 1991; Morrone, 1994; Morrone & Crisci, 1995; Rosen, 1988), which correspond to synapomorphies that define the areas of endemism (Morrone, 2014). Cluster Analysis has been used as a complementary method for biogeographic regionalization, as it recognizes groups of areas that are similar enough to be classified in the same group and identifies distinctions or similarities between groups (Legendre & Legendre, 1998). These analyses are able to display biogeographic patterns and provide biogeographic groupings that are quantitative and replicable (Kreft & Jetz, 2010).

PAE and Cluster Analysis could be performed using species' occurrence records directly; however, the relative scarcity and geographic unevenness of these records leaves many gaps (Peterson & Navarro-Sigüenza, 2016; Peterson, Navarro-Sigüenza, & Gordillo-Martínez, 2016). The use of distributional hypotheses developed through Ecological Niche Modelling (ENM) is highly valuable in this case, since gaps in information can be filled using predictive algorithms (Rojas-Soto, Alcántara-Ayala, & Navarro, 2003). Diverse ENM algorithms have been developed based on the concept of fundamental niche of Hutchinson (1957, see Peterson et al., 2011). The importance of these algorithms lies in their ability to transform the occurrence records contained in scientific collections and observational records into a synthetic understanding of the ecological conditions under which a species occurs (Peterson et al., 2011; Sánchez-Cordero, Peterson, & Escalante, 2001). One of these algorithms is the Genetic Algorithm for Rule-set Production (GARP; D. R. B. Stockwell & Noble, 1992). GARP uses a rule-set deduced from a species' occurrence records to extrapolate the ecological conditions required by a species and represent them back in geographic space (Martínez-Meyer, 2005; D. R. B. Stockwell & Noble, 1992). This method has been used in several geographic analyses of highland avifauna (e.g., Blancas-Calva, Navarro-Sigüenza, Morrone, 2010; Kobelkowsky-Vidrio, Ríos-Muñoz, & Navarro-Sigüenza, 2014; Navarro-Sigüenza & Peterson, 2004; Navarro-Sigüenza, Lira-Noriega, Peterson, Oliveras de Ita, Gordillo-Martínez, 2007), which have shown that environmental and topographic variables can influence the formation of patterns in species' distributions.

In this study, we analyzed the species richness and endemism of resident land-birds of the NCAH by developing two biogeographic regionalizations, one based on PAE and other in Cluster Analyses, in order to understand the distribution patterns of the avifauna, which has been regarded as part of the transition zone between the Nearctic and the Neotropics (Halffter, 1976). Therefore, this article aims to fill some of the information gaps about the biogeography of the fauna and provide an additional resource for identifying priority areas for conservation in the region.

Methods

The study area (Figure 1) includes the NCAH that is the surface above 1,000 m of elevation located between the Isthmus of Tehuantepec and the Nicaraguan Depression (Halffter, 1978; Morrone, 2001; Olson et al., 2001; Schuster & Cano, 2005). This region constitutes the distribution boundary for several taxa (Castoe et al., 2009; Halffter, 1978; Husley & López-Fernández, 2011; Rovito et al., 2012; Savage, 1966; Schuster & Cano, 2005; Stattersfield et al., 1998). Its vegetation consists of different kinds of temperate forests (such as pine, oak, and pine-oak), areas of subalpine vegetation, and tropical forest types like tropical rain forest and tropical dry forest (McKay, 2008; Olson et al., 2001; Rzedowski, 2006).

We selected 282 species of landbirds that are permanent residents of the NCAH (based on S. N. G. Howell & Webb, 1995; Stotz, Fitzpatrick, Parker, & Moskovits, 1996) to avoid the influence of other factors, such as seasonality or chance dispersal, on distribution patterns (Rojas-Soto et al., 2003). We used the taxonomic nomenclature of the International Ornithological Committee (IOC; Gill & Donsker, 2013). Georeferenced occurrence records for species in the region were obtained from specimens and observational records. For Mexico, we used curatorial records from the Atlas of Mexican birds (NavarroSigüenza, Peterson, & GordilloMartínez, 2002, 2003); improved in taxonomic and geographic coverage via the use of recent observational records from AVerAves (http://www.averaves.org/; Berlanga, Rodríguez, & Gómez de Silva, 2012), eBird (Sullivan, Wood, Iliff, Bonney, Fink, & Kelling, 2009), ORNIS (http://www.ornisnet.org/); and complemented with records from scientific literature (e.g., Biologia Centrali-Americana; Salvin & Godman,

