



Diversity, Endemism, Species Turnover and Relationships among Avifauna of Neotropical Seasonally Dry Forests

Authors: Prieto-Torres, David A., Rojas-Soto, Octavio R., Santiago-Alarcon, Diego, Bonaccorso, Elisa, and Navarro-Sigüenza, Adolfo G.

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Research Papers

DIVERSITY, ENDEMISM, SPECIES TURNOVER AND RELATIONSHIPS AMONG AVIFAUNA OF NEOTROPICAL SEASONALLY DRY FORESTS

DIVERSIDAD, ENDEMISMO, REEMPLAZAMIENTO DE ESPECIES Y RELACIONES ENTRE LA AVIFAUNA DE LOS BOSQUES SECOS ESTACIONALES DEL NEOTRÓPICO

David A. PRIETO-TORRES¹, Octavio R. ROJAS-SOTO², Diego SANTIAGO-ALARCON³,
Elisa BONACCORSO^{4, 5} and Adolfo G. NAVARRO-SIGÜENZA^{1*}

SUMMARY.—Neotropical seasonally dry forests (NSDF) are widely distributed across Latin America and the Caribbean. They possess important levels of species richness and endemism but few studies have assessed the diversity patterns and ecological relationships between the entire avifauna of these threatened forests. Thus, in order to analyse the macro-ecological patterns and the community structure of NSDF avifaunas, we generated species distribution models describing the current geographical distribution of 1,298 bird species inhabiting NSDF. We assessed species richness gradients in terms of distance from the Equator using both linear and polynomial regressions. Then, based on a matrix composed of the presence or absence of species in 563 quadrants, we performed cluster analyses (considering the Simpson dissimilarity index [β_{SIM}] as a distance measure) to identify the main NSDF regions and describe the avifaunal affinities among them. For the identified groups, we estimated the dissimilarity values, using both an ANOSIM test and the β_{SIM} index. Overall, we observed the lack of an equatorial peak for species diversity of NSDF avifauna in the latitudinal gradient and identified 12 avifaunistic groups. The β_{SIM} index among the NSDF avifaunal groups ranged from 0.05-0.73, showing statistically significant differences ($R = 0.894$, $p = 0.001$) in species composition among them. Species

¹ Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México. Apartado Postal 70-399, México City 04510, México.

² Red de Biología Evolutiva, Laboratorio de Bioclimatología, Instituto de Ecología, A.C, carretera antigua a Coatepec No. 351, El Haya, 91070 Xalapa, Veracruz, México.

³ Red de Biología y Conservación de Vertebrados, Instituto de Ecología, A.C., El Haya, Xalapa, Veracruz, México.

⁴ Laboratorio de Biología Evolutiva, Instituto BIOSFERA and Colegio de Ciencias Biológicas y Ambientales, Universidad San Francisco de Quito, Diego de Robles y Vía Interoceánica, 17-1200-841 Quito, Ecuador.

⁵ Biodiversity Institute, University of Kansas, Lawrence, Kansas, U.S.A.

* Corresponding author: adolfon@ciencias.unam.mx

shared between two or three NSDF groups comprised a higher proportion (~38%) than those exclusive to each group (~23%). Only 35 species were shared between the 12 groups. This information supports a separation of the NSDF avifauna into two major groups (northern and southern), as well as the idea of connections during recent geological time among the NSDF in southeastern South America (the so-called Pleistocene Arc Hypothesis). We provide a scientific framework to contextualise the importance of each NSDF nuclei in terms of their avifauna, supplying an ecological basis for future conservation decisions in order to protect their diversity. —Prieto-Torres, D.A., Rojas-Soto, O.R., Santiago-Alarcón, D., Bonaccorso, E. & Navarro-Sigüenza, A.G. (2019). Diversity, endemism, species turnover and relationships among avifauna of neotropical seasonally dry forests. *Ardeola*, 66: 257-277.

Key words: bird assemblages, community composition, endangered forests, reverse latitudinal gradient, species richness patterns.

RESUMEN.—Los Bosques Secos Estacionales del Neotrópico (BSEN) se distribuyen ampliamente en América Latina y el Caribe, y poseen importantes niveles de riqueza y endemismo de especies. No obstante, actualmente son pocos los trabajos enfocados a evaluar los patrones de diversidad y las relaciones ecológicas entre la avifauna presente en estos bosques amenazados. Por ello, con la finalidad de analizar los patrones macroecológicos y la estructura de las comunidades de la avifauna asociada a los BSEN, se generaron modelos de distribución de especies que describen la distribución geográfica de 1.298 especies de aves que actualmente habitan en estos bosques. Los patrones de riqueza de especies fueron evaluados en términos de distancia al ecuador utilizando regresiones lineales y polinomiales. Posteriormente, utilizando una matriz de ausencia y presencia de las especies en 563 cuadrantes, realizamos análisis de agrupamiento (considerando el índice de disimilitud de Simpson [β_{SIM}] como unidad de distancia) para identificar los principales grupos de BSEN y describir la afinidad entre ellos en términos de la avifauna. Para los grupos obtenidos, se estimaron los valores de disimilitud utilizando una prueba ANOSIM y el índice β_{SIM} . En general, se observó una relación inversa entre los valores de riqueza de especies y el gradiente latitudinal de distribución de estos bosques, para los cuales se identificaron un total de 12 grupos avifaunísticos. Los valores del índice β_{SIM} entre los grupos avifaunísticos oscilaron entre 0,05-0,73, con diferencias estadísticamente significativas ($R = 0,894$; $p = 0,001$) entre los grupos en términos de composición de especies. La proporción de especies compartidas entre dos y tres grupos de BSEN es mayor (~38%) que la de las especies exclusivas en cada grupo (~23%). Solo 35 especies se encuentran compartidas entre los 12 grupos. Esta información respalda la separación en dos grandes grupos (norte y sur) de la avifauna de los BSEN, así como de la existencia de conexiones potenciales entre algunos grupos de BSEN en el sureste de Sudamérica durante el tiempo geológico reciente (lo cual corresponde a la denominada Hipótesis del Arco del Pleistoceno). Este estudio proporciona un marco científico para contextualizar la importancia avifaunística de cada núcleo de BSEN, lo cual puede guiar al establecimiento de futuros esfuerzos de conservación para proteger la biodiversidad de estos bosques. —Prieto-Torres, D.A., Rojas-Soto, O.R., Santiago-Alarcón, D., Bonaccorso, E. y Navarro-Sigüenza, A.G. (2019). Diversidad, endemismo, reemplazamiento de especies y relaciones entre la avifauna de los bosques secos estacionales del Neotrópico. *Ardeola*, 66: 257-277.

Palabras clave: bosques amenazados, composición de la comunidad, ensambles de aves, gradiente latitudinal inverso, patrones de riqueza de especie.

