

Bird diversity of the Cúcuta valley (Colombia) and biogeographical affinities with dry forest avifaunas of northern South America

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ABSTRACT—Seasonally dry tropical forest is the least known and most threatened ecosystem in the Neotropics. In December 2009, we surveyed 3 tropical dry forest remnants in the arid Cúcuta valley, northeast Colombia. We recorded 140 of the 171 maximum species expected for the study area. Another 20 species were observed outside the inventory, totaling 160 species for the whole region. Results of the similarity analysis showed that the Cúcuta valley avifauna is biogeographically more related to the arid inter-Andean river valleys than to the Caribbean plains of Colombia and the Caribbean lowlands of northern Venezuela. This pattern of biogeographical affinities of dry forest bird communities in northwestern South America seems to be explained by the effect of geographic distance rather than environmental differences shaping species composition (β -diversity) and phylogenetic relatedness (phylo β -diversity) across space. Our results highlight the uniqueness and need to protect the tropical dry forest remnants of the Cúcuta valley. *Received 8 February 2016. Accepted 2 July 2017.*

Key words: avian conservation, lowland Neotropical birds, seasonally tropical dry forest, threatened ecosystem.

Diversidad de aves en el valle de Cúcuta (Colombia) y afinidades biogeográficas con avifaunas de bosque seco del norte de Suramérica

RESUMEN (Spanish)—El bosque seco tropical estacional es el ecosistema menos conocido y más amenazado del Neotrópico. En diciembre de 2009, estudiamos 3 remanentes de bosque seco tropical en valle árido de Cúcuta, noreste de Colombia. Registramos 140 especies de un máximo de 171 especies esperadas para el área de estudio. Otras 20 especies fueron registradas fuera del inventario, para un total de 160 especies en la región. Los análisis de similitud mostraron que la avifauna del valle de Cúcuta está biogeográficamente más relacionada con los valles áridos de ríos interandinos que con las planicies caribeñas de Colombia y las tierras bajas caribeñas del norte de Venezuela. Este patrón de afinidades biogeográficas de las comunidades de aves de bosque seco en el noroeste de Suramérica parece ser explicado por el efecto de la distancia geográfica más que por diferencias ambientales que moldean la composición (β -diversidad) y la cercanía filogenética (phylo β -diversidad) a través del espacio. Nuestros resultados resaltan la singularidad y necesidad de proteger los remanentes de bosque seco tropical en el valle de Cúcuta.

Palabras clave: aves neotropicales de tierras bajas, bosque seco tropical estacional, conservación de aves, ecosistema amenazado.

Seasonally dry tropical forest (SDTF) is considered one of the most threatened ecosystems in the Neotropics because of its high deforestation rate compared to other tropical forests (Janzen 1988, Miles et al. 2006, DRYFLOR 2016). More than half the global SDTF (~51%) is found in South America, mainly in Brazil, Bolivia, Colombia, and Venezuela. Approximately 60% of South American SDTF has been deforested and converted to cattle ranching and agriculture (Portillo-Quintero and Sánchez-Azofeifa 2010). In Colombia for instance, only 8% of the original dry forest area remains, with only a small area/proportion

(~36,093 ha/5%) of the original forest still protected by the National System of Protected Areas (SINAP, in Spanish; García et al. 2014).

Five major areas of SDTF are known in Colombia: the Caribbean region, the Upper Magdalena valley, the Cauca valley, the Patía valley, and the Orinoco region (IAvH 1998, García et al. 2014). Nevertheless, other remnants of dry vegetation are located in smaller inter-Andean valleys in the northern Eastern Cordillera, but knowledge of their distribution, extension, and biological composition is lacking. Ornithological surveys in Colombian SDTF have been infrequent, short-term, and geographically biased. These studies have been focused mainly in the Upper Magdalena valley (Losada-Prado and Molina-Martínez 2011, Gómez and Robinson 2014) and the Cauca valley (Naranjo 1992, Cárdenas 2000), with a few in the Caribbean and some small inter-Andean river valleys (IAvH 1997, Ayerbe-Quiones and López-O. 2011). Therefore, there is an urgent need for baseline information to design

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management and conservation programs for this poorly known and threatened ecosystem.

