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Distributional patterns of Neotropical seasonally dry forest birds: a biogeographical regionalization

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Abstract

Neotropical seasonally dry forests (NSDFs) are widely distributed and possess high levels of species richness and endemism; however, their biogeography remains only partially understood. Using species distribution modelling and parsimony analysis of endemicity, we analysed the distributional patterns of the NSDF avifauna in order to identify their areas of endemism and provide a better understanding of the historical relationships among those areas. The strict consensus trees revealed 17 areas of endemism for NSDFs, which involve four large regions: Baja California, Caribbean–Antilles islands, Mesoamerica and South America. These well-resolved clades are circumscribed by geographical and ecological barriers associated with the Gulf of California, the leading edge of the Caribbean plate, the Tehuantepec Isthmus, the Polochic–Motagua fault, the Nicaragua Depression, the Chocó forest, the Amazon basin and the Andean Cordillera. Relationships among groups of NSDFs found here suggest that evolution of their avifauna involved a mixture of vicariance and dispersal events. Our results support the idea of independent diversification patterns and biogeographical processes in each region, including those previously associated with the Pleistocene Arc Hypothesis for NSDFs of south-eastern South America. This study provides a biogeographical framework to open new lines of research related to the biotic diversification of NSDFs.

Introduction

Species heterogeneous distributions across Earth have challenged biogeographers and ecologists trying to unveil the evolutionary and ecological factors driving patterns of biodiversity. Although a variety of theoretical and methodological approaches have been applied to diverse taxonomic groups, the temporal and spatial diversification patterns of numerous biodiversity assemblages remain poorly understood (Wiens and Donoghue, 2004; Weir and Hey, 2006). This has been the case for the avifauna associated with the Neotropical seasonally dry forests (NSDFs), which involves high levels of both species richness and endemism, but has received relatively little attention compared to the avifauna of other Neotropical ecosystems (Stotz et al., 1996; Herzog and Kessler, 2002; Porzecanski and Cracraft, 2005; Ríos-Muñoz and Navarro-Sigüenza, 2012).

Despite the vast accumulation of evidence (i.e. palaeo-palynology, climatology and genetic data) highlighting the evolution and biological diversification of plant taxa (Pennington et al., 2006, 2009; Werneck et al., 2011, 2012; Banda et al., 2016), there are few studies addressing the biogeographical patterns of the avifauna associated with NSDFs at a continental scale (Ceballos, 1995; Stotz et al., 1996). Most studies have

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focused either on the taxonomy of species restricted to or associated with these forests, or on analyses describing distributional patterns of avifauna mainly within isolated NSDF patches (e.g. Cracraft, 1985; Herzog and Kessler, 2002; Porzecanski and Cracraft, 2005; Rodríguez-Ferraro and Blake, 2008; Ríos-Muñoz and Navarro-Sigüenza, 2012; Oswald and Steadman, 2015). Thus, the evolution and biogeography of NSDFs based on birds and other biological groups remain unclear, exacerbating the precarious conservation status of these forests and their associated biota (Werneck et al., 2011; Banda et al., 2016). Understanding the distribution and relationships among NSDF birds—including endemism, patterns of species richness and species turnover—would provide relevant clues for identifying diversification centres and unique biodiversity areas, which subsequently will aid in defining priority conservation units at both regional and continental scales (Gordon and Ornelas, 2000).

Currently, NSDFs show a discontinuous distribution, from north-western Mexico to northern Argentina, and from north-eastern to southern Brazil (Fig. 1). The main NSDF patches are separated from each other by different ecosystems (e.g. humid montane forests, savannas and Amazonia rain forests), showing distinct plant species composition and phenology among patches: in fact, there are no two NSDF patches that share more than half of their plant species (Pennington et al., 2000, 2006, 2009; Banda et al., 2016). Notwithstanding this, Prado and Gibbs (1993) and Pennington et al. (2000) highlighted a number of unrelated NSDF tree species that are widespread in several of the disjunct NSDF areas. These repeated distribution patterns were considered as evidence of a more widespread and perhaps continuous forest formation, with maximum extension during the Last Glacial Maximum (LGM), which may have spread at least into Amazonia, the Andean region and even to the Caribbean coast (see Pennington et al., 2000, 2009).

If any connections existed between some or all NSDFs during recent geological time (i.e. the Pleistocene Arc Hypothesis), we might expect to find clear similarities in species composition (Prado and Gibbs, 1993; Pennington et al., 2000, 2009; Linares-Palomino et al., 2011). Nevertheless, diverse studies have found that the biota of NSDFs includes different species associations and high levels of endemism in Mesoamerica and South America (Ceballos, 1995; Herzog and Kessler, 2002; Becerra, 2005; Porzecanski and Cracraft, 2005; Ríos-Muñoz and Navarro-Sigüenza, 2012; Banda et al., 2016; Oswald et al., 2017), suggesting that independent processes have shaped species compositions and diversification patterns among NSDF biota. Banda et al. (2016) identified 12 floristic groups with a clear north–south division in NSDFs, where the separation of a northern cluster (with four groups from Mexico to Colombia

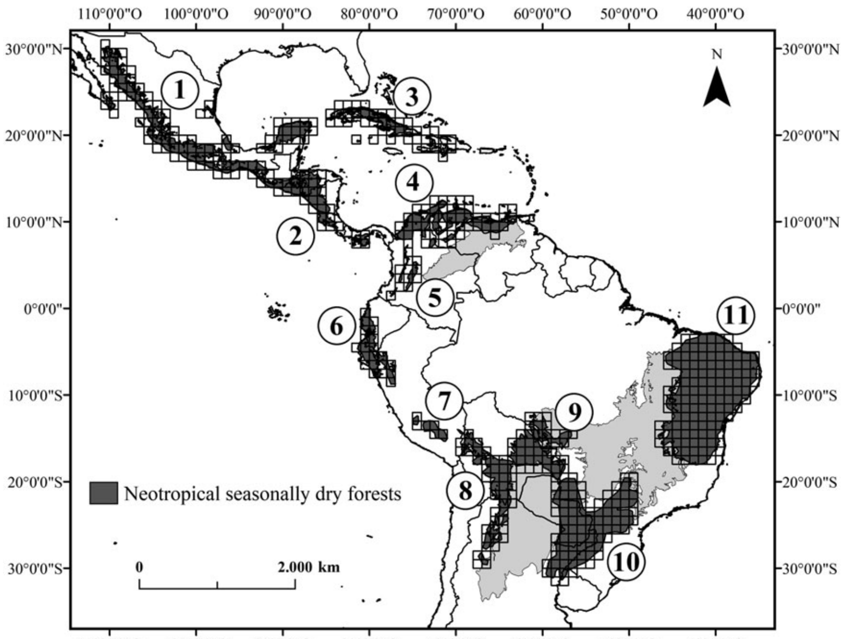

Fig. 1. Geographical distribution of Neotropical seasonally dry forests (NSDFs) showing the grid cells used for the parsimony analysis of endemicity. Numbers correspond to main NSDFs identified by Pennington et al. (2000) and Banda et al. (2016): Mexico (1); Central America (2); Caribbean–Antilles (3); Caribbean coast of Colombia and Venezuela (4); Inter-Andean valleys of Colombia (5); Pacific Equatorial (6); Inter-Andean valleys of southern Peru: Apurimac-Mantaro (7); Sub-Andean Piedmont (8); the Chiquitano forests (9); Misiones Province (10); and Caatinga (11). Light grey represents the savanna and Chaco ecosystems. Map modified from Pennington et al. (2000).