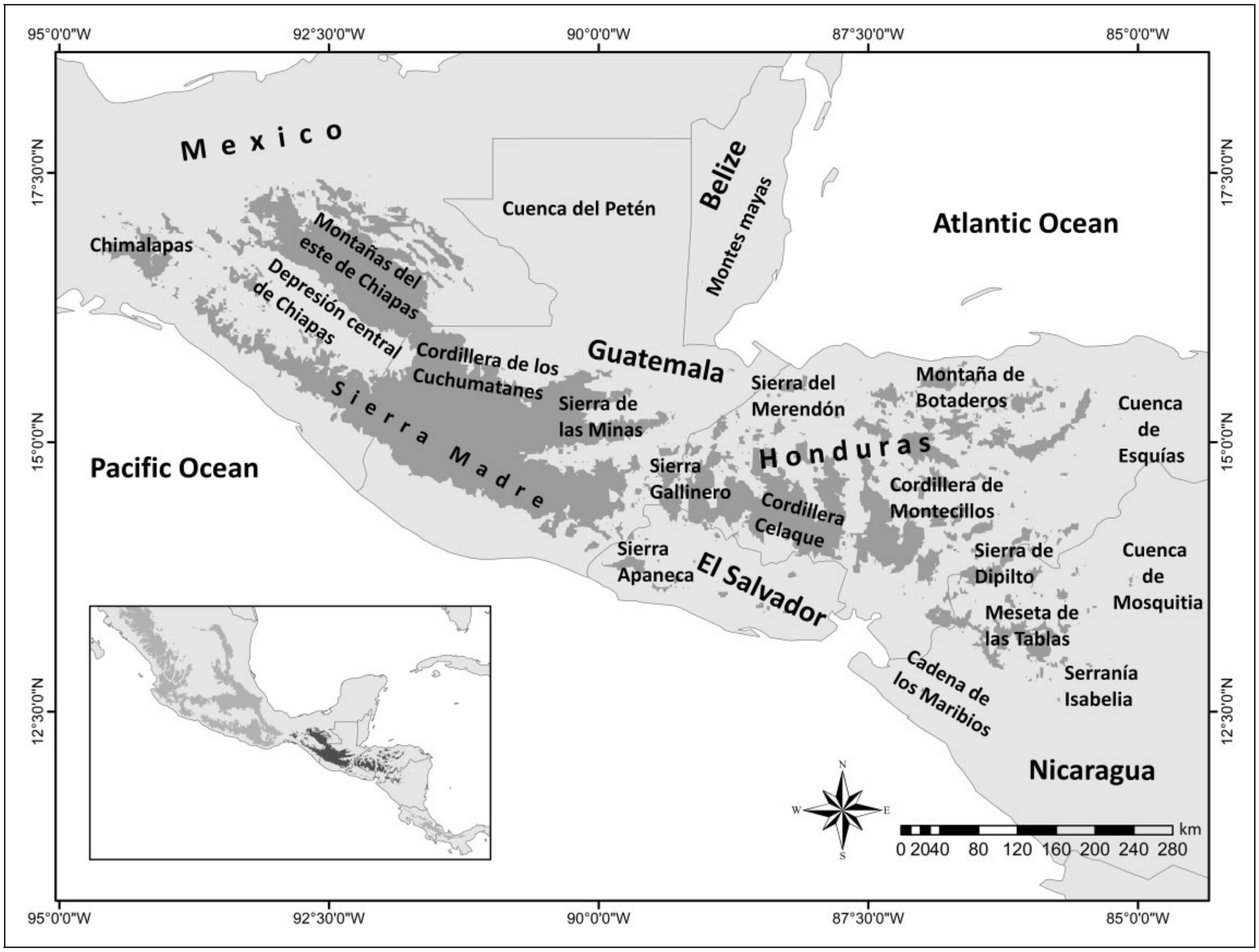

Figure 1. Montane systems in the study area (NCAH), based on McKay (2008).

1879–1904). This way, we had available a full data set of 192,674 individual records of the 282 species of landbirds, meaning 113,248 unique combinations of species/locality for developing our models.

We obtained environmental values associated with the occurrence data for each species from a set of 19 climatic variables (WorldClim Project; Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; see Supplementary Table 1) and three variables derived from topographic maps (Topographic Index, Digital Elevation Model and, Slope; Hydro1k project; http://eros.usgs.gov/#/Find_Data/-Products_and_Data_Available/gtopo30/hydro). For modeling each species, we selected a geographic area which represents the accessibility area to the taxon (region *M* sensu Soberón, 2007; Soberón & Peterson, 2005), "that represents that part of the world that is accessible to the species since its origin, or via anthropogenic or other means of introduction" (Soberón & Peterson, 2005, p. 3). This area of analysis was obtained from the World Wildlife Fund ecoregions map (Comisión para la Cooperación Ambiental, 1997; Olson et al., 2001) and obtained by the selection of regions with records of presence, under the assumption that environmental conditions are similar throughout these geographical units. To avoid the overparameterization that occurs when using all climate variables, we performed a correlation analysis of their respective environmental values for each species. We used all variables with Pearson correlation value <.85 (Elith et al., 2006; Elith, Kearney, & Phillips, 2010) and for groups of variables correlated above 0.85, only one variable per group was selected to generate the ENMs (Supplementary Table 1).

The ENMs were carried out in OpenModeller (Muñoz et al., 2009) using the GARP with Best Subsets algorithm—new openModeller implementation (Anderson et al., 2003; D. R. B. Stockwell & Noble, 1992; D. Stockwell & Peters, 1999). GARP is one of the most used algorithms in the elaboration of ENMs in the scientific literature. Although other alternative methods have been developed (e.g., Maxent; Elith et al., 2006; Phillips et al., 2006), the robustness of the method has shown that GARP is an efficient algorithm given that the bias caused by the irregularity of the biological data can be minimized (Peterson, Papes, & Eaton, 2007). We constructed 100 models for each species, using 90% of the data for training and the remaining 10% for testing, selected randomly from the full set of records. These values were adjusted according to our models as suggested by Anderson et al. (2003) and given the high number of records per species, the 10% of the data is considered sufficient for testing. Then, we selected the 20 best models (those with least omission and moderate commission) as a first selection filter, discarding those models with high omission (Anderson et al., 2003). For the evaluation of models, we applied a receiver operating characteristic curve of the internal data (Peterson et al., 2011).

To recognize the distribution patterns of bird diversity, we developed maps of total species richness, richness of endemic species, and richness of endangered species. These maps were generated in ArcMap10 (Environmental Systems Research Institute Inc., 2010) by overlapping of the maps of each species' distribution. A species was considered endemic when its distribution was restricted to only the NCAH region. The protection category for the species followed the International Union for Conservation of Nature and Natural Resources (IUCN; 2018; Least Concern, Near Threatened, Vulnerable, and Endangered), and the endemicity status was determined from the taxonomic list of the IOC (Gill & Donsker, 2013; S. N. G. Howell & Webb, 1995; Stotz et al., 1996). To understand the biogeographic affinity of resident landbirds, we grouped the species according to their geographic distribution based on the IOC (Gill & Donsker, 2013). Each of the species richness maps obtained was compared with available maps of the protected areas of Nuclear Central America using the Protected Planet map (ProtectedPlanet, https://www.protectedplanet.net/) to compare the representativeness of the different species-rich sites of highland birds in the protected areas system.

To obtain a biogeographic regionalization of the NCAH, we divided the area into 360 hexagonal cells, each 0.25° in diameter. This cell shape is better coupled to the irregularity of the NCAH physiography that the traditional square cells grid, as previously tested by Kobelkowsky-Vidrio et al. (2014). Based on the grid, we constructed a matrix of presence–absence data. Presence data were obtained from the potential distribution maps generated using ENM to avoid bias due to the lack of data points (Rojas-Soto et al., 2003). With the data matrix, we performed PAE and Cluster Analysis. PAE was performed with the Ratchet option (Nixon, 1999) in NONA (Goloboff, 1999), using Winclada (Nixon, 1999–2002). We obtained a strict consensus cladogram from the resulting most parsimonious trees. The Cluster Analysis was performed using the unweighted pair-group method with arithmetic average algorithm (Sneath & Sokal, 1973) in the *vegan* package (Oksanen et al., 2015) for R 3.4.2 (R Development Core Team, 2017), using the Jaccard similarity index to develop a phenogram. Both PAE and Cluster Analysis results are represented on a map.