SDTF in the Neotropics are considered “islands” embedded in the tropical humid forests, and the lack of connectivity through evolutionary history has been suggested as the main driver of variation in species composition among SDTF areas (Pennington et al. 2009). Two mechanisms are involved in the isolation of each area: ecological niche conservatism (i.e., retention of ecological traits of ancestors over evolutionary history) and dispersal limitation (i.e., low movement among forest cores). These mechanisms have been evaluated as drivers of floristic composition variation in SDTF simultaneously, employing analyses of species turnover across geographical and environmental gradients (Pennington et al. 2009). For example, the variation of tree species composition across the Neotropics is highly correlated with geographic configuration of the samples, implicating strong dispersal limitations (DRYFLOR 2016). Disentangling the role of environment (i.e., tropical humid forests as ecological barriers) and geography (i.e., spatial distance, rivers, orogeny, among other barriers), however, is critical to understanding the spatial distribution of SDTF areas and how they might respond to current global change scenarios. Hence, a better understanding of these processes in other taxa with contrasting dispersal abilities, such as birds, is important to understanding tropical dry forest assemblies.

The Cúcuta valley is located between the Eastern Cordillera of Colombia and the Andes of Mérida in Venezuela. The SDTF in the region, an area ~1,500 km², is one of the most important relicts of this habitat in northeastern Colombia (Soriano and Ruiz 2006). The few studies conducted in the area have focused mainly on plants, frogs, reptiles, and bats (Soriano and Ruiz 2006; Carrillo-fajardo et al. 2007; Armesto et al. 2009, 2011). Most of our knowledge of the avifauna of the Cúcuta valley comes from bird collecting expeditions during the mid-20th century by brother Nicéforo María of the Museo de La Salle (Paynter 1997; information summarized by Rodríguez-Tolosa 1985). Recently, Armesto et al. (2013) documented some bird range extensions in the area, but representative inventories or midterm studies of the avifauna from this important region are lacking.

In this study, we present results of our inventory, testing the effectiveness of our sampling, and compare results of our inventory with other dry forest bird communities of Colombia and Venezuela to evaluate the biogeographical affinities of the dry Cúcuta valley avifauna with other bird communities of dry forest in the northern South America. We also compare the species turnover across geographic and climatic differences among samples to explore potential drivers of community assembly. Finally, we discuss the uniqueness and importance of protecting the remnant tropical dry forest patches of the Cúcuta valley.

Methods

Study area

The Cúcuta valley is located near the Zulia and Pamplonita rivers. It encompasses the mountain valleys (from 400 to 1,000 m a.s.l.) close to the city of Cúcuta and adjacent towns in the department of Norte de Santander, Colombia, and around the cities of Ureña and San Cristóbal in Táchira State, Venezuela (Haffer 1967a, Soriano and Ruiz 2006; Fig. 1). A small extension of dry forest is present in this area (Espinal and Montenegro 1963), which can be categorized in the tropical subxerophytic zonobiome also present in the inter-Andean valleys of Colombia (Rodríguez et al. 2004). Low-lying and flat areas are dominated by thorn scrub, which becomes tropical dry forest and premontane humid forest as moisture increases with elevational (Soriano and Ruiz 2006). The study area is covered by forests of less structural complexity in the upper slopes (>900 m) due to deforestation and goat grazing, resulting in different types of bushy areas and eroded soils. Mean annual temperature is 27.4 °C; mean annual rainfall is 1,150 mm, and mean relative humidity is 75.0%. The annual precipitation distribution follows a bimodal pattern with 2 rainy seasons: one March–April and another October–November; the dry season is July–August (Carrillo-fajardo et al. 2007). We conducted a 9 d survey of birds in the study area in December 2009 (Fig. 1), covering most of the variation in vegetation types and topography.

Site 1—La Palma Farm, vereda Ayacucho, Municipality of San Cayetano (07°48′28.4″N, 72°35′56.8″W; 900 m), is dominated by secondary forest patches surrounded by areas of cattle