and Venezuela, including the Caribbean islands) reflects the effectiveness of the rain forests of Amazonia and the Chocó as a barrier to migration. In fact, Pennington et al. (2009) and Linares-Palomino et al. (2011) suggested that widespread species in NSDFs are an exception: only 1.43% of plant species are recorded in ~50% of the floristic nuclei defined across the region. This paucity of widespread NSDF species argues strongly against a widespread Pleistocene NSDF formation throughout the Neotropics, rather suggesting dispersal limitation in NSDF biota and a mixed evolutionary history across their distribution, with ecological similarities arising from climatic convergence (Cracraft, 1985; Mayle, 2004; Becerra, 2005; Côrtes et al., 2015; Banda et al., 2016; de Melo et al., 2016).

More than 1000 bird species are known to inhabit the NSDFs, and this avifauna is composed of a mixture of NSDF-restricted endemics, lowland taxa, and species that are more common at higher or lower elevations (Stotz et al., 1996). In addition, several species consist of highly isolated populations, often well differentiated, and with very limited or completely interrupted gene flow (Ribas et al., 2009; Rodríguez-Gómez et al., 2013; Navarro-Sigüenza et al., 2017; O'Connell et al., 2017). Although much is known regarding the biology and distribution of these birds, no recent and thorough distributional analysis has been performed within a cladistic framework. Cracraft (1985) produced the first analysis of distributional patterns and areas of endemism of the South American avifauna, whereas Ríos-Muñoz and Navarro-Sigüenza (2012) analysed species richness patterns in Mesoamerica, suggesting a first biogeographical regionalization for these forests in the region. However, these studies have only covered a fraction of the distribution of NSDFs and lack the general perspective necessary to explore the historical assemblage of NSDF avifaunas. Only studying the distribution patterns of bird species inhabiting the entire NSDFs could allow the identification of particular regions (areas of endemism) with common spatial patterns for their associated taxa and facilitate the recognition of those processes (e.g. vicariance, dispersal, extinction) that promote their evolution (e.g. Rosen and Smith, 1988; Rojas-Soto et al., 2003; Sánchez-González et al., 2008; Morrone, 2014b).

Methods using parsimony algorithms have been proposed as valuable tools for detecting similarities among biogeographical areas based on their associated taxa. One of these methods is parsimony analysis of endemicity or PAE (Rosen and Smith, 1988; Morrone, 2014c). Despite criticisms in its application (e.g. it ignores evolutionary relationships among species and is applicable only to closed ecosystems, to which the lineages under analysis should be endemic; see Brooks and van Veller, 2003; Peterson, 2008), diverse studies have argued for its utility for establishing biogeographical classifications and the relationships among these units (Morrone and Escalante, 2002; Rojas-Soto et al., 2003; Nihei, 2006; Morrone, 2014c), particularly when phylogenies for all groups are unavailable. In fact, PAE has been increasingly used to understand biological similarities between biogeographical areas, because the results obtained consist of nested or hierarchical groups of biota, where the congruent species' distributional patterns demonstrate that taxa have been affected by common factors and terminal dichotomies are interpreted as areas sharing the most recent biogeographical history (Rosen and Smith, 1988; Morrone, 2005, 2014c).

In this study we integrated species distribution models (SDMs) of ~1300 birds and PAE to identify areas of endemism for NSDF avifauna, as well as their relationships, performing a regionalization of NSDF birds across the whole Neotropical region. Given that patterns found in previous studies with NSDF plants (Linares-Palomino et al., 2011; Banda et al., 2016) have proved to be affected by dispersal to some extent, we hypothesized that birds might exhibit similar patterns, where the potential areas of endemism must be circumscribed by geographical and ecological barriers that have shaped the species composition and diversification patterns among NSDF avifauna. Our results may be used as a framework for comparison with independent sets of evidence, such as area cladograms obtained through cladistic biogeographical and phylogeographical studies (Rosen and Smith, 1988; Morrone and Escalante, 2002). Finally, these results provide a better understanding of the biogeographical relationships of NSDFs and their avifauna, which also enhance the conceptual bases for future conservation decisions—taking into account continental-level species patterns—to manage this highly threatened ecosystem.

Methods

Definition of NSDFs

Given the difficulties in defining NSDF limits from other ecosystems—including savannas, montane forests, mangroves and more recently agricultural land—we adopted a broad definition that includes all forests having a closed canopy, typically dominated (> 50%) by semi-deciduous and deciduous trees, that are present in frost-free areas, with a mean annual temperature > 25 °C, total annual precipitation of 700–2000 mm and at least three or more dry months (precipitation < 100 mm) per year (Murphy and Lugo, 1986; Sánchez-Azofeifa et al., 2005, 2013; Banda et al., 2016). This vulnerable ecosystem, which encompasses 42 ecoregions according to Olson et al. (2001), is discontinuously distributed in 18 countries (including the Caribbean islands) across the continent (Fig. 1).

Species data gathering

We created a complete list of the bird species inhabiting NSDFs, which was compiled from sources that offer information on the habitat characteristics for each species (e.g. Stotz et al., 1996; Gill and Donsker, 2015), and from a database of presence records (see below). Then, in a second selection, we excluded all the species marginally inhabiting NSDFs and those of seasonal presence (i.e. inter-tropical migrants) because they may bias the identification of patterns of endemicity (Rojas-Soto et al., 2003; Sánchez-González et al., 2008; Ríos-Muñoz and Navarro-Sigüenza, 2012). Species marginally inhabiting NSDFs were defined as those whose geographical ranges included less than 10% of NSDFs (see Species distribution models section below) because their distribution corresponded to occasional or accidental records within NSDF areas. We followed the taxonomy of Gill and Donsker (2015) for the birds of Mexico and Central America, as well as the South American Classification Committee bird list (SACC; Remsen et al., 2017) and the Clements Checklist (Clements et al., 2015) for the birds of South America.

Occurrence records for each species were gathered from: (1) the Atlas of the Birds of Mexico (Navarro-Sigüenza et al., 2002, 2003); (2) Atlas de Registro de Aves Brasileiras (ARA; http://ara.cemave.gov.br/); (3) specimen records directly obtained from ornithological collections worldwide (see Appendix S1); (4) records obtained through the first author's fieldwork in Mexico and Venezuela; and (5) online scientific collection databases [i.e. Global Biodiversity Information Facility (GBIF), eBird, and SiB-Colombia (sibcolombia.net)]. For all species, records repeated in multiple sources were removed, retaining only unique localities (within 1 km^2). In addition, to identify problematic or imprecise species occurrences, we compared the spatial distribution of obtained records with the ranges for species as defined in the websites Neotropical Birds (https://neotropical.birds.cornell.edu) and BirdLife International (https://www.birdlife.org/), removing all those mismatched records. We omitted those records with geographical information that could not be verified, as well as those records without bioclimatic data. Geographical coordinates were transformed to decimal degrees, based on the WGS84 datum.