Using the same cell/presence–absence matrix data, we performed an analysis of complementarity in order to identify the minimum number of hexagonal cells necessary to represent the total species richness of the region, as suggested by Margules and Sarkar (2009).

The matrix was analyzed in Excel 2007 through an iterative process (Humphries, van Wright, & Williams, 1991; Jacinto-Flores, Sánchez-González, & Almazán-Núñez, 2017; Venegas-Barrera & Manjarrez, 2011). For each hexagonal cell, we obtained the total number of species, and then the highest richness cell was chosen. Afterwards, the selected species were filtered and the cell with more complementary species was chosen. This iteration was performed successively until completing all the species. If two cells had the same number of complementary species, the one with the highest richness was chosen (Margules & Sarkar, 2009; Urquiza-Haas & Alarcón, 2011). Complementarity analysis results are depicted on a map. Finally, the complementarity was plotted in a species accumulation curve using EstimateS 9.1 (Colwell, 2013; Pineda & Moreno, 2015).

Results

The full database used was composed of 31,971 unique lat–long localities and 192,674 individuals from 282 species of resident landbirds. The combination of unique species/locality combinations yielded 113,248 records. Of the 282 species considered for this study, 26 are endemic to the NCAH and 13 species have a conservation status other than Least Concern according to IUCN (2018) (Table 1). The bird community is a combination of species with diverse biogeographic affinities; the most abundant were those associated with the Neotropical region (39.7%) and the Mesoamerican dominion (46.4%; Table 2).

Table 1. Number of Total, Endemic, and Endangered Species in Each Order.

Order	Total species	Endemic species	Endangered species
Accipitriformes	19	1	2
Apodiformes	29	5	0
Caprimulgiformes	2	0	0
Columbiformes	8	0	0
Coraciiformes	9	1	1
Cuculiformes	7	0	0
Falconiformes	5	0	0
Galliformes	11	3	4
Passeriformes	152	11	3
Piciformes	11	0	0
Psittaciformes	7	1	0
Strigiformes	13	3	1
Tinamiformes	4	0	1
Trogoniformes	5	0	1
Total	282	25	13

Patterns of Species Richness

The highest species richness (172–203 species) was found at elevations of 1,000–1,700 m, mainly along the Atlantic slope (Figure 2(a)). Overall, species richness decreased as altitude increased. Low richness values, of 74 to 90 species, were recorded in two montane systems with elevations >3,500 m—the Sierra Madre de Chiapas (Mexico and Guatemala) and the Sierra de los Cuchumatanes (Guatemala), as well as in central Honduras, where richness was low despite a lack of high elevation areas. Many isolated mountains with small areas (<10 km^2) had the lowest species richness values (30–73 species).

Despite having low overall species richness, high-elevation montane systems had the highest richness of endemic species (Figure 2(b)). The Sierra Madre de Chiapas, Cordillera de los Cuchumatanes, and the Sierra de las Minas had the highest concentration, with 18 to 21 endemic species. On the other hand, isolated high-elevation sites, such as northwestern Honduras, the volcanoes of El Salvador (except the Santa Ana Volcano), and northwest of the Central Chiapas Depression had the lowest values of endemic species richness (0–3 species). For endangered species (Figure 2(c)), the highest richness (8–11 species) was in the mountains of eastern Chiapas, the Sierra de las Minas, and the lowlands of the Sierra Madre of Chiapas and Guatemala. The lowest numbers of endangered species (0–3 species) were located in central Honduras and El Salvador.

Parsimony Analysis of Endemism

The PAE generated 360 equally parsimonious trees (length = 4,516, consistency index = 6, retention index = 84), which we used to obtain a strict consensus cladogram to develop a regionalization, which showed that the NCAH is divided into two main groups: Pacific slope and Atlantic slope (Figure 3(a)). Both groups are supported by two synapormophic species (*Nyctidromus albicollis* and *Herpetotheres cachinnans*). In the Pacific slope clade, there are four mountain systems in a successively nested pattern: center, southwestern, and eastern

Table 2. Number of Resident Landbird Species in the NCAH According to General Geographic Distribution.

General geographic affinity	Number of species
Neotropical region	112
Mesoamerican dominion	131
Nearctic and Neotroprical regions	18
Nearctic region and Mesoamerican dominion	19
Holarctic realm and Mesoamerican dominion	1
Holarctic and Holotropical realms	1