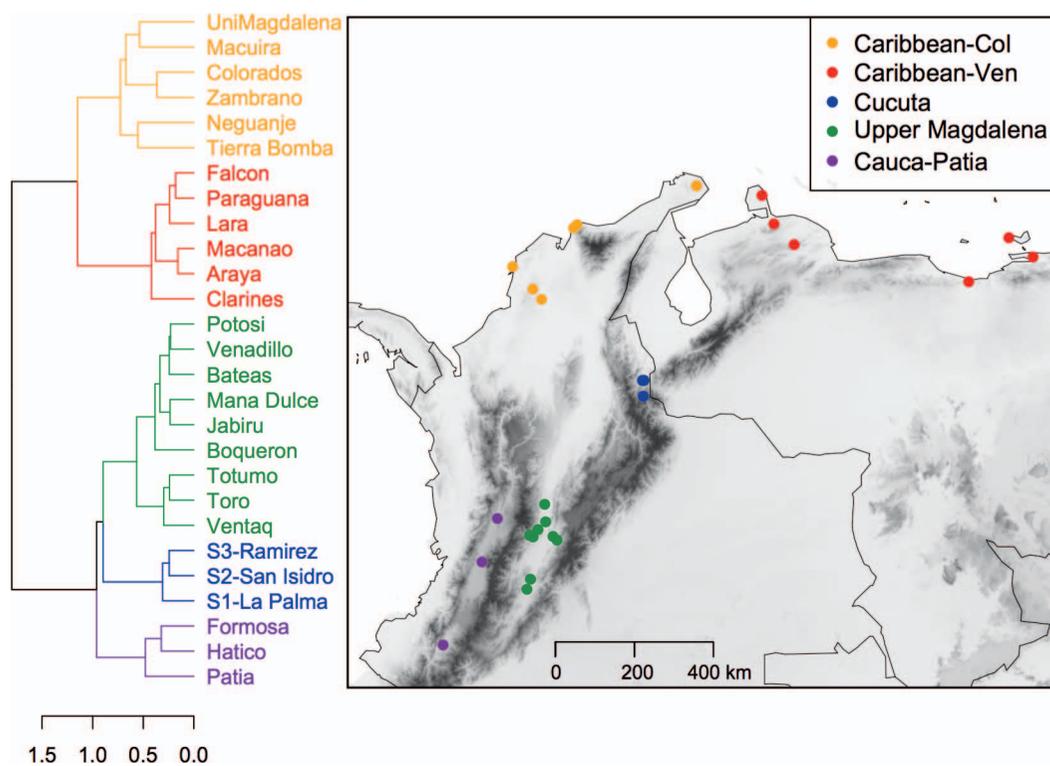


Figure 1. Colombia and Venezuela, highlighting the locations of the SDTF bird communities used in the dendrogram analysis. On the left, cluster analysis employing the Sorensen dissimilarity index as a distance measure. The avifauna of the Cúcuta valley (blue) is more related to arid inter-Andean valleys, such as the Upper Magdalena, Cauca, and Patía in Colombia, than to the Caribbean lowlands of Colombia and Venezuela. Details of localities included in the analysis are presented in Table 1.

grazing and coffee plantations (Infante-Betancur 2009). These fragments show a well-defined vertical strata and a canopy height of ~12–15 m. Streams are common in the area, facilitating the proliferation of ferns (*Adiantum* sp.). Coal mining is incipient, but its impact on soils and vegetation is evident. Fieldwork was conducted 13–15 December 2009.

Site 2—San Isidro, vereda El Tabiro, Corregimiento Carmen de Tonchalá, Municipality of Cúcuta (07°49'37.2"N, 72°35'01.0"W; 400 m), consists of small forest patches of forests dominated by trees of *Tabebuia* (Bignoniaceae), *Psidium* aff. *arayan* (Myrtaceae), and *Ficus* (Moraceae). The understory is marshy and dominated by herbs like *Anthurium* (Araceae), *Calathea lutea*, *C. cf. inocephala* (Marantaceae), and *Costus* sp. (Costaceae; Infante-Betancur 2009). This area is crossed by the Tonchalá River and is surrounded by steep slopes with a smaller and less complex forest. The vegetation gradually turns to

bushes of different height and grasslands in the summits. Coal mining is common in the lower sectors, whereas cattle grazing is observed in the upper parts of the valley. The area is currently part of the San Isidro Nature Reserve owned by the regional environmental authority (CORPONOR). Fieldwork was conducted 16–18 December 2009.

Site 3—Ramírez Farm, vereda Ayacucho, Municipality of San Cayetano (07°49'37.0"N, 72°37'0.0"W; 400–600 m), is covered by secondary forest regenerated from pastures abandoned since the end of the 1950s. The forest presents an open canopy of 8 m height, dominated by *Esenbeckia* sp. (Rutaceae). The steepest slopes are more conserved, with taller trees and a closed canopy 12–14 m. These areas includes trees of *Pouteria* (Sapotaceae), *Ficus* (Moraceae), and *Brownea* (Caesalpiniaceae). In some more disturbed areas, lianas and vines such as *Tetrapteris*, *Banisteriopsis* (Malpighiaceae), *Mandevilla hirsuta* (Apocynaceae), *Tournefortia* (Boraginaceae),

and representatives of Fabaceae and Asteraceae are common, particularly along forest edges and roads (Infante-Betancur 2009). The upper slopes (>900 m) are totally transformed to grasslands and shrubs because of current and past timber extraction and goat grazing. Field work was conducted 19–21 December 2009.