Species distribution models

Traditionally, PAE has been performed using data from individual specimens and localities. Unfortunately, for most species, few observations and/or specimens are available, and when they exist, data are generally biased by site accessibility (Peterson, 2001). Thus, considering the immense efforts required to define maps for the species' distributional ranges, the use of computational algorithms to generate species distribution models (SDMs) represent a good alternative to obtain accurate species' distribution maps (Peterson, 2001; Soberon and Peterson, 2005). Using SDMs has the advantage of minimizing spatial gaps inherent to species' distributional information, improving the resolution of biogeographical hypotheses in PAE by filling in poorly known and/or non-surveyed areas (e.g. Rojas-Soto et al., 2003; Sánchez-González et al., 2008; Ríos-Muñoz and Navarro-Sigüenza, 2012).

Although recent studies have shown that there are uncertainties when forecasting species distributions depending on the algorithm used (Heikkinen et al., 2006), we decided to use the maximum entropy machine-learning algorithm (MaxEnt) given its proven performance in calculating the most likely distribution of the focal species as a function of occurrence localities and environmental variables (Elith et al., 2006, 2011; Elith and Leathwick, 2007). For each species, we obtained a potential SDM using MaxEnt 3.3.3k (Phillips et al., 2006). To characterize the potential distribution based on ecological niche modelling, we used the environmental data from WorldClim 1.4 (Hijmans et al., 2005), which includes a set of 19 climatic variables summarizing aspects of precipitation and temperature at 30-arc second resolution (~1 km^2 cell size). Although procedures for SDMs using the 19 climatic variables have been discussed extensively elsewhere (e.g. Graham, 2003b; Peterson et al., 2011; Dormann et al., 2013), we used all 19 variables to simplify the process of modelling the distribution of the large number of species selected for analyses (~1300). The MaxEnt algorithm compensates for co-linearity between variables using a method for regularization that deals with feature selection, ranking the contribution of each one throughout the analysis; thus, there is less need to remove correlated variables (Elith et al., 2011).

On the other hand, given that SDMs must consider historical factors affecting the species distributions, we used specific areas for model calibration (i.e. accessible area or M) for each species (Soberon and Peterson, 2005; Barve et al., 2011). These calibration areas were established based on the intersection of occurrence records with the Terrestrial Ecoregions (Olson et al., 2001) and the Biogeographical Provinces of the Neotropical region (Morrone, 2014a). Such consideration was based on the assumption that these regions may define the historical accessible areas for each species in geographical space.

Because low sample size in occurrence records may affect model performance (Pearson et al., 2007; Owens et al., 2013), we only modelled species with five or more records for those that were geographically restricted (Stotz et al., 1996; Ríos-Muñoz and Navarro-Sigüenza, 2012; Gill and Donsker, 2015). For widely distributed species, we only considered those with at least 20 independent occurrence records. SDMs for species that had between five and 20 records were developed using all presence data and assessed with a Jackknife test (Pearson et al., 2007), while SDMs for species with > 20 records 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). In this last case, performance of the MaxEnt models was evaluated by calculating the commission and omission error values (Anderson et al., 2003) and the Partial-ROC curve test (Peterson et al., 2008). All models were run with no extrapolation to avoid artificial projections of extreme values of ecological variables (Peterson, 2008; Elith et al., 2011) and all other MaxEnt parameters were set to default.

In all cases, we used the logistic response to obtain digital maps containing the values for habitat suitability (continuous probability from 0 to 1; Phillips et al., 2006; Elith et al., 2011), which were subsequently converted into binary presence–absence data based on the ‘tenth percentile training presence’ (TPTP) as threshold value (Liu et al., 2013). This threshold represents a criterion that minimizes commission errors—rejecting the lowest (10%) suitability values of training records—in our final binary maps, allowing for a better recovery of species distributional areas (Escalante et al., 2013; Owens et al., 2013). To generate only the “best hypothesis map” for each species to use in subsequent analysis, we compared our final maps against available distributional information of each species (e.g. Cracraft, 1985; Gordon and Ornelas, 2000; Herzog and Kessler, 2002; Schulenberg et al., 2010; Gill and Donsker, 2015; Herzog et al., 2016) discarding those with high commission errors and/or those that were statistically not significant.

Considering these final maps, we determined the species’ ecosystem specificity in order to identify those NSDF-restricted species. This step was developed based on two approaches: (1) calculating the degree of coverage of the geographical distributions for each species across the Neotropical ecosystems; and (2) using the modification proposed by Sánchez-González and Navarro-Sigüenza (2009) for published endemicity indices (Crisp et al., 2001; Linder, 2001). For the first approach, we divided the species’ range area predicted in each ecosystem by the total species’ range area predicted in the SDM. For the second approach, we obtained the index of restriction (IR) by substituting the number of quadrants (see Crisp et al., 2001; Linder, 2001) for the number of ecosystems in which a given species was reported as present by our models. This information was compared with the databases of Stotz et al. (1996), which offer information about the habitat for each species in order of preference. For both analyses, the area per ecosystem was delimited by selecting the terrestrial ecoregions of the world (Olson et al., 2001), which provides a framework for the identification of, and comparisons among, representative habitats, along with the approximate boundaries of natural communities and ecosystems prior to major land-use change. Based on this idea, we subdivided the terrestrial Neotropical area into 14 major ecosystems—which involved 263 ecoregions (Olson et al., 2001)—and overlapped them with each SDM map.

Parsimony analysis of endemicity (PAE)

To assess the relationships among NSDFs and to identify areas of endemism, we implemented a PAE (Rosen and Smith, 1988; Morrone and Escalante, 2002). This method joins areas (analogous to terminal taxa), based on their shared taxa (analogous to characters), according to the most parsimonious explanation (Morrone, 2014c). First, we divided the study area into 563 grid cells of size 1° × 1° (Fig. 1), and constructed a species presence/absence binary matrix (coded as “1” if present or “0” if absent) on each cell (Appendices S2 and S3), based on the individual SDM maps for all species (hereafter “complete species matrix”). From a continental (broad) scale, this grid size could be considered a fine-grained resolution, which allows us to connect small cells when locality data points are scattered and produce low data resolution (Gutiérrez-Velázquez et al., 2013).

Then, given that Pennington and Lavin (2016) argued that—at least for trees—NSDFs show phylogenies that are geographically structured (contrary to the pattern found in rain forests and savannas), we built an additional binary matrix employing only those species defined as NSDF-restricted (hereafter “restricted species matrix”; see Appendix S2). This last step is important because it allows us to assess and compare the distributional patterns of NSDF avifauna considering different but parallel histories, providing a better understanding of the historical relationships among geographical areas (Ricklefs, 1987; Wiens and Donoghue, 2004; Weir and Hey, 2006; O’Connell et al., 2017). For both cases, an extra hypothetical area coded only with “0” was added to the matrices and used to root the cladogram, which would be equivalent to a hypothetical “ancient” area without taxa (Rosen and Smith, 1988; Morrone and Escalante, 2002; Morrone, 2014c).