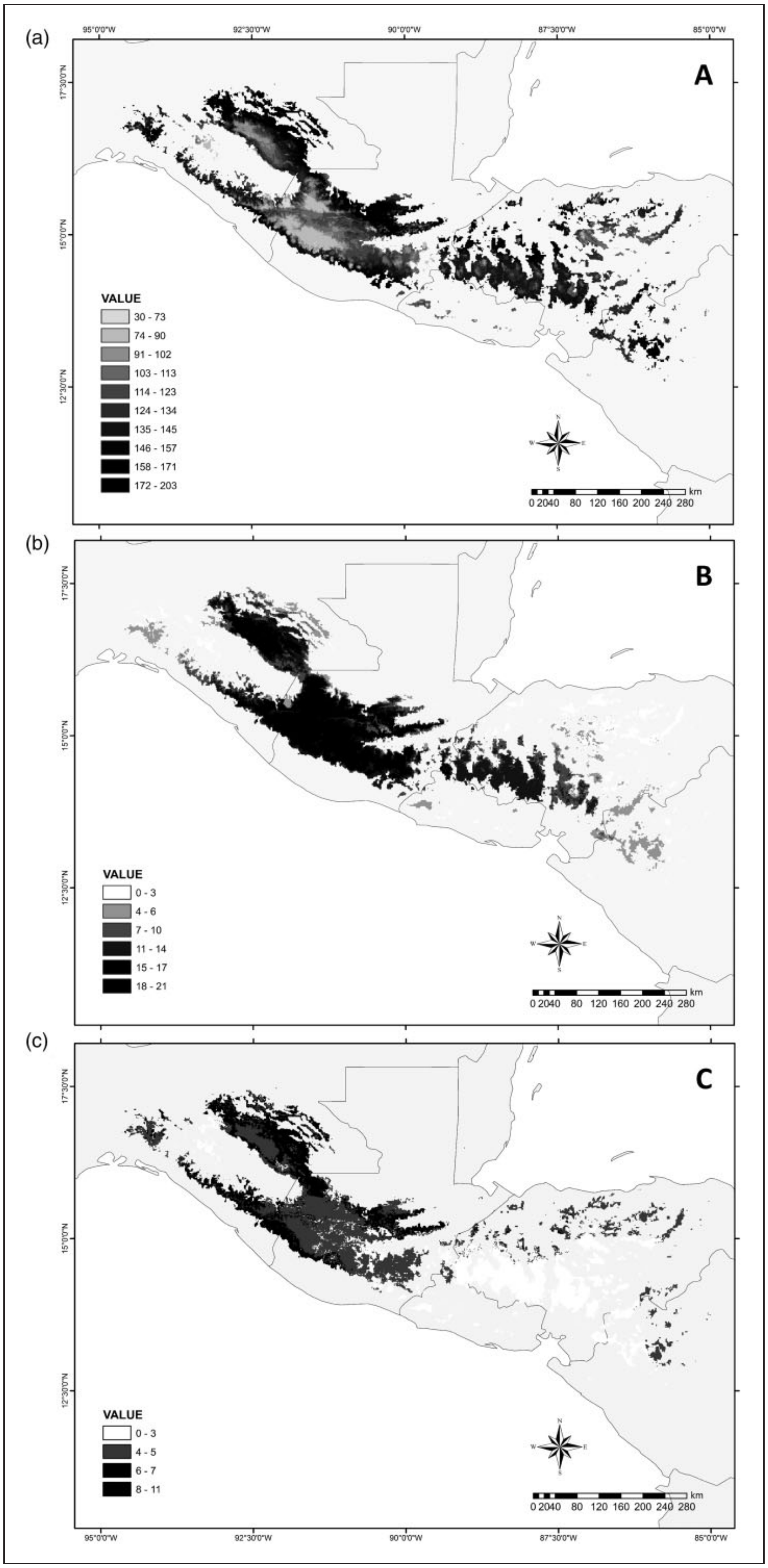

Figure 2. Maps of species richness of the resident landbirds of the NCAH. (a) Total species richness, (b) richness of endemic species, and (c) richness of endangered species.

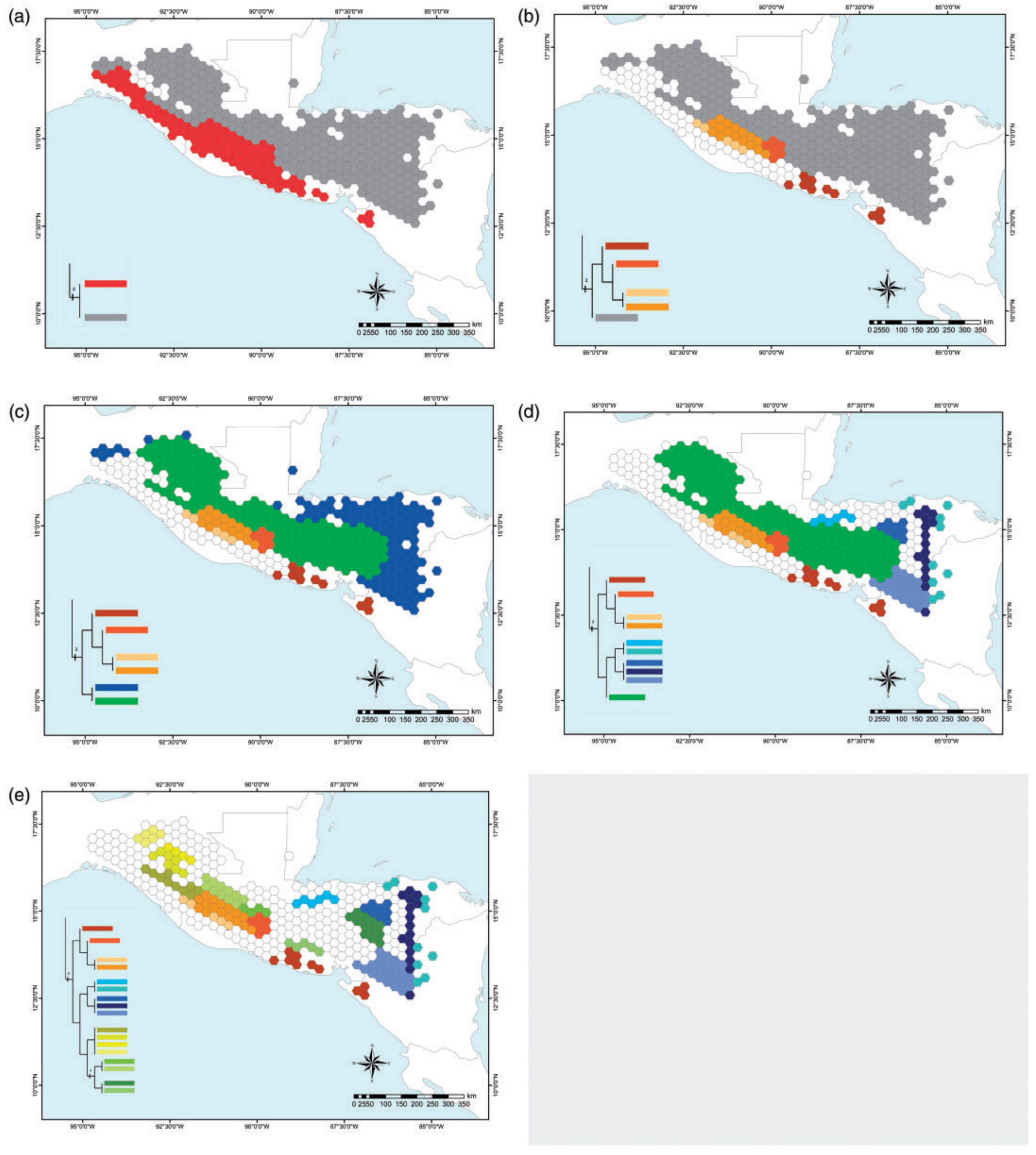

Figure 3. Cladograms and geographic representation of the Parsimony Analysis of Endemism. (a–e) Representation of the process of grouping of the regions. The altitude and both Pacific and Atlantic slopes play an important role in the formation of the areas of endemism. The colors in the cladograms represent the grids grouped in the clade.

Guatemala, and El Salvador to western Nicaragua (Figure 3(b)). The Atlantic slope clade is divided into two groups, the lower altitude and higher altitude areas (Figure 3(c)). In Figure 3(d), the cordilleras of northern and eastern Honduras are grouped with western Nicaragua. Lastly (Figure 3(e)), there is a polytomy between the mountains that surround the Central Chiapas Depression and the mountains of eastern Chiapas, while central Honduras and eastern Guatemala form a clade together with southern Honduras, supported by the synapormophic species *Atlapetes albinucha*.