Fieldwork

We sampled birds during 3 days on each study site using a combination of methods (i.e., direct observations, digital recordings, and mist-netting), conducting a more efficient inventory because of the short time available (Remsen 1994, Stiles and Bohórquez 2000). On sites 1 and 2, we set up 108 m of mist nets (36 mm, 12 × 2.2 m) over 2 days from 0600 to 1800 h (total 216 net/h). Birds were examined for any sign of breeding or molting. We collected some rare birds caught in the nets, but other rare species and those difficult to catch in nets were collected using air rifles. Specimens were deposited in the Ornithological Collection of the Instituto de Ciencias Naturales of Universidad Nacional de Colombia (ICN), Bogotá, and tissue samples were deposited at the Banco de Tejidos of Universidad de los Andes, Bogotá (ANDES-T). Usually one researcher stayed at the nets and the other 2 members of the team walked along 2–5 km transects to visit all available habitats while observing and recording birds. We recorded vocalizations with a unidirectional microphone (Sennheiser ME67) and a digital recorder (Marantz PMD 620). At site 3 we were unable to set up mist nets because of the steep topography in the area.

Data analyses

Diversity estimates—First we tested the effectiveness of our sampling, running incidence-based estimates that use the frequencies of species in a collection of samples (Oksanen et al. 2016). We selected *bootstrap* and *jackknife 2* (second-order jackknife), considered the most accurate when using small sample sizes (Colwell and Coddington 1994). *Bootstrap* uses the frequency of each species and the number of sites in the collection, whereas *jackknife 2* uses information on the frequency of rare species in a sample to estimate the number of undetected species in an assemblage (Oksanen et al. 2016).

Biogeographical affinities (beta and phylbetadiversity)—We evaluated the avifaunistic relationships between the Cúcuta valley and other areas of SDTF from the Caribbean and northern inter-Andean valleys located in Colombia and Venezuela (Fig. 1). SDTF has been defined as a closed canopy forest, occurring on fertile soils with less than ~1,800 mm of rainfall per year and a 3–6 month dry season when precipitation is <100 mm per month and vegetation becomes mostly deciduous (Murphy and Lugo 1986, DRYFLOR 2016). We used these criteria to select the regions we included in the analyses. Thus, we compiled 24 published bird inventories of SDTF localities of the northern inter-Andean valleys and Caribbean lowlands dry areas and built a binary matrix of species versus sites, plus our 3 sites in the Cúcuta valley (Table 1; Supplemental Table S1). Migratory and aquatic species were excluded from the analysis, migrants because sampling in different seasons might affect comparisons among bird communities, and water birds because of their dependence on the presence of waterbodies and rivers (Ruiz-Guerra 2012). Given the reduced habitat specialization among dry forest birds, they frequently occur in adjacent humid habitats; therefore, dry forest bird communities analyzed in this study represent a mix of species drawn from arid and humid habitats (Stotz et al. 1996). Taxonomy and English names follow the South American Classification Committee (SACC; Remsen et al. 2017).

We ran a cluster analysis employing the Sorensen dissimilarity index as a distance measure and applied the hierarchical Ward's clustering method using the function *hclust* of the package *vegan* (Oksanen et al. 2016) to construct the dendrogram implemented in the R programming language (R Development Core Team 2016). After defining the most important clusters of the northern inter-Andean valleys, we tested the significance of the resulting clusters, especially seeking to understand the relationships of the Cúcuta valley with other dry areas in northern South America, but also exploring the relationship between other areas of SDTF. For this task we used the nonparametric method of analysis of similarities (ANOSIM), which offers a way to test statistically if significant differences exist between groups of sampling units (Clarke 1993, Oksanen et al. 2016). If 2 groups of sampling units are really

Table 1. Localities of seasonally dry tropical forest from Colombia and Venezuela with ornithological surveys used in the similarity analysis.