The data matrices were analysed with a heuristic search based on the New Technology algorithm in TNT ver. 1.5 software (Goloboff and Catalano, 2016), finding the minimum length five times. After performing several tests surveying the weighting value, we used a homoplasy penalization (k) equal to 3, as proposed by Goloboff (1993), which preserved the clades obtained with lowest values, restricting homoplasy severely and maximizing the number of synapomorphies. The obtained strict consensus trees were analysed in WinClada (Nixon, 1999) and plotted (Appendices S4 and S5) in a geographical map using ArcMap 10.2 (ESRI, 2010). Areas of endemism were recovered based on at least two synapomorphies (Platnick, 1991), also including taxa with consistency index (CI) = 0.5 (only if taxa showed reversions), because they may represent a distinctive feature of occurrence (autopomorphies) that is coded as unique presence to a given area (Escalante, 2015). Nodal support in cladograms was assessed by performing a bootstrap analysis with 1000 replicates in TNT.

Because some authors have discussed the need to increase the historical signal for finding relationships among study areas and confer a “dynamic interpretation” to PAE (Rosen and Smith, 1988; Cracraft, 1991; Nihei, 2006; Vázquez-Miranda et al., 2007), we performed two additional analyses taking into consideration the hierarchical information from genera and species together (Cracraft, 1991; Porzecanski and Cracraft, 2005). In this sense, our results from PAE could be tested by a cladistic biogeographical analysis and compared with available phylogenies of taxa inhabiting the areas investigated (Rosen and Smith, 1988; Morrone, 2005; Sánchez-González et al., 2008). However, we did not observe any difference in general patterns (i.e. NSDF regions identified) between the “species” and “species-genera” approaches (Appendices S4 and S5). The results shown herein are based on strict consensus cladograms (i.e. complete species vs. NSDF-restricted species) only from the analyses using species information.

Finally, considering that patterns of relationships among areas are easily retrieved within well-defined geographical clades (Grismer, 2000; Morrone, 2014c), we performed two additional PAEs (i.e. complete and restricted species approaches) based on the 17 NSDF geographical groups or regions identified in the cladograms for the 563 sampled grids (Appendix S4). This last step allowed us to increase the numbers of synapomorphies, grouping cell grids where data quantity is low and splitting quadrants that generate conflict (Morrone and Escalante, 2002), determining the relationships among areas (Morrone, 2014c). The resulting geographical groups were supported by taxa as synapomorphies (see Results, Table 1). In all cladograms, we performed a bootstrap analysis with 1000 replicates to assess nodal support. The 17 NSDF regions identified herein were named based on a proposal by Pennington et al. (2000) and Banda et al. (2016).

Results

The occurrence database contained ~1 248 000 records from 1298 bird species (from 78 families and 511 genera) selected in this study. For the 1242 species containing more than 20 independent occurrence records, all SDMs showed high AUC (Area Under Curve for Receiver Operating Characteristic) values (ranking from 0.7 to 0.99) and Partial-ROC ratios (ranking from 1.15 to 1.99). For the remaining 56 species, the Jackknife test showed that models were statistically significant ($P < 0.01$). Thus, performance values for both modelling approaches indicated that models of the species’ potential distributions were accurate.

Based on the SDMs, we observed that 36.4% of bird species have at least 40% of their distribution within NSDFs, while 30.4% were between 25% and 40%, and 33.1% had between 10% and 25% overlap with NSDF areas. Additionally, the values of ecosystem/ecological specificity showed that 40.9% of species tended to be present in more than three ecosystems (IR < 0.2), while only 13.7% are present between one and two (IR > 0.5). Most of the NSDF bird species (45.4%) are present in at least three ecosystems (IR = 0.3). From these approaches, we determined that ~43% (n = 557) of species initially considered are highly associated and/or endemic to NSDFs (Appendix S2). Final species selection was established based on those with at least 33% of their distribution within the NSDF and an IR ≥ 0.3, where the NSDF represented the main ecosystem occupied.

For the complete species matrix approach (representing 563 sampled grids) we obtained a strict consensus cladogram of 16 367 steps [CI = 0.07, retention index (RI) = 0.86], while for the restricted species matrix approach the consensus cladogram consisted of 4172 steps (CI = 0.13, RI = 0.89). Both analyses revealed 17 NSDF geographical groups, showing ~53% coincidence in the areas of endemism between the two approaches (i.e. complete and restricted species) and containing almost the same synapomorphies (Table 1). Individual cladograms and their geographical correspondence with the grid cell groupings for both approaches are presented in Appendix S4.

Subsequently, for PAE considering the 17 NSDF regions in the complete species approach, we obtained a strict consensus cladogram with 2040 steps (CI = 0.63, RI = 0.75), while the restricted species approach showed 705 steps (CI = 0.78, RI = 0.80). Both cladograms were the base to propose our biotic regionalization of the NSDF (Fig. 2). In this proposal, we observed that Baja California is the sister group (at the base of the tree) of the rest of NSDF clades; the Caribbean–Antilles islands are separated from the well-defined clade that includes the Mesoamerican and South American areas. The complete species cladogram

Table 1
Synapomorphic species for the clades (i.e. potential areas of endemism, PAE) for avifauna of the Neotropical seasonally dry forests (NSDFs), considering both approaches (matrices of information): complete vs. NSDF-restricted species. Individual cladograms and the geographical correspondence obtained for the grid cells are presented in the supplementary material (Appendix S4)