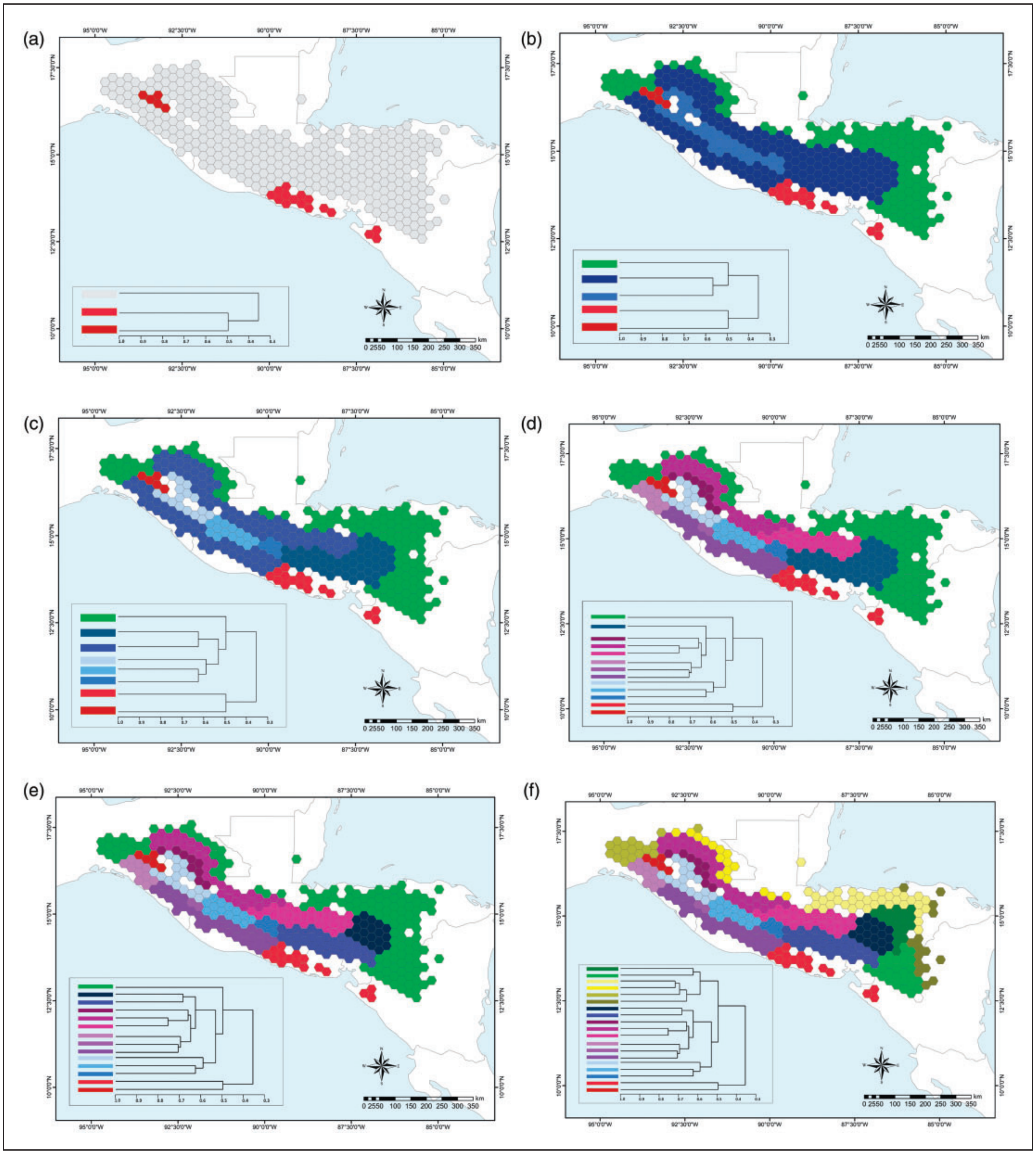

Figure 4. Phenograms and geographic representation of the Cluster Analysis. (a–f) Representation of the process of grouping of the regions. (f) The final groups are very similar to the physiographic aspect of the montane systems. The colors in the phenograms represent the grid grouped in this group.

Cluster Analysis

The regionalization based on the phenogram obtained from the Cluster Analysis showed an initial separation of two main groups (with a similitude of 0.35) that represent the driest areas of the NCAH (Figure 4(a)). Next (Figure 4(b)), the low-altitude areas of the Atlantic slope (green) diverged from all other montane systems and high plains (blue). In Figure 4(c), the central zone, characterized by having high plains, was further divided into three groups, then the montane systems diverged into two groups. In Figure 4(d), the cordilleras of the Pacific slope are divided into three groups: northwest central Chiapas, central Chiapas to western El Salvador, and the Tacaná Volcano to the Tajumulco

Volcano. On the other hand, the Atlantic slope is grouped as follows: eastern Guatemala to western Honduras, eastern Chiapas, and eastern Chiapas to central Guatemala. Subsequently, southern Honduras diverged, as shown in Figure 4(e). The phenogram concluded with the division of the Atlantic slope into six groups (Figure 4(f)).

Highland Birds and Protected Areas

Figure 5 depicts the distribution of species richness maps compared with the protected areas system. Although all the species analyzed are present in at least one protected area, the protected areas of Nuclear Central America are mainly located in tropical lowland ecosystems. A few