INTRODUCTION

Studies of bird assemblages have contributed significantly to the understanding of community ecology and biogeography, but

not all bird communities have been equally well studied (Stotz *et al.*, 1996; Herzog & Kessler, 2002; Weir & Hey, 2006; Rodríguez-Ferraro & Blake, 2008). In particular, the temporal and spatial diversification patterns

for some bird communities associated with endangered ecosystems, such as the Neotropical seasonally dry forests (NSDF), remain only partially understood at both regional and continental scales (Weir & Hey, 2006; Wiens & Donoghue, 2004). Although NSDF are widely distributed and hold high levels of species richness and endemism, these forests have received relatively little attention from ecologists and conservationists (Miles *et al.*, 2006; Sánchez-Azofeifa *et al.*, 2013). Overall, both sample sizes and sampling effort for NSDF bird communities are often unsatisfactory (e.g., Ríos-Muñoz & Navarro-Sigüenza, 2012; Prieto-Torres *et al.*, 2018b). For this reason, many researchers have supported the idea of maintaining an information network, such as DRY-FLOR (see www.dryflor.info/), to aid in the protection of NSDF by standardized protocols, combining ecological research, remote sensing and social sciences, that allow comparisons between different areas. Evidence of this fact is the growing interest in identifying NSDF regions that may have high conservation priority (Miles *et al.*, 2006; Portillo-Quintero & Sánchez-Azofeifa, 2010; Albuquerque *et al.*, 2012; Banda *et al.*, 2016; Prieto-Torres *et al.*, 2016, 2018a; Escribano-Ávila *et al.*, 2017).

Considering that the financial resources available for biodiversity conservation are limited, information on species richness and endemism levels, including species turnover and the historical relationships among regions, have been identified as important metrics for estimating the conservation value of different areas (Myers *et al.*, 2000; Gordon & Ornelas, 2000). Theoretically, regions or ecosystems containing the largest numbers of ecologically restricted species are the most sensitive to ecological disturbance and alteration; consequently, they must be considered as conservation priorities (Gordon & Ornelas, 2000; Duckworth & Altwegg, 2018). However, and despite there being

numerous studies of NSDF plants (e.g., Pennington *et al.*, 2000; 2006; Linares-Palomino *et al.*, 2011; Banda *et al.*, 2016), few studies have assessed the diversity patterns and historical relationships among the entire NSDF avifauna across the Americas (Ceballos, 1995; Stotz *et al.*, 1996; Prieto-Torres *et al.*, 2018b). Most of the information collected in NSDF avifaunal studies only applies to a small number of areas, which makes it difficult to formulate generalisations on biota dynamics due to the lack of replication. Therefore, many questions have yet to be answered regarding the biogeography and macroecological patterns of the NSDF avifauna.

Several studies provide contrasting perspectives of the historical distribution of NSDF, casting doubts on the value of biological comparisons among different NSDF areas in order to understand their biogeography, in particular when considering NSDF to be a single and widely distributed biogeographical unit (e.g., Becerra, 2005; Werneck *et al.*, 2011; Côrtes *et al.*, 2015; de Melo *et al.*, 2016; Prieto-Torres *et al.*, 2018b). This unified interpretation is important for both biogeographical inference and setting conservation priorities in NSDF because, based on the idea of connections during recent geological time, we could expect to find high species similarity, including low levels of endemism and species turnover, between the NSDF areas (Linares-Palomino *et al.*, 2011). Nevertheless, recent avifaunal studies show high levels of endemism among NSDF in the Caribbean Islands, the Mesoamerican, and the South American NSDF as consequences of independent evolutionary processes and diversification patterns among them (e.g., Cracraft, 1985; Herzog & Kessler, 2002; Porzecanski & Cracraft, 2005; Ríos-Muñoz & Navarro-Sigüenza, 2012; Prieto-Torres *et al.*, 2018b). In fact, some authors suggest that no single NSDF formation contains even a third of the total NSDF bird species pool

(Ceballos, 1995; Stotz *et al.*, 1996; Prieto-Torres *et al.*, 2018b). These characteristics illustrate the possible distinctiveness of the species pools found within NSDF across the Americas, and the need to define the avifaunal relationships of such disjunct NSDF areas. In addition, even though it is known that evolutionary processes such as selection, genetic drift, and gene flow vary in strength and importance over latitude (Martin & Tewksbury, 2008), the consequences of this geographical variation on the NSDF biota are poorly understood (Gentry, 1995; Banda *et al.*, 2016). It is thus important to identify the areas of greatest species diversity and endemism –i.e., unique biodiversity areas– providing a framework to define the conservation significance of each separate NSDF region, as has been done for other threatened ecosystems, for example the South American Atlantic forest (Cardoso da Silva *et al.*, 2004).

In this study, we applied a macro-ecological approach to analyse the spatial variation of the bird assemblages inhabiting NSDF, partly employing the methodology used by Banda *et al.* (2016) for woody plants. We aimed to: (i) quantify and map the current avian diversity in NSDF, (ii) assess species richness patterns in terms of distance from the Equator (i.e. latitudinal gradient); and (iii) characterise NSDF areas in terms of species composition (i.e. patterns of species richness and endemism, as well as species turnover among regions). Our results offer a better understanding of the macro-ecological distribution patterns of NSDF avifauna, which will aid future ecological studies and conservation efforts in these highly threatened forests. This type of information is particularly critical in ecosystems such as the NSDF, where strong anthropogenic disturbances (e.g., agriculture, cattle ranching, mining, and urbanization) are dramatically decreasing biodiversity via loss of original vegetation, reduction of species ranges and the imposition of low connectivity or even complete

isolation among populations (Miles *et al.*, 2006; Portillo-Quintero & Sánchez-Azofeifa, 2010; Sánchez-Azofeifa *et al.*, 2005).

METHODS

Study area

We defined NSDF as ecosystems typically dominated (>50%) by deciduous trees, which are present in frost-free areas, with a mean annual temperature >25°C, a total annual precipitation of 700-2,000mm and at least three or more dry months (precipitation < 100mm) per year (Murphy & Lugo, 1986; Pennington *et al.*, 2000; Sánchez-Azofeifa *et al.*, 2005; 2013). The vegetation is heterogeneous, including formations ranging from tall forests to cactus-dominated scrub, but mostly dominated by semi-deciduous to deciduous trees (Murphy & Lugo, 1986; Pennington *et al.*, 2000, 2006; Sánchez-Azofeifa *et al.*, 2005). This endangered ecosystem, which encompasses 42 ecoregions according to Olson *et al.* (2001), is discontinuously distributed in 18 countries across Meso- and South America (Figure 1). In Mesoamerica, NSDF are located in Mexico, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica and Panama. In South America, NSDF are distributed in Venezuela, Colombia, Ecuador, Peru, Bolivia, Argentina, Paraguay and Brazil. Important NSDF fragments are also located in the Caribbean islands in Cuba, the Dominican Republic and Haiti.