		Nodes in PAE	
NSDF region	Species	Complete	Restricted species
Caribbean–Antilles Islands	*Tachornis phoenicobia*, *Quiscalus niger*	a	–
Cuba (Cu)	*Coccyzus merlini**, *Contopus caribaeus**, *Corvus nasicus**, *Icterus melanopsis**, *Margarobyas lawrencii**, *Melanerpes superciliaris**, *Myiarchus sagrae**, *Spindalis zena**, *Tiaris canorus**	c	a
Haiti, Dominican Republic and Puerto Rico (HP)	*Amazona ventralis*, *Chlorostilbon swainsonii*, *Coccyzus longirostris*, *Contopus hispaniolensis*, *Corvus leucognaphalus*, *Dulus dominicus*, *Euphonia musica*, *Icterus dominicensis*, *Melanerpes striatus*, *Mellisuga minima*, *Microligea palustris Myiarchus stolidus*, *Nesoctites micromegas*, *Patagioenas inornata*, *Phaenicophilus palmarum*, *Psittacara chloropterus*, *Spinus dominicensis*, *Todus angustirostris*, *Todus subulatus*, *Tyto glaucops*, *Vireo nanus*	b	–
Baja California (BC)	*Basilinna xantusii*, *Geothlypis beldingi*, *Toxostoma cinereum*	d	–
Mesoamerican mainland	*Amphispiza quinquestriata*, *Camptostoma imberbe**, *Megascops guatemalae**, *Molothrus aeneus*, *Pachyramphus aglaiae**, *Stelgidopteryx serripennis*, *Turdus rufopalliatus*	e	g
Sonora to Panama	*Arremonops rufivirgatus*, *Geothlypis poliocephala*, *Vireo hypochryseus*	f	–
Northwestern Mexico (PS)	*Amphispiza quinquestriata*, *Polioptila nigriceps*, *Turdus rufopalliatus*	–	h
Northern Oaxaca (SP)	*Aimophila notosticta*, *Calothorax pulcher*	–	i
Yucatán Peninsula (YP)	*Cyanocorax yucatanicus**, *Melanoptila glabrirostris**, *Melanerpes pygmaeus**, *Meleagris ocellata*, *Myiarchus yucatanensis*, *Nyctiphrynus yucatanicus*	g	j
Central America (CAm)	*Cantorchilus modestus*, *Zimmerius vilissimus*	h	–
North Central America (CAmN)	*Campylopterus rufus**, *Icterus maculialatus**	i	k
South Central America (CAmS)	*Geothlypis chiriquensis*, *Thamnophilus bridgesi*	j	–
Northern South America	*Campylorhynchus griseus**, *Icterus nigrogularis**, *Myiarchus apicalis*, *Picumnus granadensis*, *Picumnus squamulatus*, *Sporophila intermedia*	k	e
Caribbean coast of Colombia and Venezuela (CCV)	*Campylorhynchus nuchalis**, *Crax daubentoni*, *Crypturellus erythropus*, *Euphonia trinitatis**, *Icterus icterus**, *Inezia caudata*, *Myiarchus venezuelensis**, *Ortalis ruficauda**, *Saltator orenocensis**, *Synallaxis cinnamomea**, *Thamnophilus melanonotus**, *Thraupis glaucocolpa**	l	f
Pacific Equatorial (PE)	*Amazilia amazilia**, *Arremon abeillei**, *Basileuterus trifasciatus**, *Chaetocercus bombus**, *Columbina cruziana**, *Contopus punensis**, *Cyanocorax mystacalis**, *Dives warczewiczi**, *Geothlypis auricularis*, *Mecocerculus calopterus**, *Melanopareia elegans**, *Mimus longicaudatus**, *Myiodynastes bairdii**, *Sturnella bellicosa**, *Thamnophilus bernardi**	m	c
Sub-Andean piedmont (SA-P)	*Arremon torquatus**, *Leptotila megalura**, *Megascops hoyi*, *Microstilbon burmeisteri*, *Psilopsiagon aymara**, *Rhynchotus maculicollis**, *Sappho sparganurus*	n	b
Caatinga (CaB)	*Casiornis fuscus**, *Herpsilochmus sellowi**, *Pseudoseisura cristata**, *Paroaria dominicana**, *Picumnus pygmaeus**	o	d

*Synapomorhic species reported for both PAEs.

differed from the restricted one, because the northernmost limit of NSDFs (SS group; Fig. 2a) appears in the former as sister group of the Mesoamerican and South American mainland grid cells, whereas in the restricted species cladogram these grid cells appear within north-western Mexico (Fig. 2b).

Following the nested pattern, NSDFs showed a clear division into two main well-defined clades: one contains the Mesoamerican region, from north-western Mexico to Panama, and another comprises all of the South American areas. Focusing in the Mesoamerican region, we observed that the Yucatan Peninsula (YP) is sister to all other NSDF groups located in Central America and north-western Mexico (Fig. 2). However, it is noteworthy that the Panama region (Pa group; Fig. 2b), which represents the southernmost limit of Mesoamerican NSDF range, is the most basal subclade for the restricted species approach, whereas it is geographically included within the South Central America group (CAmS in Fig. 2a) for the complete species cladogram. However, despite the slight differences in topology between the two cladograms (complete and restricted species) for the main NSDF in Mesoamerica, where some are completely nested

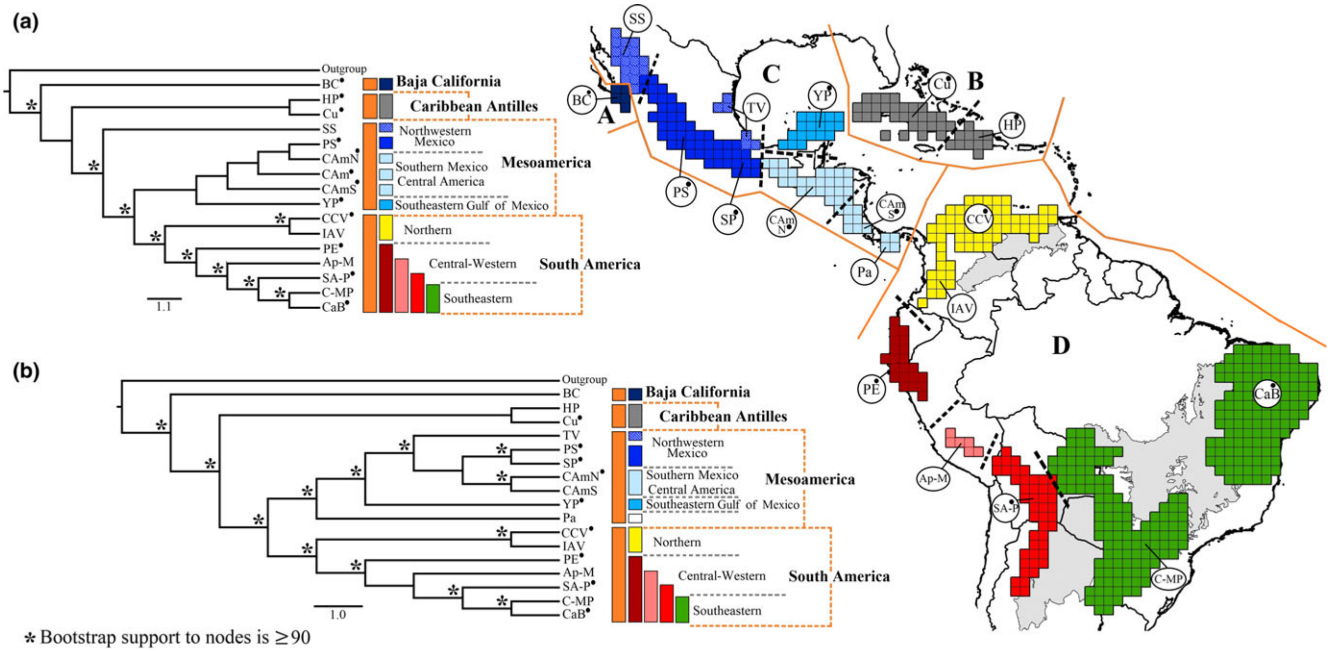

Fig. 2. Regionalization of the Neotropical seasonally dry forests (NSDFs) based on the avifauna distribution and their relationships considering complete (a) vs. NSDF-restricted (b) species approaches (matrices of information). The cladograms revealed 17 NSDF geographical groups, which involved four large regions: The Baja California (A), Caribbean–Antilles islands (B), Mesoamerican (C) and South America (D). Acronyms in both cladograms and the map correspond to identified NSDF regions and areas of endemism [more than two synapomorphies (species; represented with a black circle]: BC = Baja California; Cu = Cuba island; HP = Haiti, Dominican Republic and Puerto Rico islands; SS = Sonora and Sinaloa forests; PS = Mexican Pacific slope lowlands; SP = northern Oaxaca in southern Mexico; TV = Tamaulipas–Veracruz states; YP = Yucatan Peninsula; CAmN = northern Central America; CAmS = nouthern Central America; CAm = Central America; Pa = Panama; IAV = Inter-Andean Valleys of Colombia; CCV = Caribbean Colombia–Venezuela; PE = Pacific Equatorial; Ap-M = Apurimac-Mantaro; SA-P = Sub-Andean Piedmont; C-MP = Chiquitano forests and Misiones Province; CaB = Brazilian Caatinga. These well-resolved clades are circumscribed by geographical and ecological barriers (dotted black lines) associated with the Gulf of California, the leading edge of the Caribbean plate, the Tehuantepec Isthmus, the Polochic–Motagua fault, the Nicaragua Depression, the Chocó forest, the Amazon basin and the Andean Cordillera (including the Inter-Andean Valleys). Well-supported clades [more than two synapomorphies (species)] are shown with a black circle in the acronyms of NSDF regions (see Table 1 for a complete description).