Region	Locality	Species richness ^a	Species included in analysis ^b	Source
Caribbean Lowlands, Ven	Paraguaná Peninsula	39	35	Rodríguez-Ferraro and Blake (2008)
Caribbean Lowlands, Ven	Falcón lowlands	51	48	Rodríguez-Ferraro and Blake (2008)
Caribbean Lowlands, Ven	Lara lowlands	50	50	Rodríguez-Ferraro and Blake (2008)
Caribbean Lowlands, Ven	Clarines-Píritu región	82	78	Rodríguez-Ferraro and Blake (2008)
Caribbean Lowlands, Ven	Araya Peninsula	47	42	Rodríguez-Ferraro and Blake (2008)
Caribbean Lowlands, Ven	Macanao Peninsula	37	34	Rodríguez-Ferraro and Blake (2008)
Upper Guajira, Col	Serranía de la Macuira	141	92	Marinkelle (1970), Andrade and Mejía (1988)
Caribbean Lowlands, Col	Zambrano: Finca Forestal Monterey, Dpto. Bolívar	86	68	IAvH (1997)
Caribbean Lowlands, Col	Los Colorados: SFF Los Colorados, Dpto. Bolívar	86	81	IAvH (1997)
Caribbean Lowlands, Col	Tierra Bomba: Isla de Tierra Bomba, Dpto. Bolívar	33	30	IAvH (1997)
Caribbean Lowlands, Col	Neguanje: NW PNN Tayrona, Dpto. Magdalena	55	47	IAvH (1997)
Caribbean Lowlands, Col	UniMagdalena: Universidad del Magdalena, Dpto. Magdalena	186	93	Strewe et al. (2009)
Upper Magdalena valley, Col	Laguna El Toro, Dpto. Tolima	161	122	Losada-Prado and Molina-Martinez (2011)
Upper Magdalena valley, Col	El Totumo, Dpto. Tolima	137	110	Losada-Prado and Molina-Martinez (2011)
Upper Magdalena valley, Col	Laguna de Ventaquemada, Dpto. Tolima	125	91	Losada-Prado and Molina-Martinez (2011)
Upper Magdalena valley, Col	Jibirú	176	146	Gómez and Robinson (2014)
Upper Magdalena valley, Col	Mana Dulce	157	143	Gómez and Robinson (2014)
Upper Magdalena valley, Col	Venadillo	119	110	Gómez and Robinson (2014)
Upper Magdalena valley, Col	Boquerón	93	85	Gómez and Robinson (2014)
Upper Magdalena valley, Col	Potosí	115	95	Gómez and Robinson (2014)
Upper Magdalena valley, Col	Bateas	115	95	Gómez and Robinson (2014)
Cauca River valley, Col	Hda. Formosa: Dpto. Valle del Cauca	141	82	Naranjo (1992)
Cauca River valley, Col	Reserva El Hatiko: Dpto. Valle del Cauca	134	89	Cárdenas (2000)
Upper Patía valley, Col	Patía valley: Dpto. Cauca	211	144	Ayerbe-Quiñones and López-O. (2011)
Cúcuta valley, Col	Site 1: La Palma	101	92	This study
Cúcuta valley, Col	Site 2: San Isidro	99	88	This study
Cúcuta valley, Col	Site 3: Ramírez	84	76	This study

^a Reported by the respective source.

^b After excluding migratory and aquatic birds.

different in their species composition, then compositional dissimilarities between the groups must be greater than those within the groups (Clarke 1993). We conducted 6 analyses of similarities (ANOSIM) to examine the sensitivity of the results to different groups of localities: (1) all 5 clusters identified by the clustering analysis; (2) Upper Magdalena valley and Cauca valley; (3) Cúcuta valley and Upper Magdalena valley; (4) Cauca

valley and Cúcuta valley; (5) Upper Magdalena valley, Cauca valley, and Cúcuta valley; and (6) Caribbean and Cúcuta valley.

We also explored species turnover (β -diversity) and phylogenetic turnover (phylo β -diversity) among our communities of dry forest with geographical and environmental distances (Graham and Fine 2008). The phylo β -diversity measures how phylogenetic relatedness changes across

Table 2. Results of the analyses of similarities (ANOSIM) among 5 SDTF areas from northern South America. When the Cúcuta valley is grouped with the Upper Magdalena valley (UMV) the R-statistics increased to their highest values, but when Cúcuta is grouped with Cauca the R-statistics decreased.