Species occurrence records and distribution models

Analyses were based on records of 1,298 terrestrial native bird species inhabiting NSDF, which were obtained from ornithological collections (see Supplementary Material, appendix 1) and online databases (i.e.,

the Global Biodiversity Information Facility [GBIF], eBird and the SiB Colombia). The complete checklist of bird species inhabiting NSDF is provided in Prieto-Torres *et al.*

(2018b). For the final species list, all names follow those proposed by Gill and Donsker (2015) for Mesoamerica, as well as the South American Classification Committee (Remsen

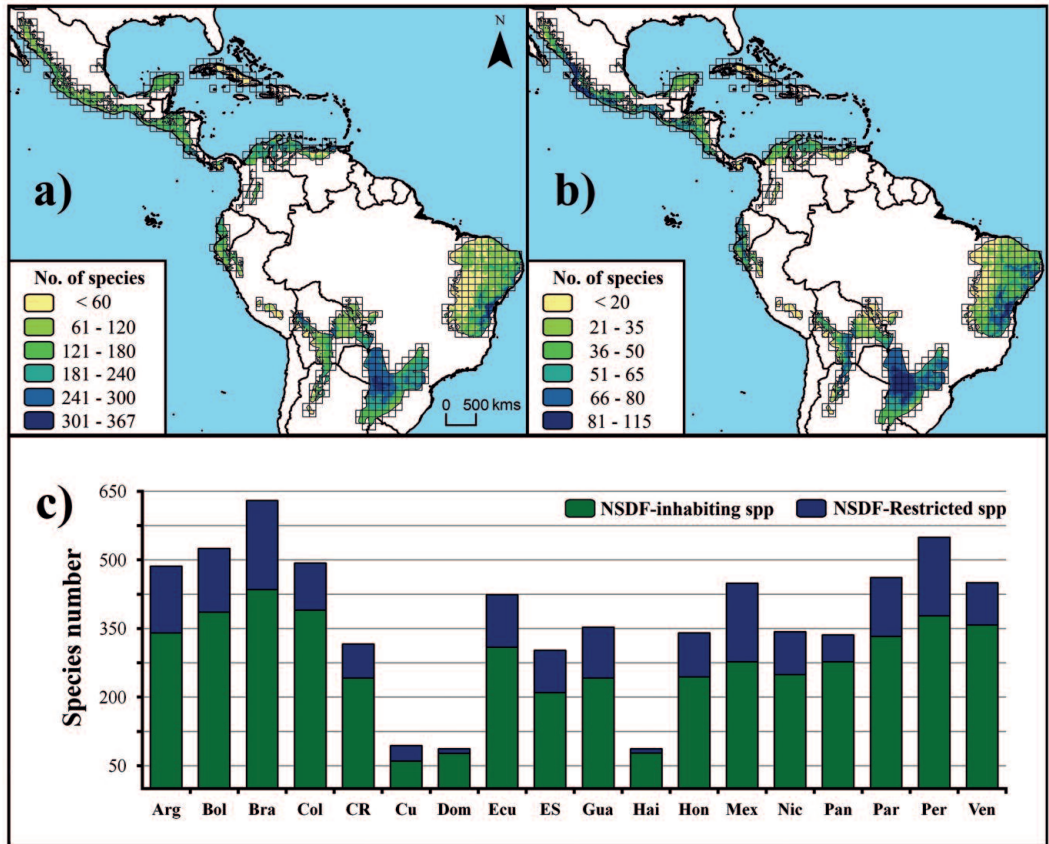


FIG. 1.— Spatial patterns of species richness and endemism for 1,298 bird taxa throughout the Neotropical seasonally dry forest (NSDF) distribution. Geographical species richness patterns across NSDFs were estimated in two ways: (a) all species vs. (b) only NSDF-restricted species. Acronyms in (c) correspond to countries that have expanses of NSDF: Argentina (Arg), Bolivia (Bol), Brazil (Bra), Colombia (Col), Costa Rica (CR), Cuba (Cu), Dominican Republic (Dom), Ecuador (Ecu), El Salvador (ES), Guatemala (Gua), Haiti (Hai), Honduras (Hon), Mexico (Mex), Nicaragua (Nic), Panama (Pan), Paraguay (Par), Peru (Per) and Venezuela (Ven).

[*Patrones espaciales de riqueza de especies y endemismos para 1.298 taxones de aves a lo largo de la distribución de los Bosques Secos Estacionales del Neotrópico (BSEN). Los patrones geográficos de riqueza de especies en el BSEN se estimaron considerando dos enfoques: todas las especies (a) vs. “solo especies restringidas” (b). Las siglas en (c) corresponden a países con extensiones de NSDF: Argentina (Arg), Bolivia (Bol), Brasil (Bra), Colombia (Col), Costa Rica (CR), Cuba (Cu), República Dominicana (Dom), Ecuador (Ecuador), El Salvador (ES), Guatemala (Gua), Haití (Hai), Honduras (Hon), México (Mex), Nicaragua (Nic), Panamá (Pan), Paraguay (Par), Perú (Per), y Venezuela (Ven).]*

Jr. *et al.*, 2017) and the Clements Checklist (Clements *et al.*, 2015) for the birds of South America. In addition, the conservation status of each species follows IUCN (2014).

For most species, few observations and/or specimens are available, and where they exist data are generally biased by site accessibility (Peterson, 2001; Peterson *et al.*, 2018). Thus, such techniques as species distribution models (SDMs) have been developed to obtain more accurate species distribution maps, based on identifying environmentally suitable areas. Using SDMs has the advantage of minimising the spatial biases inherent to species distribution information, filling in gaps in poorly known and/or non-surveyed areas (Peterson, 2001; Soberón & Peterson, 2005; Peterson *et al.*, 2018). Thus, SDMs have become a widely used tool in ecology, evolution, conservation and management (e.g., Soberón & Peterson, 2005; Ortega-Andrade *et al.*, 2015; Prieto-Torres & Pinilla-Buitrago, 2017; Peterson *et al.*, 2018).

The SDMs were obtained with MaxEnt 3.3.3 (Phillips *et al.*, 2006), which uses the maximum entropy principle to calculate the most likely distribution of focal species as a function of occurrence localities and environmental variables (Elith *et al.*, 2011). To characterise the potential distribution –based on ecological niche modelling–, we downloaded interpolated climate data (30''-resolution: ~1km² cell size) from the WorldClim project 1.4 (Hijmans *et al.*, 2005). All models were run with no extrapolation to avoid artificial projections of extreme values of ecological variables (Elith *et al.*, 2011; Owens *et al.*, 2013). Other MaxEnt parameters were set to default. In addition, for each species we used a geographical clip based on the intersection of Terrestrial Ecoregions (Olson *et al.*, 2001) and the Biogeographical Provinces of the Neotropic (Morrone, 2014) in order to create an area for model calibration by species (or *M sensu* BAM diagram; see Soberón & Peterson, 2005; Barve *et al.*, 2011). Such con-

siderations were based on the assumption that these regions may define the accessible historical area and specific restriction region for each species.