(Fig. 2a) and others showed some reciprocally monophyletic groups (Fig. 2b), the division is clear between the north-western Mexico [including the sections of Tamaulipas and Veracruz (TV), Pacific Mexican forest (PS), and Northern Oaxaca in southern Mexico (SP)] and the Central American (from southern Mexico to Panama) regions. This last region is subsequently divided into two main subgroups: (1) the northern (CAmN; from southern Mexico to Nicaragua) and (2) the southern subgroup (CAmS; from Nicaragua to Panama).

Furthermore, for both approaches we observed that NSDFs in South America involved a well-resolved clade divided into two reciprocally monophyletic groups (Fig. 2). One group comprises the grid cells that correspond to northern South America, containing all areas throughout the inter-Andean valleys (IAV; from Colombia to the Caribbean coast), as well as the north-western stretch of the Orinoco river (including the Cordillera de la Costa and the Maracaibo Lake depression, in Venezuela) and the dry forests located in the western slope of the Sierra de Perijá (from La Guajira to Santander-Córdoba Departments in Colombia; CCV subgroup). The second group is formed by the forests located throughout the Pacific Equatorial (PE) region (an area of endemism located from western Ecuador to north-western Peru, including the central Andean Valleys) and a sister clade that includes the dry valleys located in southern Peru [i.e. Apurímac-Mantaro and Tarapoto-Quillabamba forests (Ap-M)] as well as the south-eastern South America areas (i.e. NSDFs from western Bolivia and north-eastern Argentina to north-eastern Brazil). For this last South American group, two well-supported subgroups are formed consecutively and separately: one contains the endemism area at the Sub-Andean piedmont forests (SA-P) of north-western Argentina and western Bolivia, and the other corresponds to the Chiquitano and Misiones Province [i.e. south-eastern Bolivia, north-eastern Argentina, Paraguay and Uruguay (C-MP)], and the endemism area of Caatinga (CaB; located in north-eastern Brazil).

Discussion

The Baja California's NSDF

In regional cladograms the Cape of Baja California forms a distinct unit, which supports the idea of a somewhat independent biogeographical history, as has been suggested in previous avian regionalizations. Isolation of the NSDF in the Cape region from those in western Mexico (5.5–4.0 Mya) by the Gulf of California has promoted the differentiation and a high degree of endemism associated with the Cape of diverse groups, including mammals, birds, snakes and insects (Grismer, 2000; Rojas-Soto et al., 2003; Ríos-Muñoz and Navarro-Sigüenza, 2012; O'Connell et al., 2017). However, given the closest affinities of avian species with the nearby continent at the northern portion of the Peninsula (Rojas-Soto et al., 2003), it seems clear that the Cape avifauna originated through a terrestrial route from the northern to the southern tip of the Baja California Peninsula (Rojas-Soto et al., 2003; O'Connell et al., 2017).

The Caribbean–Antilles avifauna

As found in previous biogeographical studies (e.g. Crother and Guyer, 1996; Zink et al., 2000; Graham, 2003a,b; Vázquez-Miranda et al., 2007), our analyses support a monophyletic origin for groups of organisms inhabiting this region. However, a potential difficulty in explaining this monophyly is posited by the question of how birds reached those islands, given that the complex geological history of the region included "at least eight events of fragmentation and seven of hybridization" (Rosen, 1985). In our study, we observed that several taxa acted as homoplasies, which can be interpreted as the result of either dispersal or extinction events (Vázquez-Miranda et al., 2007). Considering that ~41% (n = 56 species) of NSDF avifauna is endemic and, of these, only eight species (two of which are synapomorphies) were shared among the three islands (Cuba, Haiti, Puerto Rico), the observed pattern is more probably explained by a mixture of vicariance and dispersal events, especially because those islands have had relatively recent bird exchanges (Vázquez-Miranda et al., 2007). This idea is more parsimonious than assuming concordant dispersal patterns of individual taxa, particularly considering the biota's affinities with both Central America and/or South America (Crother and Guyer, 1996; Zink et al., 2000; Graham, 2003a,b).

Despite the existence of vicariance models explaining affinities between the avifauna of this region with the mainland (e.g. the temporal separation of the leading edge of the Caribbean plate [beginning in the Late Cretaceous and finishing in the Miocene–Middle Pleiocene]; Rosen, 1985; Iturralde-Vinent and MacPhee, 1999; Graham, 2003a,b; Morrone, 2014b), it is important to consider that dispersal events could have contributed to defining the avifaunistic assemblages of this region, as apparently occurred in the history of the woodpecker genus *Melanerpes* (Navarro-Sigüenza et al., 2017). It is difficult to compare the present study with earlier studies because they used different islands, different taxa and different continental regions as a reference. Therefore, further studies are needed to assess the relative age of these diversification centres and their biogeographical relationships.

The Mesoamerican NSDFs

The division of this clade into sub-groups supports the long isolation history of the identified Mesoamerican regions. Our results highlight the importance of the Mexican Plateau and the Tehuantepec Isthmus in shaping the distribution of Mesoamerican biotas in both highlands and lowlands (Becerra, 2005; Sánchez-González et al., 2008; Ríos-Muñoz and Navarro-Sigüenza, 2012; Banda et al., 2016). The clear differentiation of the groups on both sides of the Tehuantepec Isthmus (north-western Mexico, Yucatan Peninsula and Central America; Fig. 2), as well as the subdivisions observed within the northern Mexican regions [Sonora-Sinaloa (SS), northern Oaxaca (SP) and Tamaulipas–Veracruz (TV) areas] might be explained by higher diversification rates compared to other dry forest areas, as detected for example in the hummingbird *Amazilia cyanocephala* (Rodríguez-Gómez et al., 2013; O'Connell et al., 2017). Although the age of Mesoamerican NSDFs is not known, the fossil record and dated phylogenies suggest a Miocene–Pliocene age at least in north-western Mexico (Becerra, 2005). These forests probably expanded to Central America (where fossil evidence seems to suggest that it invaded only after 2.5 Mya; Graham and Dilcher, 1995) after the Sierra Madre Occidental and the Transmexican Volcanic belt were formed, creating conditions for the establishment and persistence of NSDFs.