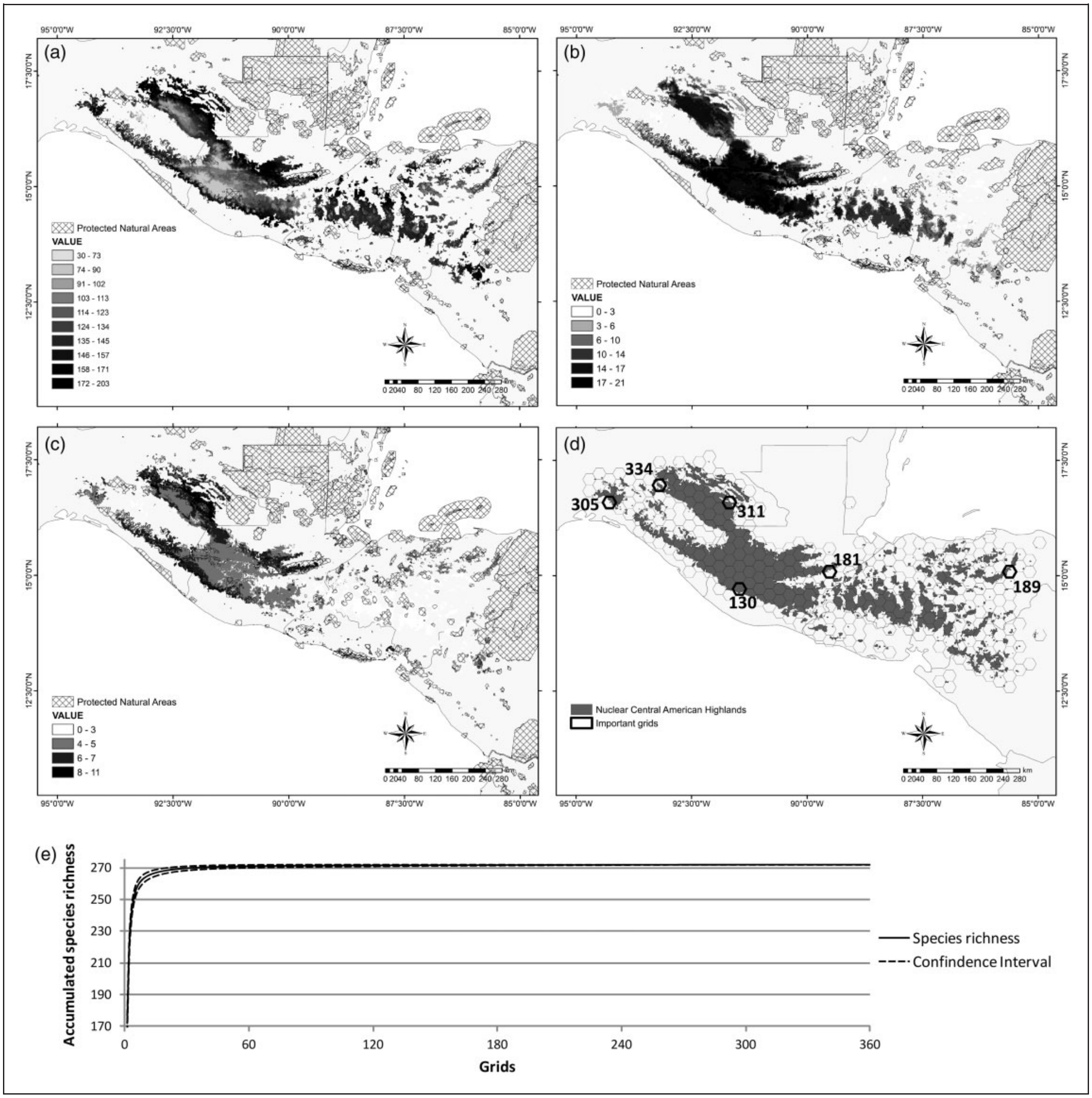

Figure 5. Protected areas on maps of species richness of the resident landbirds of NCAH and complementarity analysis. (a) Total species richness, (b) richness of endemic species, (c) richness of endangered species, (d) complementary grids, and (e) species accumulation curve of NCAH.

regions of the montane systems have a notably high number of protected areas, like the Sierra Madre de Chiapas, the Sierra de las Minas, the volcanoes of El Salvador, and the Honduras summits. However, there are large gaps along the Guatemalan high plateaus, the mountains of eastern Chiapas, the Cuchumatanes, and the lower areas of Honduras mountains. The protected areas located in the Sierra de las Minas and Sierra Madre de Chiapas are notable also for simultaneously protecting an important species richness of resident, endemic, and endangered species (Figure 5).

Complementarity Analysis

The complementarity analysis shows that 6 of the 360 cells, distributed along the whole area mainly in middle elevations (Figure 5(d)), hold the total number of 282 species of resident landbirds. All the species of conservation concern are concentrated in the two hexagonal cells with more complementary species, and the endemic species are all present in the combination of the first four hexagonal cells with more complementary species (Table 3). The species accumulation curve evidences that all the species are represented in a few hexagonal cells, reaching the asymptote with just one sixth of the cells (Figure 5(e)).

Discussion

The resident landbird fauna of the NCAH is a reflection of the geological and evolutionary history of the region that is located in a complex transition zone. The species composition is mainly conformed of species of Neotropical and Nearctic affinities that are present there as a result of multiple dispersal and vicariance events (Halffter, 1976; Rovito et al., 2012; Sánchez-Osés & Pérez Hernández, 2005; Stattersfield et al., 1998; Webb, 2006; Weir et al., 2009). However, most of the species have affinity to the Neotropical region and especially the Mesoamerican domain. The region also holds a number of species of Neotropical migrants with affinity to the Nearctic region, which constitute an important component of the bird diversity (Navarro-Sigüenza et al., 2014), although they were not considered in our analyses.

Patterns of Species Richness and Endemism

The highest concentration of species richness is located in middle elevations, between 1,000 and 1,700 m, where tropical and temperate ecosystems coexist (Mid-domain effect; Colwell & Hurtt, 1994; Colwell & Less, 2000; Colwell et al., 2004; Zapata, Gaston, & Chown, 2005). This area includes the cloud forest and its great biodiversity (Gual-Díaz & Rendón-Correa, 2014; Rzedowski, 2006). The high species richness found on the Atlantic slope is an extension of a pattern that starts in eastern Mexico south to South America, which is an effect of the great diversity of Neotropical species present in south-eastern Mexico (Navarro-Sigüenza et al., 2014).

Our data also show a difference of 173 species between the sites with the lowest and those with the highest species richness. The low species richness found on the small isolated mountains may be due to ecological differentiation from the other montane systems caused by the Massenerhebung effect (Flenley, 1995), in combination with geographical barriers such as valleys and depressions which cause abrupt changes in humidity and temperature (Lim, Rahman, Lim, Moyle, & Sheldon, 2011; Robin, Vishnudas, Gupta, & Ramakrishnan, 2015). These phenomena shape variation in humidity, influencing ecological factors important for birds, such as altitudinal distribution of vegetation and structure among different types of mountains (Bruijnzeel et al., 1993; Terborgh, 1977).

The decrease in species richness at higher altitudes corresponds to a general pattern that has been documented in many taxa (Campbell & Vannini, 1989; Schuster & Cano, 2005; Terborgh, 1977). In the case of birds, the gradual decrease in the biodiversity from lowlands to summits corresponds with the simplification of the vegetation structure and the reduction of available resources (e.g., food; Terborgh, 1977). However, there are exceptions to this overall pattern in individual

Table 3. Number of Complementary Species per Grid of the Total Species Richness, Richness of Endemic Species and Richness of Endangered Species.