CLUSTER	R	P
Carib-Col + Carib-Ven + UMV +Cauca + Cúcuta	0.86	0.0001
Carib-Col + Carib-Ven + (UMV +Cauca) + Cúcuta	0.80	0.0001
Carib-Col + Carib-Ven + (UMV + Cúcuta) + Cauca	0.87	0.0001
Carib-Col + Carib-Ven + (Cauca + Cúcuta) + UMV	0.78	0.0001
Carib-Col + Carib-Ven + (UMV +Cauca + Cúcuta)	0.83	0.0001
(Carib-Col + Carib-Ven + Cúcuta) + Cauca + UMV	0.31	0.001

space (i.e., the length of the shared branches in phylogeny between 2 samples), much like β -diversity, measures how species composition changes over space (Graham and Fine 2008). To study phylo β -diversity we built a hypothesized phylogenetic tree for all tree species found in our Colombian and Venezuelan SDTF dataset based on a comprehensive avian phylogeny (Jetz et al. 2012; Supplemental Material S2). To calculate the compositional turnover (hereafter β -diversity) and phylogenetic turnover (hereafter phylo β -diversity), we employed the Sorensen and the phylogenetic Sorensen's similarity index (PhySor), respectively. The PhySor was calculated using the function *phylosor.query* implemented in the package PhyloMeasures (Tsirogiannis and Sandel 2016).

We correlated these metrics of turnover with the geographic and environmental distances. Geographic distances were estimated as the log-transformed Euclidean distance between each pair of geographic coordinates; environmental distances were calculated as the Euclidean distances for the 19 bioclimatic variables for each locality extracted from WorldClim (Hijmans et al. 2005). We then used a multiple regression on distance matrix (Goslee and Urban 2007) to evaluate the correlation of each of the turnover metrics and these dependent variables. Finally, we applied a variance partitioning analysis (Borcard et al. 1992, Legendre and Legendre 2012) to separate the effect of environment and the spatial structure of the

environment in the species and phylogenetic turnover. These analyses were performed using the betapart library in R programming language (R Development Core Team 2016).

Results

Cúcuta valley diversity

In the Cúcuta valley we recorded 160 species; 140 species were detected during our sampling, but for the final inventory we included an additional 15 occasional species recorded when we were moving among our 3 study sites and 5 other species previously recorded in the area by JEA during a 2003 expedition (Supplemental Table S3). Local species richness was similar between S1 (100 species) and S2 (99 species) while S3 had fewer species (84 species). We captured 160 individuals of 54 species, observed 126 species, and listened to 89 species. We tape recorded 52 species and collected 97 individuals of 60 species. Catalogue numbers of specimens at ICN and information of sound recordings uploaded in xeno-canto.org are available in Supplemental Table S3.

Results of our inventory were close to the expectations for the study area. *Bootstrap* estimated an alpha diversity of 152 species and *jackknife 2* estimated 171 species for the Cúcuta valley. These estimations suggest our inventory is between 81% to 92% of the possible total alpha diversity for the whole area; however, other cryptic, occasional, or species that exhibit intra-tropical migrations could be overlooked but can be part of the final inventory (Morton 1977, Levey 1988).

Biogeographical affinities

Our clustering analysis identified 5 clusters (Fig. 1, Table 2): Caribbean of Colombia and Venezuela, Upper Magdalena, Cauca-Patía, and Cúcuta valleys (Fig. 1). We also found strong support for these clusters based on the analysis of similarities (ANOSIM; Table 2). When we grouped the Cauca-Patía valley with either the Cúcuta or Upper Magdalena valley, the ANOSIM R-statistics decreased, but when we grouped Cúcuta with the Upper Magdalena valley, the ANOSIM R-statistics increased to the highest value, suggesting that the avian community of the Cúcuta valley is compo-

Table 3. Partition of variance for β -diversity and phylo β -diversity explained by geographical and environmental distance.

Variance component	Proportion explained (%)	F-value	P-value
β-diversity			
Total	0.47	158	0.001
Geography	0.45	289	0.001
Environment	0.23	105	0.001
Geography (Environment)	0.24	162	0.001
Environment (Geography)	0.02	15	0.001
Phyloβ-diversity			
Total	0.39	112	0.001
Geography	0.37	205	0.001
Environment	0.19	85	0.001
Geography (Environment)	0.19	112	0.001
Environment (Geography)	0.02	12	0.001

sitionally more similar to the Upper Magdalena valley (Table 2). Additionally, when we grouped the Cúcuta valley with the dry forest of the Caribbean, the R-statistics decreased to the lowest value.