We converted the obtained logistic values of suitability (continuous probability from 0 to 1; Phillips *et al.*, 2006) into a binary presence/absence map by setting the “tenth percentile training presence” as the decision threshold. We decided to use this threshold because it allows reducing commission errors (i.e., overprediction of areas) in our final binary maps, recovering more conservative species distributional ranges (Liu *et al.*, 2013). The performance of the MaxEnt models for species that had between five and 20 records ($n = 56$ spp.: 4.31% of database) was developed using all presence data and assessed with a Jackknife test (Pearson *et al.*, 2007). For species with more than 20 records ($n = 1,242$ spp.: 95.69%), performance was evaluated by calculating the commission and omission error values and the Partial-ROC curve test (Peterson *et al.*, 2008). For this last case, it is important to note that SDMs were generated using a random sampling of 90% of the locality records for model training and the remaining 10% for internal model evaluation (i.e. testing data).

Finally, based on the obtained individual SDMs, we determined a species ecosystem specificity value in order to define those NSDF-restricted species. This step was based on two approaches (see Prieto-Torres *et al.* [2018b] for more details): (1) calculating the degree of coverage of the geographical distribution for each species across the Neotropical ecosystems; and (2) using the index of restriction (IR) proposed by Sánchez-González and Navarro-Sigüenza (2009), which corresponds to a modification of published endemism indices (Crisp *et al.*, 2001; Linder, 2001). NSDF-restricted species were defined (Supplementary Material, appendix 2) herein as those that had at least 33% of their distribution within the NSDF and an IR ≥ 0.33 .

Richness, endemism and species turnover amongst NSDF

We summed all species binary maps in order to obtain the potential species richness patterns across NSDF considering two approaches: all species *vs.* NSDF-restricted only. In order to highlight geographical differences throughout the Neotropics, these maps employ a colour key to indicate species richness levels. In addition, given that we obtained a species list for each grid cell, we performed both linear and polynomial regressions between the absolute latitude, the total number of species and NSDF-restricted species. These analyses allowed us to evaluate the richness gradients (i.e., all species, NSDF-restricted) in terms of distance to the Equator (Banda *et al.*, 2016).

Subsequently, we divided the study area into 563 grid cells ($1^\circ \times 1^\circ$; Figure 1) and constructed two binary species matrices (i.e., all species *vs.* NSDF-restricted only), coding presence as “1” and absence as “0” for each site based on the individual SDM maps obtained. We used these matrices to identify the main NSDF regions and describe the avifaunal affinities between them. However, when we compared results from the all species and NSDF-restricted analyses, we did not observe differences in the major NSDF regions identified (see below). Thus, the results below are based only on a strict consensus dendrogram of analyses using all-species information. We used this approach because it allows assessing and comparing the distributional patterns of NSDF avifauna considering different but parallel histories, providing a better understanding of the historical relationships between geographical areas (Ricklefs, 1987; Wiens & Donoghue, 2004; Weir & Hey, 2006).

To identify the main NSDF regions and describe the avifaunal affinities among them, we first performed ordination and classifi-

cation analyses of sites using the Simpson dissimilarity (or β_{SIM}) index as a distance measure and the Unweighted Pair-Group Method with Arithmetic mean (UPGMA) as the linkage method. We decided to use the β_{SIM} to calculate pairwise avifaunal distances because this index is less affected by variations in species richness (Baselga, 2010; Colwell *et al.*, 2012). To avoid the effects of the order of the sites in the matrix (especially when pairwise distance values are equal), we used the Recluster package (Dapporto *et al.*, 2016) performing 10,000 random site re-orderings. All analyses were run in the R software (R Core Team, 2018).

We then described the relationships amongst the NSDF identified groups based on a UPGMA hierarchical clustering using the Pvcust package (Suzuki & Shimodaira, 2006). This allowed us to assess the support for each node in the dendrogram, calculating probability values (p-values) based on 1,000 bootstrap resamplings. For this classification, we pooled the species lists for each grid cell into a single list and conducted clustering analyses on a species (rows) \times NSDF group (columns) matrix. We calculated expected species accumulation curves (to assess how well the bird assemblage is captured in our dataset) for each NSDF group using a sample-based rarefaction method (Colwell *et al.*, 2012) from the species accumulation (specaccum) function in the vegan library (Oksanen *et al.*, 2018). Finally, in order to determine the degree of differences among the bird assemblages identified, we estimated the dissimilarity values (including the number of shared and exclusive species) amongst the NSDF regions based on the β_{SIM} dissimilarity index and the ANOSIM test (i.e., Analysis of similarities; Clarke, 1993) in the R software. This last step allowed us to test statistically whether there is a significant difference between two or more groups of the identified NSDF region.

RESULTS

Species distribution modelling and species richness patterns

Of 1,298 bird species –belonging to 24 orders, 78 families and 511 genera– inhabiting NSDF (Supplementary material, appendix 2), we found that ~21% (n = 275) are widely distributed across the Neotropical region, while ~55% (n = 707) are geographically restricted to South America, ~20% (n = 260) to Mesoamerica, and only ~4% (n = 56) are restricted to Caribbean Islands. For these species, we observed that ~25% (n = 323 spp.) have at least 50% of their distribution within NSDF, while ~42% (n = 545) of species have between 25-50% of their distribution within NSDF.

Other ~33% (n = 430) species have ranges that overlap by 10-25% with NSDF areas. Likewise, the species ecosystem specificity values showed that only 13.7% (n = 178) of species are present in only one (i.e., NSDF) or two ecosystems (IR > 0.5), whereas most (45.4%; n = 589 spp.) are distributed in one to three ecosystems (IR ≥ 0.33). An additional 40.9% (n = 531) of species tended to be distributed in more than three ecosystems (IR < 0.25). Based on these patterns, we determined that ~43% (n = 557) of species were highly associated with, and/or restricted to, NSDF.

From a national boundaries perspective, we found that the countries with the highest species richness were Brazil (n = 630 spp.), Peru (n = 549), Bolivia (n = 525) and Co-

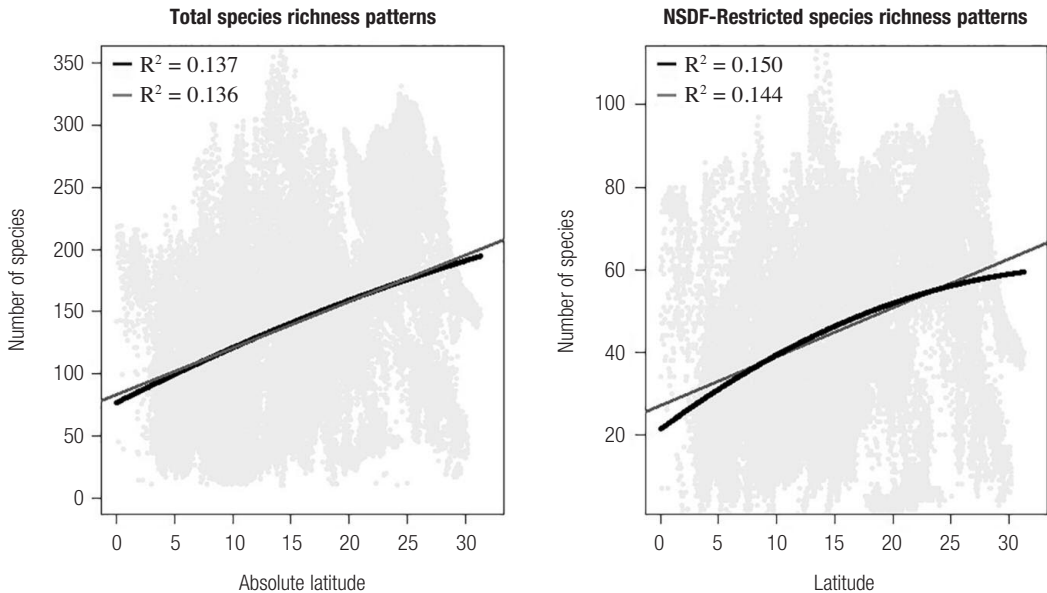


FIG. 2.—Fitted line plots for linear (grey line) and polynomial (black line) regression of absolute latitude (i.e., distance from the Equator) versus total number of species for the avifauna associated with Neotropical seasonally dry forests (NSDF).