The clear separation observed for the Sonora-Sinaloa (SS) subgroup and the rest of the Mesoamerican mainland (Fig. 2a) could be explained by the high affinities with Nearctic biota of this northernmost area (Stotz et al., 1996). In fact, despite the high species turnover (n = 188) observed between the Sonora-Sinaloa subgroup and the rest of the Mesoamerican NSDFs, these northernmost forests shared 54 species (95%) with those reported for the Baja California region. Furthermore, we propose a region formed by all areas west of the Tehuantepec Isthmus located in Mexico [including NSDF in Tamaulipas–Veracruz (TV) and except those corresponding to Baja California (BC)], which is supported by previous biogeographical hypotheses, and also suggested that the north-eastern Gulf of Mexico is biogeographically distinct from the southern and south-eastern part of the Gulf coast (Liebherr, 1994; Hernández-Baños et al., 1995; Marshall and Liebherr, 2000; Ríos-Muñoz and Navarro-Sigüenza, 2012).

On the other hand, separation within the south-eastern Isthmus groups (light blues in Fig. 2) supports the biogeographical hypothesis of vicariant processes associated with the Polochic–Motagua fault and the Nicaragua Depression in the region (Morrone, 2001; Schuster et al., 2003; Liede and Meve, 2004). Here, we identified at least three distinct regions, suggesting the existence of bird assemblages with independent biogeographical histories, probably shaped by new immigrants from dispersal events between South and North America after the establishment of the Panama Isthmus (Smith and Klicka, 2010). For instance, we observed that ~73% of the NSDF avifauna is shared between southern Central America and northern South America (with ~72% of NSDF-restricted species shared between the NSDF from Panama and northern South America), confirming the existence of strong affinities between the two regions (Linares-Palomino et al., 2011; Ríos-Muñoz and Navarro-Sigüenza, 2012; Banda et al., 2016).

In the Panama region, differences in the affinities between the cladograms for this region may be influenced by the inclusion (i.e complete approach) or the exclusion (i.e. restricted approach) of species widely distributed in the region and inhabiting other ecosystems surrounding NSDFs. In this sense, such differences could be explained by different temporal patterns of speciation documented for taxa associated with humid and dry habitats across the Isthmus of Panama (Smith et al., 2012). The Panama area has had a history of expanding and contracting processes for both the dry and the humid forests, and even when both habitats consist of "young" and "old" species, the dry habitat species are geographically more distant from their nearest counterpart in Central America and northern South America, compared with species from the humid habitats in these regions (Oswald and Steadman, 2015; Oswald et al., 2017). This phenomenon, if generalized, is probably an important contributor to biogeographical patterns in the southernmost section of the Mesoamerican region (Sánchez-González et al., 2008; Ríos-Muñoz and Navarro-Sigüenza, 2012; Smith et al., 2012).

South American NSDF areas and the Pleistocene Arc Hypothesis

Previous studies of distributional patterns within the South American biota have accepted the hypothesis that areas of endemism have arisen by isolation of more widespread biotas. This scenario is commonly associated with paleogeographical changes, alterations in river systems, Pleistocene climatic fluctuations or a mixture of all these processes (Herzog and Kessler, 2002; Werneck et al., 2012). However, we find little support for widespread Pleistocene NSDF formation throughout South America, because few species (10.33%; $n = 100$ species) are widespread and shared by more than 75% of South American areas. This result is concordant with NSDF plant patterns recently reported by Linares-Palomino et al. (2011) and Banda et al. (2016), as well as with the restricted climatic corridors found by Werneck et al. (2011), which suggest that LGM climate was probably too dry and cold to support large tracts of NSDFs across the continent.

Some authors suggest that long-distance ancient dispersal events of unrelated taxonomic groups are less likely than vicariant associations (Werneck et al., 2011; de Melo et al., 2016). Likewise, there is substantial support that NSDF is a dispersal-limited biome given the phylogenetic niche conservatism and strong geographically structured phylogenies for woody plant clades (Pennington et al., 2009; Pennington and Lavin, 2016). Thus, an allopatric-vicariance explanation—delineated by major geographical or ecological barriers before the Pleistocene—seems more plausible to explain the evolution and relationships among all these forest areas, which is supported by results based on endemic taxa. For instance, the biogeography of *Brotogeris* parakeets implies a dynamic history for South American biomes since the Pliocene, corroborating that geological evolution of Amazonia has been important in shaping its biodiversity with taxa endemic to NSDFs and other biomes (Ribas et al., 2009). In this sense, our results suggest that the wide distributions of a relatively low proportion of NSDF species and ecological similarity among them (including specialists and generalists) may reflect only limited recent long-distance dispersal events and species exchange (Dick et al., 2003, 2004; Mayle, 2004).

The separation of a northern South American clade (Fig. 2) suggests an effect of the Amazonia rain forests, the wet Chocó forest and the final uplift of the northern Andes as barriers for the dispersal of dry forest species (Amorim, 2001; Garzione et al., 2008; Hoorn et al., 2010; Morrone, 2014b; Banda et al., 2016). Clusters of the northern inter-Andean valleys (located along the Magdalena and Cauca Rivers) together with Caribbean coastal areas reflect the heterogeneity of dry Andean regions (with important species turnover with Mesoamerica and Caribbean–Antilles), where few species are distributed all the way from the northern to the southern Andes (Nores, 2004; Vázquez-Miranda et al., 2007). These results are also consistent with those previously reported for other taxonomic groups in the region that are associated with NSDFs (Linares-Palomino et al., 2011; Morrone, 2014b).

Although our analyses generally agree with the Pleistocene Arc Hypothesis proposed originally by Prado and Gibbs (1993)—formation of a once extensive and largely contiguous seasonal woodland comprising the Caatingas, the Misiones and Sub-Andean Piedmont nuclei—the clear separation among NSDFs from central–south-western and south-eastern South America supports the idea that both uplift of the Andes and historical (Cenozoic and Quaternary) climatic regimes of north-western Ecuador–Peru and western Bolivia-Argentina are probably responsible for the high endemism and distributions of their NSDF bird communities (Hoorn et al., 2010; Morrone, 2014b). These communities have been biogeographically separated from neighbouring Bolivian lowland sites (Herzog and Kessler, 2002; Herzog et al., 2016). In fact, previous Andean NSDF legume phylogenies showed consistently high geographical structure throughout their distribution, suggesting that at least the NSDF flora has been assembled gradually over the past ca. 19 Myr, with processes of *in situ* diversification, largely undisturbed by new immigrants (Särkinen et al., 2012). From this perspective, the NSDF on the slopes of central–south-western South America constitutes an important biogeographical area with ecological and geographical long-term stability, and probably originated by convergence scenarios resulting from ancient dispersal events that involved low niche differentiation and strong dispersal limitation from other NSDF patches (Pennington et al., 2009; Särkinen et al., 2012). This also suggests that NSDFs from Ecuador and northern Peru to western Bolivia–Argentina might constitute remnants of a previously wider expansion according to the Pleistocene NSDF formation (Särkinen et al., 2012; Côrtes et al., 2015; de Melo et al., 2016). Passerine fossils support this hypothesis and suggest that some NSDF species had wider distributions in the past (Oswald and Steadman, 2015), with the Andean valleys (e.g. the Marañón and Apurimac Valleys) having direct influence on divergence and extinction processes by acting as semi-permeable barriers (Särkinen et al., 2011; Smith et al., 2014; Winger and Bates, 2015).