Geography was a better predictor of β and phy β turnover than climate (Table 3), with the effect of geographical distance more important in explaining β -diversity than phylo β -diversity turnover (Table 3, Fig. 2). This result was unexpected in that compositional turnover is better explained than phylogenetic turnover ($R^2 = 0.54$; $P < 0.001$ vs. $R^2 = 0.43$; $P < 0.001$, respectively) when we included both geography and environment as

predictors in the multiple regression models. In addition, the variance partitioning analysis showed that the effect of climate is due to the spatial structure of the variables used (i.e., temperature and precipitation) rather than the strong effect of the climatic restrictions on the species responses. This pattern and the overall biogeographical affinities of the dry forest bird communities studied are better explained by the effect of geography than environmental distance.

Discussion

Bird diversity

In the present study we reported 160 species for the arid Cúcuta valley, a low diversity value compared to the diversity reported in humid tropical forests from Colombia (Laverde-R et al. 2005, Gómez and Robinson 2014). Bird communities in SDTF have low diversity compared to other Neotropical ecosystems such as humid or montane forests (Stotz et al. 1996, Gómez and Robinson 2014), a difference attributed mainly to the climatic or physical conditions. For example, little variation in precipitation along 65 km strongly influences plant species diversity, which in turn affects avian diversity; therefore, mean annual precipitation seems to be a good predictor of bird species richness (Rompré et al. 2007, Gómez and Robinson 2014).

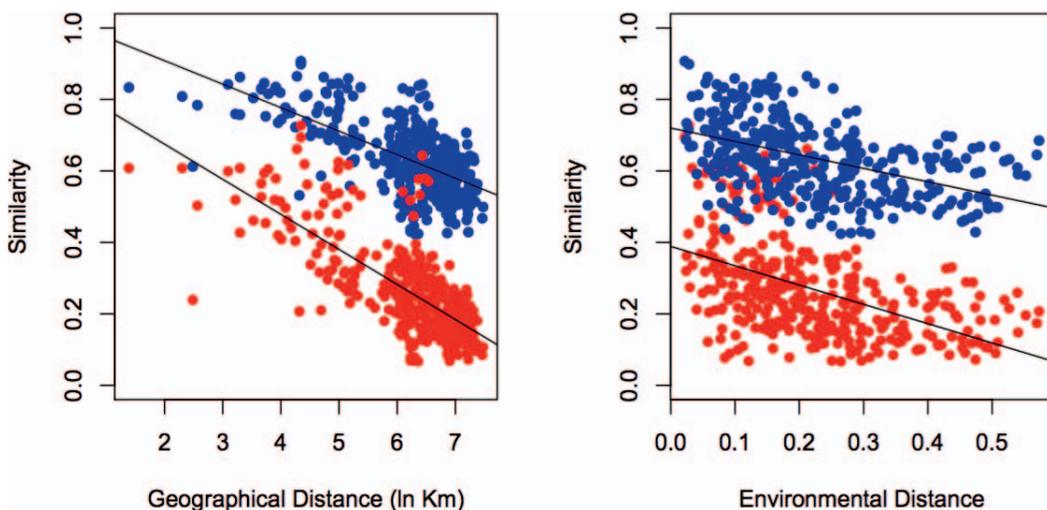


Figure 2. Changes in β -diversity (red) and phylo β -diversity (blue) along geographical and environmental distance.

The effects of forest deforestation and degradation, however, have been poorly evaluated and may be modifying species composition and local species richness. For example, within our study area, species diversity was similar among our study sites, although site 3 showed the lowest diversity due to the possible effect of timber extraction, goat grazing, and mining. These activities might have reduced suitable habitats for some species present in the other sampled sites (e.g., *Ortalis ruficauda*, *Cranioleuca subcristata*, *Cantorchilus leucotis*). These anthropogenic processes are widely distributed across SDTF and may be jointly responsible with environmental variables for the low diversity of this ecosystem. Nevertheless, 160 bird species are a relatively high diversity value for a dry forest, possibly related to the combined effect of the heterogeneous landscape in the region, the diversity of sampled habitats, and the possible influence of other nearby humid habitats in the foothills of the Eastern Cordillera and the Catatumbo lowlands (Rodríguez-Tolosa 1985). Indeed, when excluding migratory and strictly aquatic birds, species richness in the Cúcuta valley is similar, and in some cases higher, to that reported for SDTF bird communities in Colombia and Venezuela with similar sampling effort (Table 1). Therefore, our results suggest that the arid Cúcuta valley harbors one of the richest SDTF bird communities in Colombia and north-western South America.