[Gráfico de dispersión de puntos y líneas ajustadas para los valores de regresión lineal (línea gris oscura) y polinomial (línea negra) entre los valores de latitud absoluta (es decir, distancia desde el ecuador) versus el número total de especies para la avifauna asociada a los Bosques Secos Estacionales del Neotrópico (BSEN).]

lombia (n = 493). The number of NSDF-restricted species was also higher in Brazil (n = 195) and Peru (n = 171), as well as in Mexico (n = 172) and Argentina (n = 146). The lowest values for both species richness and endemism were reported in Haiti (n = 87 spp.: 9 NSDF-restricted), the Dominican Republic (n = 87 :10), Cuba (n = 94 :34) and Panama (n = 336 :59). According to Figure 1, we observed that species richness patterns in the NSDF avifauna tended to increase in some areas considered boundaries (i.e., ecotones) with other species-rich environments (e.g., montane forests, tropical rainforests), whereas the lowest species richness values were observed in ecotones with other dry ecosystems, such as savannahs (the Llanos in Venezuela and Colombia) and the Cerrado (in northeastern Brazil). Although 51.1% (n = 663 spp.: including 181 NSDF-restricted spp.) and 31.1% (n = 404 :94) of the NSDF avifauna is shared with the Chaco and savannahs, respectively, the highest proportion (85.7%; n = 1,112 :410) is shared with ecosystems that are altitudinally higher than NSDF.

Interestingly, both line plots for linear and polynomial regression models showed a lack of an equatorial peak in the latitudinal pattern (Figure 2). Overall, both regression models showed that species richness increases directly and significantly ($p < 0.05$) with distance from the Equator, explaining between 13-15% of the variation in richness patterns. In fact, the southernmost NSDF in Bolivia, Argentina, Paraguay and Brazil (which reach the Tropic of Capricorn), as well as the northernmost Mexican NSDF (that reach the Tropic of Cancer) have higher species numbers than most of Caatinga and the Pacific Equatorial areas (close to the Equator; see Figure 1). These results suggest, as observed recently for NSDF plants (Banda *et al.*, 2016), the existence of a “reverse latitudinal gradient” throughout the distribution of the NSDF biota.

Relationships and species turnover amongst NSDF

The average number of species per NSDF quadrats (i.e., $1^\circ \times 1^\circ$ grid cells) was 259 (SD = 91, median = 276; range: 50-448). Based on the classification analyses of the 563 grid cells, we recognised 12 main groups from the species pool (Supplementary Material, appendix 3) most of them encompassing more than one country (Figure 1). Species accumulation curves (Figure 3) reached an asymptote for the 12 NSDF groups, indicating that very few new species remain to be recorded in all areas. Thus, the avifaunistic inventories are sufficiently complete for these areas. Tables 1 and 2 show the detailed description of taxonomic richness (including the percentage of exclusive and shared species) for each NSDF group, as well as the dissimilarity indexes values among them. Overall, the β_{SIM} dissimilarity index among these 12 avifaunistic groups ranged from 0.05-0.73 (Table 2), showing statistically significant differences ($R = 0.894$, $p = 0.001$) among the avifaunal composition of NSDFs.

Despite the clear distinction between the compositions of avian assemblages among different NSDF groups (Table 2, Figure 4), we observed that species shared between two and three NSDF groups represented a higher proportion (~38%; n = 491 spp.) than those restricted or exclusive to each NSDF group (~23%; n = 294 spp.). The proportion of species shared among at least half (six) of the groups was ~23% (n = 303 spp.), whereas only ~20% (n = 259 spp.) were shared among seven or more groups. We found only 35 (2.69%) species that were shared among all 12 NSDF regions (Supplementary Material, appendices 2). Similar patterns were observed for the NSDF-restricted species, with ~44% (n = 244) of species shared among two and three NSDF groups and ~38% (n = 210 spp.)

TABLE 1

Description of avifaunistic groups identified for Neotropical seasonally dry forests (NSDF): number of sites (grid cells) and taxonomic diversity (including number of species, the percentage of widely-distributed species and those exclusive to the NSDF group, as well as the number of threatened species [including those in the Data Deficient, Vulnerable, Endangered and Critically Endangered categories]).
 [Descripción de los grupos avifaunísticos identificados para los Bosques Secos Estacionales del Neotrópico (BSEN): número de sitios (celdas) y diversidad taxonómica (incluido el número de especies, el porcentaje de especies ampliamente distribuidas y aquellas exclusivas dentro del grupo de BSEN), así como el número de especies amenazadas [considerando las categorías: Datos Deficientes, Vulnerable, Amenazada y Criticamente Amenazadas].]

Group	Number of sites	Number of Families	Number of genera	Number of species (*)	Median of species per site	% wide-distributed species	% exclusive species	Number of threatened species (**)
(1) Caribbean-Antilles	41	43	104	137 (39)	79.01	42.34	40.87	11 (10)
(2) Western Mexico	70	59	229	383 (135)	186.62	41.51	9.66	20 (8)
(3) Eastern Mexico and Central America	64	51	268	492 (162)	269.45	48.98	9.76	20 (5)
(4) Caribbean Colombia-Venezuela	52	63	292	447 (94)	319.37	56.60	10.74	18 (6)
(5) Northern Inter-Andean valleys	13	62	267	390 (56)	304.92	63.08	0.51	10 (-)
(6) Pacific Equatorial	16	62	260	402 (121)	260.68	47.51	7.46	31 (11)
(7) Northern Peru valleys	5	61	247	372 (89)	311.60	45.43	0.27	17 (-)
(8) Southern Peru valleys and Northwestern Bolivia	15	65	315	482 (129)	283.40	34.23	0.00	12 (-)
(9) Sub-Andean Piedmont (Bolivia)	34	66	225	478 (130)	261.94	32.85	0.63	14 (1)
(10) Chiquitano Forests and Central Brazil	54	68	249	547 (162)	285.09	29.80	0.18	20 (-)
(11) Misiones Province	72	64	333	505 (134)	313.78	29.90	1.78	16 (-)
(12) Caatinga	127	65	335	510 (163)	272.52	30.20	11.57	42 (28)

(*) Values in parentheses correspond to the number of NSDF-restricted species reported for each group.