Grid number	Complementary species	Accumulated species richness	Percentage	Endangered species	Accumulated species richness	Percentage	Endemic species	Accumulated species richness	Percentage
181	247	247	87.6	10	10	76.9	17	17	65.4
334	23	270	95.7	3	13	100	1	18	69.2
130	7	277	98.2	0	13	100	7	25	96.2
189	3	280	99.3	0	13	100	1	26	100
311	1	281	99.6	0	13	100	0	26	100
305	1	282	100	0	13	100	0	26	100

taxa; for example, our results show that the resident species of the families Emberizidae, Corvidae, Fringillidae, and Turdidae have higher species richness at higher altitudes (Stotz et al., 1996).

The distribution of endemic species richness occurs in a pattern that is opposite to the distribution of total species richness. The highest concentration of endemic species is found in the highest areas of Guatemala and southern Chiapas, and the values decline as altitude decreases. The high endemic species richness in the Sierra Madre de Chiapas, the Cordillera de los Cuchumatanes, and the Sierra de las Minas is likely a consequence of isolation due to the presence of large mountain chains surrounded by plains (Lim et al., 2011; Robin et al., 2015). In these areas, speciation is the product of multiple vicariant events (Rovito et al., 2012). High geological activity created mountains and plains, such as the Motagua fault, the Isthmus of Tehuantepec, and the Nicaraguan Depression, which eventually served as biogeographical barriers to biotic dispersal (Castoe et al., 2009; Husley & López-Fernández, 2011; Rovito et al., 2012). These biogeographical barriers also played an important role in the dynamics of species formation in the NCAH, as has been evidenced in birds and other taxa, such as pit vipers (Crotalinae; Castoe et al., 2009), freshwater fishes (Husley & López-Fernández, 2011), and salamanders (Rovito et al., 2012). Sánchez-González, Morrone, and Navarro-Sigüenza (2008) suggested that the high number of endemic species is evidence of long isolation of the region and asynchronous colonizations. On the other hand, Weir et al. (2009) mentioned that geological dynamics at different times during the formation of Central America (GABI) also allowed the interchange of avifaunas that had been previously isolated in North and South America.

The number of bird endemics in the NCAH led to its recognition as an Endemic Bird Area, in addition to its biological importance in some other aspects like taxonomic diversity (Stattersfield et al., 1998). We found slight discrepancies in the number of endemic species. For example, BirdLife International records only 20 endemic species (BirdLife International, 2015; http://www.birdlife.org/) compared to the 26 reported in this article. This might be the result of using different taxonomic approaches; for instance, the approach used here (following Gill & Donsker, 2013) recognizes more species because it considers evolutionary allopatric units to be separate species where other traditional species concepts would recognize only one species (see Navarro-Sigüenza & Peterson, 2004; Peterson & Navarro-Sigüenza, 2009) that have proved to give a finer resolution to biogeographic (Bertelli et al., 2017) and conservation analyses (Peterson & Navarro, 1999). Despite these differences, the general patterns of altitudinal and regional variation of species richness and endemism, as they represent different species assemblages, have implications in the understanding of the biogeography of the region and especially in the conservation perspective, given that conservation not only involves the care of areas with pristine vegetation and high species richness, but also represent biotic interactions and evolutionary processes (Blois, Zarnetzke, Fitzpatrick, & Finnegan, 2013; Fjeldsa, 1994; Margules & Sarkar, 2009).

Regionalization of Nuclear Central American Highlands

PAE suggests a complex pattern of biogeographic structuring resulting also from a complex history, also giving avifaunistic identity to each of the groupings formed in the analysis. PAE showed that the NCAH is divided into two main clades—the Pacific slope and the Atlantic slope. This pattern of distribution is largely influenced by the presence of species that are mostly associated with lowlands that are at the upper limits of their altitudinal range in the region. These species are found mainly along the tropical lowlands of the Gulf of Mexico, Yucatan Peninsula, lowlands of the Caribbean coast, the lower parts of the NCAH, and some along the Pacific lowlands of the region. Unlike the lowland species, the distribution of the highland-associated species does not strictly follow the pattern associated with slopes. Rather, some of these species, like those associated with less-humid vegetation such as drier pine and oak forests, are distributed either only in the NCAH or along both slopes of the mountain chains of Mesoamerica. Species associated with more humid highland forests, such as cloud forests, also show a particular pattern in the NCAH. Sánchez-González et al. (2008) analyzed the biogeography of the avifauna of the Neotropical cloud forests and obtained a clade conformed of cloud forests from eastern Mexico to north-central Nicaragua. This is interesting because bird communities of cloud forests that grouped the NCAH with eastern Mexico also have endemic species that give biogeographical identity to the NCAH. Another example includes the volcanoes of El Salvador and Cadena de los Maribios that are characterized by being isolated and surrounded by lowlands and dry tropical forests. In this case, the regionalization of birds of dry tropical forests by Ríos-Muñoz and Navarro-Sigüenza (2012), this mountainous region forms a clade called Inner Central America.

The areas of endemism obtained here partially coincide with those suggested by Schuster, Cano, and Cardona (2000) using beetles (Coleoptera, Passalidae). The coinciding areas are located in the Sierra Madre, eastern Chiapas mountains, Cordillera de los

Cuchumatanes, Sierra de las Minas, Sierra del Merendón, and Sierra Gallinero-Cordillera Celaque. However, our results suggest other areas of endemism in the volcanoes of El Salvador-Cordillera de los Maribios, Cordillera de Montecillos, great volcanoes of Sierra Madre, Sierra de Dipilto-Meseta de las Tablas, and Cuenca de Esquías-Cuenca de Mosquitia. In the same group of beetles, Schuster and Cano (2005) found that altitudinal distribution does not correspond with clade formation, surely due to the Massenerhebung effect (Flenley, 1995). Our data suggest the same pattern overall, in the border of the NCAH region both along the Pacific and Atlantic slopes. This can be attributed to the different elevation and isolation of the mountains but also to the presence of lowland species that arrive to the highlands along both slopes.