Biogeographical affinities

In northern South America (i.e., Colombia and Venezuela), SDTF occurs in 6 different geographical regions: the Patía valley, the Cauca valley, the Middle and Upper Magdalena valley, Santander and Norte de Santander in Colombia, the Caribbean coast, and the Orinoco region in Colombia and Venezuela (Gómez and Robinson 2014). In our analyses we included 5 of these 6 regions; the Orinoco region was excluded because recent and complete inventories were lacking.

Our results showed that the avifauna of the Cúcuta valley is more similar to the arid inter-Andean river valleys than to avifaunas from the arid Caribbean lowlands of Venezuela and Colombia (Fig. 1). Recent studies on bats and reptiles have found a similar biogeographical pattern; the Cúcuta valley fauna is more similar to Andean

enclaves of Venezuela and Colombia rather than to La Guajira and Caribbean lowlands of Venezuela (Soriano and Ruiz 2006, Armesto et al. 2011). In addition, floristic composition analyses revealed that the arid regions located in the north of South America form a northern cluster of dry forests separated from other dry forest regions further south in South and north in Central America, suggesting that the humid forest of Amazonia and the Chocó formed an effective barrier for colonization of dry forest species from other areas (DRYFLOR 2016). These results support that Cúcuta valley could be considered an inter-Andean valley influenced by other sources of species, such as from mountains and humid forests, that increase its regional species pool; however, its proximity to the Caribbean and other Andean SDTF increases the colonization probability from other regions.

Evidence suggests a relevant influence of the inter-Andean river valleys in shaping the current fauna of the Cúcuta valley. Haffer (1967a, 1967b) proposed that the inter-Andean valleys were colonized from the northern Caribbean plains during dry periods of the Pleistocene and post-Pleistocene, a period that promoted the expansion of open habitats and arid areas from northern Colombia southward. Whether colonization of the Cúcuta valley occurred through an arid corridor across the Maracaibo basin, where humid conditions seem to have served as a barrier between the peri-Caribbean and Cúcuta avifaunas, or if dispersal could have occurred by crossing the Eastern Cordillera through the Ocaña depression (Hernández-Camacho et al. 1992, Cadena et al. 2016), as recently documented for several bird species (Avendaño et al. 2013), is unclear. Therefore, the Cúcuta valley may be serving as a stepping stone among 2 or 3 dry forest regions (Caribbean, inter-Andean valleys, and Llanos), a process that historically has positively modified its species diversity and explains its singularity.

Conservation

The connection between the arid Cúcuta valley and adjacent dry forest areas located west of the Eastern Cordillera and Llanos during recent geological times has possibly prevented the differentiation of endemic species or subspecies in the region (Haffer 1967a). Despite the absence

of local endemics, the remnant SDTF in the Cúcuta valley harbors a rich community of birds characterized by a mixture of both inter-Andean and Caribbean species, although a higher number of species is shared among the valleys.

The position of the Cúcuta valley as a branch distinct from the other inter-Andean valleys has resulted in the presence of some species exclusive to the Cúcuta valley (*Myiothlypis flaveola*). Other species are shared with the eastern plains (Llanos) of Colombia (*Amazilia viridigaster*, *Tangara cayana*) or with the Caribbean plains but have not reached the Upper Magdalena and Cauca River valleys (e.g., *Ortalis ruficauda*, *Columbina squamata*, *Phaethornis augusti*, *Thamnophilus melanonotus*). Moreover, within this assemblage, some species such as the Black-backed Antshrike (*T. melanonotus*) stands out because of its high level of habitat specialization to the SDTF (Stotz et al. 1996), whereas the presence of the endangered Recurve-billed Bushbird (*C. alixii*) and the Red Siskin (*Spinus cucullatus*; Pacheco and Álvarez 2016) urges the implementation of controlled management actions (e.g., integrated management districts) that regulate coal mining, cattle, and agricultural activities in remaining forest patches between the Pamplonita and Zulía rivers. This action would require extensive knowledge of habitat associations and dynamics of the SDTF bird communities, including ecological interactions with adjacent humid habitats such as gallery forests and tropical wet forests along the base of the Eastern Cordillera and the Catatumbo lowlands. This region could be an important site of historical connection among dry forests, assuming that dispersal is limited by environmental and geographic barriers, these step-stone-like areas are critical to maintaining regional dry forest diversity and should be urgently protected.

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