(**) Values in parentheses correspond to the number of threatened species reported as exclusive for each group.

TABLE 2

Dissimilarity values based on Simpson index (below diagonal) and shared species (above diagonal) of bird among Neotropical seasonally dry forests (NSDF) groups. Deeper grey shade indicates greater numbers of shared species, corresponding to line widths in Figure 4. [Valores de disimilitud, basados en el índice de Simpson (debajo de la diagonal), y número de especies de aves compartidas (arriba de la diagonal) entre los grupos de Bosques Secos Estacionales del Neotrópico (BSEN). Tonos grises oscuros indica los más altos valores de especies compartidas entre grupos, los cuales son correspondientes a los anchos de línea representados en la Figura 4.]

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)	(11)	(12)
(1) Caribbean-Antilles	—	63	75	64	57	53	46	48	48	48	47	49
(2) Western Mexico	0.54*	—	345	159	155	135	117	114	111	112	103	103
(3) Eastern Mexico and Central America	0.45*	0.09*	—	247	238	187	163	158	151	155	144	146
(4) Caribbean Colombia-Venezuela	0.53*	0.58*	0.45*	—	355	242	233	251	239	257	238	242
(5) Northern Inter-Andean valleys	0.58*	0.60*	0.39*	0.09*	—	255	245	256	239	249	225	227
(6) Pacific Equatorial	0.61*	0.65*	0.53*	0.40*	0.34*	—	333	259	240	238	199	194
(7) Northern Peru valleys	0.66*	0.68*	0.56*	0.37*	0.34*	0.10*	—	293	270	267	229	221
(8) Southern Peru valleys and Northwestern Bolivia	0.65*	0.70*	0.67*	0.44*	0.34*	0.36*	0.21*	—	449	446	369	329
(9) Sub-Andean Piedmont (Bolivia)	0.65*	0.71*	0.68*	0.47*	0.39*	0.40*	0.27*	0.06*	—	452	384	328
(10) Chiquitano Forests and Central Brazil	0.65*	0.71*	0.69*	0.43*	0.36*	0.41*	0.28*	0.07*	0.05*	—	459	410
(11) Misiones Province	0.66*	0.73*	0.71*	0.47*	0.42*	0.51*	0.38*	0.23*	0.20*	0.09*	—	428
(12) Caatinga	0.64*	0.73*	0.70*	0.46*	0.42*	0.52*	0.41*	0.32*	0.31*	0.19*	0.15*	—

* Results of pairwise test of ANOSIM were significant ($R > 0.8$, $p < 0.01$).

restricted/exclusive to one NSDF group. Approximately 7% ($n = 38$) of NSDF-restricted species are shared by at least six NSDF groups and only two species are distributed among the 12 groups.

The UPGMA hierarchical clustering showed that relationships amongst the 12 NSDF groups involved two well-resolved higher-level clusters (Figure 4). The first

major group, corresponding to the northern cluster, involved the NSDFs located in three clearly differentiated and well-supported regions: (1) the Caribbean islands, (2) north-western Mexico and (3) Central America (from southeastern Mexico to Panama). The second higher-level group, corresponding to the southern cluster, comprised areas located in South America, which were subsequently

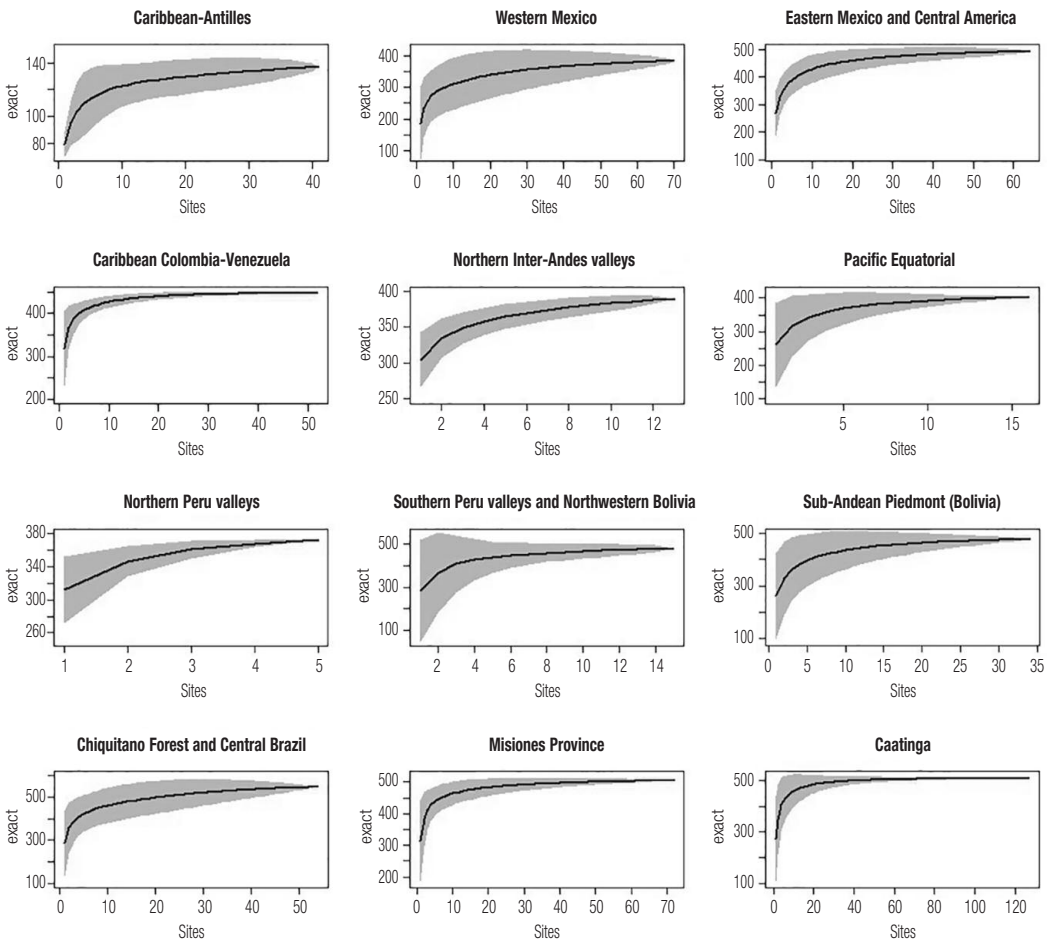


FIG. 3.—Species accumulation curves for each avifaunistic group calculated using a sample-based rarefaction method. Gray shade represents the 95% confidence intervals for the best fit estimate of species numbers.