On the other hand, regions formed by the Cluster Analysis are congruent with the overall physiography of the montane systems. First, the volcanoes of El Salvador, Cadena de los Maribios, and part of the Central Chiapas Depression are grouped, characterized by being the most isolated and driest areas of the NCAH. Possibly, their grouping is a consequence of the presence of species that are mainly distributed in the tropical dry forest. Ríos-Muñoz and Navarro-Sigüenza (2012) presented two groupings that are similar to the previous areas, although these do not form a monophyletic group. The next group corresponds to the areas bordering the Atlantic slope, that at some sites coincide with the regions of highest species richness. This grouping is influenced by species shared among the lowlands of the Atlantic slope and the lowest elevations of the NCAH. The distribution of these (typically lowland) species only in the lowest altitudes of the NCAH generates greater similarity among sites with lower altitudes than between adjacent sites. This influence allows, for example, Monte Victoria (Belize) to be grouped with Sierra Merendón and Montaña Botaderos, despite these sites are geographically isolated from each other.

The effects of both geological and climatic changes, adaptation processes, continuous dispersion, biotic interactions, altitude, and biogeographical barriers have shaped the bird community of the NCAH (Chapin & Körner, 1996; Körner, 2004; Lim et al., 2011; Robin et al., 2015). It is noticeable that many groupings coincide among the PAE (Figure 3) and the Cluster Analysis (Figure 4), such as the volcanoes of El Salvador and Cadena de los Maribios (Nicaragua), Meseta de las Tablas and Sierra Dipilto (Nicaragua), Cuenca de Esquías and Mosquitia (Nicaragua), Cordillera de los Montecillos (Honduras), Sierra del Merendón (Honduras), Tacaná and Tajumulco volcanoes (Guatemala), Guatemalan high plains, and central Chiapas (México). Other groupings only coincide partially, such as Sierra Gallinero (Honduras), Cordillera de los Cuchumatanes, and Sierra de las Minas (Guatemala), and the volcanoes of central Guatemala (see Figure 1). Only three regions do not coincide: the western central Honduras, western Chiapas, and north-eastern Chiapas.

The patterns of distribution here described follow some general patterns outlined in previous works, but our results now provide a more detailed figure of such regions having unique combinations of bird species: the Atlantic slope, the Pacific slope, and the Highlands (Álvarez del Toro, 1964, 1971; T. R. Howell, 2010; Jolón-Morales, 2005; Komar, 1998). Moreover, regionalization presented herein partially coincides with that of Schuster et al. (2000), improved by the finding of additional areas of endemism. Thus, our study adds biogeographic data on the avifauna that were scarce (Peterson et al., 1998), improving the framework on which both further research and conservation decisions can be designed.

Implications for Conservation

The highest concentration of endangered species coincides with sites where the total species richness is also high. The endangered endemics *Oreophasis derbianus* and *Tangara cabanisi* (EN; IUCN, 2018) are restricted to cloud forest. According to this category, habitat loss or change has a negative impact on species population size. There are five vulnerable species (VU; IUCN, 2018) that face habitat or population decrease; these species are the regional endemics *Penelopina nigra, Megascops barbarus*, and *Cardellina versicolor*, as well as the more widespread *Crax rubra* and *Electron carinatum*. Also, six species are categorized as Near Threatened (NT; IUCN, 2018), at risk because they are particularly sensitive to habitat loss due to their ecological specialization and therefore restricted distribution, like *Xenotriccus callizonus* and *Pharomachrus mocinno* (Dayer, 2010; S. N. G. Howell & Webb, 1995). On the other hand, other species listed have ampler ranges: *Colinus virginianus* is widely distributed in lowlands and North America, and *Tinamus major*, *Harpyhaliaetus solitaries*, and *Spizaetus ornatus* are distributed largely in the lowlands and South America.

The function of conservation areas is to protect samples of biota so that evolution may act on them in the future; for that reason, we should aim to have the highest representativeness of species possible in protected areas (Margules & Sarkar, 2009; Whittaker et al., 2005). Among the areas protected in the NCAH, those that stand out as important sites for regional avifauna are located in Sierra de las Minas and Sierra Madre (Chiapas and Guatemala). These areas protect a high richness of resident species, endemic species, and endangered species. However, both montane systems belong to very close groups according to the Cluster Analysis (Figure 4(f)) and do not match any area of endemism (Figure 3(e)). This leads us to deduce that they protect high species richness but of very similar bird communities. Despite their similarity, the analysis also suggests that the two sites are complementary and together they contain more than 95% of the species, 69% of endangered species, and all the endemic species. This is a common problem; therefore, it is recommended that conservation areas complement each other to protect a greater representation of species diversity (Justus & Sarkar, 2002; Margules & Sarkar, 2009; Whittaker et al., 2005).

Another important point is the inclusion of rare species, which are defined by their area of distribution, habitat specificity, or local population size (Margules & Sarkar, 2009). In the case of the high plains of Guatemala region, overall species richness is not particularly high, but it concentrates the majority of endemic species; it also forms a distinct group in the Cluster Analysis (Figure 4(f)) and is an area of endemism (Figure 3(e)). Despite its characteristics, the protected area located there is smaller than in the montane systems. Similar to the high plains of Guatemala, eastern Chiapas requires more protected areas because it concentrates high species richness, especially of endangered species, it is an important area of endemism (Figure 3 (e)), and Cluster Analysis shows it to be a distinct group (Figure 4(f)). Added to this, degradation and loss forest due to social development and drug trafficking are a problem in the NCAH (McSweeney et al., 2014; Redo et al., 2012). Increasing the coverage of protected areas in these zones would benefit the complementarity and the conservation of communities and habitats that do not have an adequate representation in existing protected areas of the NCAH. Another issue is that even when protected areas conserve complementary and distinctive communities, if they are not adjacent they lead to an *archipelago* of disconnected protected areas (Margules & Sarkar, 2009).

Our results offer a new view on the regional understanding of bird diversity patterns and the biogeographical processes that have shaped regional richness. We believe that these maps of both species richness and regionalization can serve as a useful tool for conservation biologists and authorities in implementing strategies for the protection of natural areas in NCAH. However, more work is still needed to obtain a more complete picture of the complexities of bird diversity in the northern Neotropics. Prioritization of conservation areas must take into account the different sets of information, as the ones provided herein. A combination of areas detected by different sets of data like with high species richness (e.g., Sierra de las Minas), high endemism (e.g., Sierra Madre), and those with avifaunistic identity detected by the biogeographic regionalization analyses (e.g., eastern Honduras highlands), would be ideal. However, more exhaustive field evaluation of the representation of taxa within protected natural areas, analysis of the complementarity between these areas, possibilities of connectivity among highland areas through its connection via the lowlands (e.g., the Mesoamerican Biological Corridor, CONABIO 2018), and assessment of the vulnerability of their habitat are all necessary in order to arrive at adequate conservation strategies for this unique avifauna.

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Supplemental Material

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