Finally, we found a stretch of NSDF from north-eastern Brazil south to Paraguay–Argentina and north towards eastern Bolivia (Fig. 2), which is concordant with previous studies, showing a well-supported grouping among these forests and suggesting the existence of a historical stable unit known as the Open Dry Diagonal (Mayle, 2004; Porzecanski and Cracraft, 2005; Linares-Palomino et al., 2011; Werneck et al., 2011, 2012). Today, many dry habitat sister taxa are geographically distant from one another, suggesting that these species have either undergone long-distance dispersal across large tracts of humid forests, or that arid regions were once connected (Oswald et al., 2017). The absence of synapomorphies within the Chiquitano and Misiones Province forests (Table 1; Appendix S4) provides some evidence for the recent formation of bird assemblages in this area (Herzog and Kessler, 2002; Smith et al., 2014), as was found for woody plants (Linares-Palomino et al., 2011; Banda et al., 2016). In fact, several authors suggest climatic and floristic characteristics closer to Atlantic rain forests than to NSDFs for these areas (Olson et al., 2001; Oliveira-Filho et al., 2006), which were probably colonized by dry forest species during drier and cooler periods of the Pleistocene. These colonization processes were probably favoured by a potential narrow east–west corridor connecting NSDF in the extremes of north-eastern Brazil and south-western South America during the LGM (Werneck et al., 2011). This connection could serve as a biogeographical link sheltering floristic and faunistic dispersal routes, resulting in partial expansions of NSDFs in some areas of Amazonia (Werneck et al., 2011, 2012). As a consequence of this last idea, the long-distance dispersal hypothesis of NSDFs in south-eastern South America proposed by Mayle (2004) remains a scenario that still needs independent testing.

Final considerations

Our study suggests that evolution of the well-differentiated avifaunas in the four major geographical groups herein identified might have involved a mixture of vicariance and dispersal events, which provides new insights into the diversification centres and historical relationships for the distributional patterns of this ecosystem and its associated avifauna. Despite some species being shared among different clades (regions), and that this probably increased after closure of the Panama Isthmus (Morrone, 2014b) and during the maximum extension of forests at the LGM (Banda et al., 2016), we observed a clear differentiation among the main areas, with high degrees of endemism (Fig. 2). This agrees with the idea of independent evolutionary histories among NSDF nuclei across their distribution (Becerra, 2005; Côrtes et al., 2015; de Melo et al., 2016).

Differences observed with previous studies (e.g. Porzecanski and Cracraft, 2005; Ríos-Muñoz and Navarro-Sigüenza, 2012) are largely due to taxonomic uncertainties (i.e. species concepts and new species that have been described or recognized since those studies; Jetz et al., 2002), as well as by differences in the definition of sampling area sizes and algorithms used for analyses. For PAE, there is a trend to decrease the absolute number of steps and to increase the number of synapomorphies as the size of the area increases (Morrone and Escalante, 2002). Likewise, it is important to note that this approach depends on detailed primary biodiversity occurrence data. In studies like this, with large data numbers, it is worth noting that observed patterns of species distributional data could be influenced by diverse sources of error (e.g. taxonomic uncertainties, identification errors, or errors on locality information associated with species occurrences). Thus, it is important to promote the constant update of the taxonomic status of specimens deposited in collections, as well as the procedures for cleaning and revising biodiversity data from heterogeneous sources (Navarro-Sigüenza et al., 2003; Bloom et al., 2017).

Although our results mostly apply to the geographical scale and taxa used for this study, the NSDF avifauna distribution patterns we found are non-random and congruent with those for other organisms (Becerra, 2005; Porzecanski and Cracraft, 2005; Pennington et al., 2009; Ríos-Muñoz and Navarro-Sigüenza, 2012; Oswald and Steadman, 2015; Banda et al., 2016). The general pattern identified here implies the need to continue to study these areas of endemism, which certainly could have a much longer history than the temporal framework of the Pleistocene. Thus, from a conservation perspective, most historical areas of endemism must be considered as priorities and incorporated into efforts of conservations planning (e.g. Nori et al., 2016), because they reflect an unique history of the Earth and its biota. A failure to protect them would result in major losses of unique species diversity for this highly threatened ecosystem. The observed distributional patterns of the avifauna, as well as their relationships across the NSDFs, constitute evidence of the great complexity of the biogeography of this ecosystem, in which each particular pattern should be considered a stepping stone along a true arc, recognized as the biogeography of the Neotropics.

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Conflicts of interest

The authors declare no competing interests in this study.

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Supporting Information

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

Appendix S1 Ornithological collections of international museums that kindly provided data analysed in this study.

Appendix S2 List of the 1298 bird species of Neotropical seasonally dry forests considered in the parsimony analysis of endemicity.

Appendix S3 Matrix of all species and cells used in this study.

Appendix S4 Cladogram and geographical correspondence of the groupings of grid cells obtained from the potential distributional data in the parsimony analysis of endemicity considering the complete (a) vs. Neotropical seasonally dry forest (NDSF)-restricted (b) species matrices from "species information" analyses. Letters in cladograms show the groups supported by synapomorphies included in Table 1. Well-supported clades [more than two synapomorphies (species)] are shown with a black circle. Black square in the cladogram corresponds to the outgroup. Acronyms in maps correspond to identified NDFS regions and areas of endemism: BC = Baja California; Cu = Cuba island; HP = Haiti, Dominican Republic, and Puerto Rico islands; SS = Sonora and Sinaloa forests; PS = Mexican Pacific slope lowlands; SP = northern Oaxaca in southern Mexico; TV = Tamaulipas–Veracruz; YP = Yucatan Peninsula; CAmN = northern Central America; CAmS = Southern Central America; CAm = Central America; Pa = Panama; IAV = Inter-Andean Valleys of Colombia; CCV = Caribbean Colombia–Venezuela; PE = Pacific Equatorial; Ap-M = Apurimac-Mantaro; SA-P = Sub-Andean Piedmont; C-MP = Chiquitano forests and Misiones Province; CaB = Brazilian Caatinga.

Appendix S5 Cladogram and geographical correspondence of the groupings of grid cells obtained from the potential distributional data in the parsimony analysis of endemicity considering the complete (a) vs. Neotropical seasonally dry forest (NDSF)-restricted (b) species matrices from "species-genera information" analyses. Letters in cladograms show the groups supported by synapomorphies. Well-supported clades [more than two synapomorphies (species)] are shown with a black circle. Black square in the cladogram corresponds to the outgroup. Acronyms in maps correspond to identified NDFS regions and areas of endemism: BC = Baja California; Cu = Cuba island; HP = Haiti, Dominican Republic and Puerto Rico islands; SS = Sonora and Sinaloa forests; PS = Mexican Pacific slope lowlands; SP = northern Oaxaca in southern Mexico; TV = Tamaulipas–Veracruz; YP = Yucatan Peninsula; CAmN = northern Central America; CAmS = southern Central America; CAm = Central America; Pa = Panama; IAV = Inter-Andean Valleys of Colombia; CCV = Caribbean Colombia–Venezuela; PE = Pacific Equatorial; Ap-M = Apurimac-Mantaro; SA-P = Sub-Andean Piedmont; C-MP = Chiquitano forests and Misiones Province; CaB = Brazilian Caatinga.