[Curvas de acumulación de especies para cada grupo avifaunístico calculadas utilizando el método de rarefacción basado en muestreos. El tono gris representa los intervalos de confianza del 95% para la estimación de línea de mejor ajuste de números de especies.]

divided in two well-supported sub-clusters. One sub-cluster comprised the grid cells of northern South America (including the Caribbean coast from Colombia and Venezuela, as well as the inter-Andean valleys from Colombia) and those grid cells that included the NSDFs of central-western South America (from western Ecuador to northwestern Peru). The second sub-cluster is formed by the forests located throughout southeastern South America, which is further divided in other two well-supported groups: one contains the NSDFs located at higher altitudes (i.e. Sub-Andean Piedmont; from Apurímac-Mantaro and Tarapoto-Quillabamba forests to western Bolivia), and the other is formed

by the Chiquitano forests-Central Brazil, the Misiones province, and the Brazilian Caatinga (Figure 4).

DISCUSSION

Community structure of the NSDF avifauna: history meets ecology

Our study provides a clear picture of the uniqueness of the NSDF regional avian groups across the Neotropics, supporting the idea of independent evolutionary histories for bird assemblages at different NSDF nuclei despite their environmental similarities (as

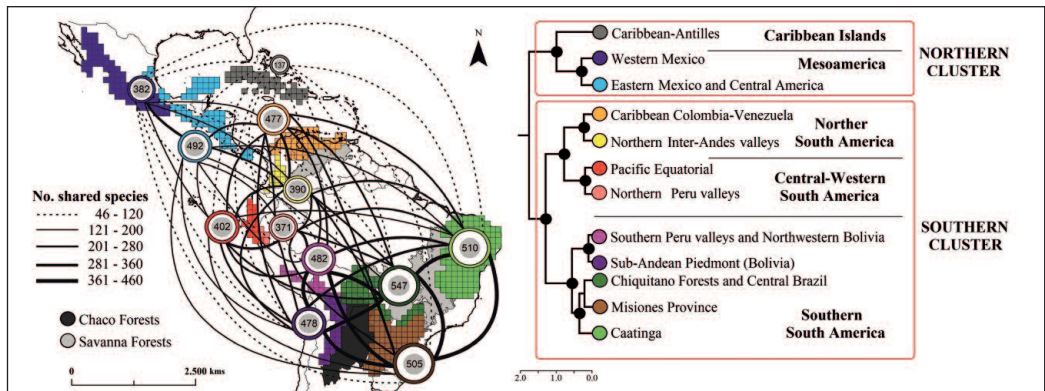


FIG. 4.—Geographical patterns for the hierarchical classification and ecological relationships of the twelve faunistic groups identified based on bird species associated with Neotropical seasonally dry forests (NSDF). Classification of groups was based on the UPGMA clustering of 563 grid cells using the Simpson dissimilarity index as a measure of distance (see supplementary material appendix 3). Size of the circles in the map is proportional to the number of species per group (Table 1), while the number of species shared among areas (Table 2) is described by line widths. Black circles in the dendrogram correspond to probability values (p -value $\geq 80\%$; for each node based on 1,000 bootstrap repetitions). The higher-level clusters are indicated by the rectangles.

[Patrones geográficos para la clasificación jerárquica de los doce grupos faunísticos identificados considerando las especies de aves asociadas a los Bosques Secos Estacionales del Neotrópico (BSEN). La clasificación de los grupos se basó en el agrupamiento UPGMA de 563 celdas utilizando el índice de disimilitud de Simpson como una medida de la distancia (véase Material Suplementario, apéndice 3). El tamaño de los círculos en el mapa es proporcional al número de especies por grupo (Tabla 1), mientras que el número de especies compartidas entre áreas (Tabla 2) se describe por el ancho de línea. Los círculos negros en el dendrograma corresponden a valores de probabilidad ($p \geq 80\%$; con base a las 1.000 repeticiones de bootstrap). Los grupos de nivel superior se indican con los rectángulos.]

proposed by Porzecanski & Cracraft, 2005; Ríos-Muñoz & Navarro-Sigüenza, 2012; Prieto-Torres *et al.*, 2018b). In fact, the identified spatial richness and endemism patterns were similar to those found for other NSDF taxa (e.g., woody plants, herpetofauna, mammals) either at regional or continental scales (Ceballos, 1995; Linares-Palomino *et al.*, 2011; Banda *et al.*, 2016). This concordance among biogeographic patterns of NSDF biota supports the existence of unique associations (with high levels of geographical restriction and faunal turnover) across the NSDF distribution (Becerra, 2005; Côrtes *et al.*, 2015; de Melo *et al.*, 2016; Prieto-Torres *et al.*, 2018b), leading to different time-events of adaptation to dry environments –in the case of birds– within northern and southern ranges (see Barker *et al.*, 2015). These results are likely since birds are following historical patterns of NSDF plant species distributions (see Banda *et al.*, 2016; Prieto-Torres *et al.*, 2018b).

Our data confirmed that the degree of isolation and historical colonisation patterns play an important role in shaping bird assemblages in NSDF. We observed that few species are widespread and shared across diverse NSDF groups. Most species shared among at least half of the groups involved birds considered as widespread ecological generalists, such as the Black Vulture *Cathartes aura*, Burrowing Owl *Athene cunicularia* and Tropical Kingbird *Tyrannus melancholicus* (Stotz *et al.*, 1996; Gill & Donsker, 2015). This low number of shared species among more than three NSDF groups strongly argues against the idea of connections during recent geological time throughout the Neotropics for a widespread NSDF formation (Pennington *et al.*, 2009; Linares-Palomino *et al.*, 2011; Prieto-Torres *et al.*, 2019). Hence, based on current evidence, we rather suggest a mixed evolutionary history across the NSDF distribution, with ecological similarities among some NSDF nuclei arising from convergence

and dispersal limitations. As suggested by Werneck *et al.* (2011), the climatic regimes during the LGM were probably too dry and cold to support large tracts of NSDF –connecting all regions or favouring the long-distance dispersal of taxa. This idea is supported by the important geographical and ecological barriers circumscribing NSDF groups, such as the Leading edge of the Caribbean plate, the Tehuantepec Isthmus, the Polochic-Motagua fault, the Nicaraguan Depression, the Chocó forest, the Amazon basin and the Andean Cordillera (Porzecanski & Cracraft, 2005; Ríos-Muñoz & Navarro-Sigüenza, 2012; Banda *et al.*, 2016; Prieto-Torres *et al.*, 2018b).

Although there is no support for historical interconnection of NSDFs across their entire geographical distribution, it is important to note that avifaunal affinities found between two NSDF regions in southeastern South America (Figure 4) support the so-called Pleistocene Arc Hypothesis as originally proposed by Prado and Gibbs (1993). In this respect, our results and those obtained for plant taxa (Banda *et al.*, 2016) suggest that these regions were probably once interconnected within recent time (i.e., the Late Pleistocene; Werneck *et al.*, 2011). As a consequence, the long-distance dispersal hypothesis of NSDF in southeastern South America, proposed by Mayle (2004), remains a feasible scenario that requires further study.

Geographical distribution of species richness

Compared to other Neotropical ecosystems such as montane forests and tropical rainforests, species richness and endemism in the NSDF is low (Gordon & Ornelas, 2000; Porzecanski & Cracraft, 2005; Rodríguez-Ferraro & Blake, 2008; Ríos-Muñoz & Navarro-Sigüenza, 2012). This avifauna is composed of a mixture of NSDF-restricted

endemics, lowland taxa and species that are more common at higher elevations (Stotz *et al.*, 1996). In fact, most of the bird species (~57%, $n = 741$) inhabiting NSDF are primarily associated with other ecosystems (Stotz *et al.*, 1996). However, NSDF bird assemblages also have a unique composition as a result of a diverse array of ecological conditions across the surrounding ecosystems (e.g., montane cloud forests, rainforests, savannas, and dunes) and the altitudinal gradient involved across the forests distribution (e.g., García-Trejo & Navarro-Sigüenza, 2004; Ríos-Muñoz & Navarro-Sigüenza, 2012). This scenario of mixed community structure (e.g., the five Andean avifaunistic groups in Figure 4) reflects the great heterogeneity of regions and confirms the existence of complex transition zones (i.e., ecotones) among the ecosystems surrounding NSDFs (Prieto-Torres & Rojas-Soto, 2016; Dexter *et al.*, 2018).

Evidently, avian species richness and endemism patterns are also tightly associated with floristic composition and seasonality of precipitation across the distribution of NSDFs (Olmos *et al.*, 2005; Martin & Tewksbury, 2008; Albuquerque *et al.*, 2012). For instance, during the rainy season the phenology of NSDF resembles that of montane and rainforests, which favours the movements of animal species into NSDF, increasing richness values in bordering areas (Stoner & Timm, 2004; 2011). Therefore, ecotones frequently represent heterogeneous environments that are considered reservoirs of biological diversity (Búrquez & Marínez-Yrizar, 2010). Likewise, the notable “*reverse latitudinal gradient*” of species richness—originally suggested by Gentry (1995) for woody plants—could also be related to differences in ecological conditions along the gradient, which enhance the coexistence of highly variable climatic areas with more stable ecoclimatic regions (e.g., Sánchez-González & Navarro-Sigüenza, 2009). In

fact, most NSDF regions differ greatly—along their latitudinal gradient—in terms of surface area, climate, topography and geological history. This complex geological history, with extensive environmental changes in the Neotropics, may have promoted the local evolution or persistence of high species diversity and the retention of ancient lineages (see Pearson & Dawson, 2003; Bush *et al.*, 2004); consequently, producing a higher concentration of species in certain places that are currently reflected in the different NSDF groups or nuclei (Rodríguez-Ferraro & Blake, 2008; Ríos-Muñoz & Navarro-Sigüenza, 2012; Banda *et al.*, 2016; Prieto-Torres *et al.*, 2018b). For instance, larger areas (such as western Mexico and Misiones Province) that are surrounded by other ecosystems, harboured more species than isolated areas such as the Caribbean islands and the northern Peru valleys. Likewise, this pattern probably reflects different post-glacial sources for recolonising formerly glaciated regions at low latitudes, as well as environmental barriers that limit the ranges of species from both northern and southern extremities to the equator (e.g., Qian *et al.*, 2009).

Alternatively, results can be explained by an integrated time and area-size factor that involved low niche differentiation and strong dispersal limitation of organisms from the other NSDF nuclei (Pennington *et al.*, 2009; Banda *et al.*, 2016). Thus, high diversity of NSDF-restricted species is distributed as patches along NSDF distribution (Figure 1). This last idea, suggests ecological and geographical stability for several NSDF patches (i.e. refuges), as well as older clades, favouring the highest values of species diversity and endemism (see Barker *et al.*, 2015). For instance, although the age of Mesoamerican NSDF is not known, Becerra (2005) suggested a Miocene-Pliocene age for north-western Mexico forest based on dated phylogenies of the genus *Bursera*. Thus, it would be important to incorporate more molecular

phylogeographic information and paleo-distribution models (e.g., Côrtes *et al.*, 2015; de Melo *et al.*, 2016), dating divergence times among NSDF endemic lineages and their close relatives. We expect oldest divergence times and stronger phylogeographic structure for these refuge areas, which would be associated with the latitudinal patterns observed here: higher species richness values for both extremes of distribution than for Equatorial areas.

Conservation implications

Our results show strong avifaunal differentiation between the 12 identified NSDF regions, the high levels of geographically restricted species (up to 23%) and the high species turnover (beta diversity) among most groups supporting their taxonomic uniqueness (Table 2). Thus, failure to protect each of the identified NSDF groups would result in major losses of unique species diversity and evolutionary history. An example of this scenario are the Andean dry forests (divided into five avifaunistic groups and with 44 threatened species; Table 1), where current protection falls short of expectations (i.e., Aichi target; UNEP, 2010), in particular given current levels of habitat transformation and destruction by human activities (Miles *et al.*, 2006; Lessmann *et al.*, 2014; Banda *et al.*, 2016).

Considering that NSDF is one of most threatened ecosystems globally, we argue that the IUCN red list shows a worrying (and maybe outdated) perspective on the conservation status of the birds that inhabit this ecosystem (Table 1; Supplementary Material, appendix 2). We note that only 9.6% of species are considered threatened (these including 87 NSDF-restricted species), while 4.8% are listed as “Near Threatened” (NT). Currently, most species (85.6%) are considered to be of ‘Least Concern’ (LC) by the

IUCN. In fact, considering that current protected areas cover only 8.4% of NSDF and represent on average ~10% of the total distribution of the avifauna inhabiting these forests (Prieto-Torres *et al.*, 2018a), it is clear that the level of protection for unique NSDF biotas is woefully inadequate. Much biodiversity still remains unprotected. Thus, studies describing basic diversity patterns are urgently required for the Neotropics because they provide baseline information that is relevant for both in-depth ecological studies on ecosystem dynamics and conservation planning (Rodríguez-Ferraro & Blake, 2008; Duckworth & Altwegg, 2018). From this perspective, contextualizing the avifaunistic relevance of each separate NSDF nucleus, we hope that our results become a basis for future ecological studies and conservation decisions that take into account continental-level faunistic patterns, in order to protect the maximum possible diversity of these highly threatened forests.

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AUTHOR CONTRIBUTIONS.—DAP-T designed the study. DAP-T, ORS, EAB, AGN-S performed the species' selection. DAP-T and AGN-S conducted data collection. DAP-T performed the ecological niche and species distribution modelling. DAP-T, ORS, DS-A performed data analyses. All authors drafted the manuscript.

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SUPPLEMENTARY ELECTRONIC MATERIAL

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Appendix 1. Ornithological collections of international museums that kindly provided data analysed in this study.

Appendix 2. Bird species of the 12 avifaunistic groups identified here for Neotropical seasonally dry forests (NSDF).

Appendix 3. Fifty percent majority rule consensus tree based upon 10,000 random site order-addition hierarchical clustering analyses of 563 grid cells corresponding to distribution of Neotropical seasonally dry forests (NSDF).

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