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Dissecting bird diversity in the Pantepui area of endemism, northern South America

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Abstract

The Pantepui region harbors one of the most distinctive endemic montane bird faunas in the Neotropics, and is located across the tepuis of northern South America. We made an extensive literature review to understand large-scale distribution patterns of birds in the Pantepui. The core avifauna of the tepuis is composed of 138 bird species, most forest-dwelling insectivores, of which 43 are endemic. In addition, 167 subspecies of birds are endemic to these mountains. The number of endemic species peaks between 1251 and 2000 m, whereas the diversity of non-endemic species is highest between 751 and 1000 m. A high proportion (28%) of endemic taxa (species plus subspecies) is restricted to a single mountain. Tepuis are distributed along a longitudinal gradient, and bird species compositions of mountains located in the eastern and western portion of this gradient are clearly differentiated. Maximum altitude of the mountains and their distance from the Andes are the best predictors of species richness and composition across the Pantepui. Also, bird species composition at site level exhibits significant nested patterns which are affected by maximum altitude, isolation and geographic position of the mountains. The unique bird assemblage of the Pantepui area of endemism is structured through a combination of the spatial distribution of the mountains, habitat diversity, and complex historical events.

Keywords Neotropical montane birds · Elevational gradients · Longitudinal diversity gradient · Nested biotas · Deconstruction approach

Zusammenfassung

Analyse der Vogeldiversität in der von starkem Endemismus geprägten Pantepui-Region im nördlichen Südamerika
Die Tafelberge in der Tepui-Region im nördlichen Südamerika bilden die Pantepui-Region, ein Gebiet mit hoher Endemismus-Rate und einer der ausgeprägtesten Bergvogel-Faunen der Neotropen. Mithilfe einer umfassenden Literaturstudie wollten wir die weiträumigen Verbreitungsmuster der Vögel des Pantepuis zu verstehen versuchen. Die Kern-Avifauna der Tafelberge dort besteht aus 138 Vogelarten, überwiegend waldbewohnende Insektenfresser, von denen 43 Arten endemisch sind. Außerdem sind in diesen Bergen weitere 167 Vogel-Unterarten endemisch. Die Anzahl der endemischen Arten ist in 1251–2000 Metern Höhe am größten, die Vielfalt der nicht-endemischen Arten zwischen 751 und 1000 Metern. Ein großer Anteil (28%) der endemischen Arten (plus Unterarten) ist auf einen einzigen Berg begrenzt. Die Tafelberge verlaufen entlang eines longitudinalen Gradienten, und die Zusammensetzung der Vogelarten westlich und östlich dieses Gradienten ist klar unterschiedlich. Die Höhe der Berge und ihre Entfernung von den Anden sind der beste Prediktor für den Artenreichtum und die–zusammensetzung entlang des Pantepui. Auch an anderen Standorten zeigt die Artenzusammensetzung ausgeprägte Muster, die von der Meereshöhe, der räumlichen Isolation und der geographischen Position der Berge abhängen. Die

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einzigartige Zusammensetzung der Vogelarten in der endemitischen Pantepui-Region wird von einer Kombination von räumlicher Anordnung der Berge, Vielfalt der Habitate und komplexer historischer Vorgänge strukturiert.

Introduction

Mountains around the world commonly have a high diversity of species with narrow geographic ranges, making these ecosystems "cradles of biodiversity" (Fjeldså et al. 2012). In addition, mountains have a high conservation priority since they harbor many endemic and threatened species (Stattersfield et al. 1998). Four principal montane regions are found in South America: the Andes, running the entire western length of the continent; the mountain chains of eastern Brazil; the Coastal Cordillera of northern Venezuela; and the Guayana Highlands or tepuis of southern Venezuela and adjacent countries (Körner et al. 2017).

Tepuis are ancient montane formations famous for their mesa-like summits and high diversity of endemic plants (Maguire 1970; Huber 1995; Berry and Riina 2005; Huber 2005). The Pantepui area of endemism, located across the tepui mountains, is a biogeographic unit characterized by the restricted distribution of birds, plants and other organisms (Mayr and Phelps 1967; Cracraft 1985; Maguire 1970; Huber 1988; Hoogmoed 1979; McDiarmid and Donnelly 2005).

Tepuis host one of the most distinctive avifaunas in South America (Renjifo et al. 1997; Sánchez-González et al. 2008), and ornithological studies carried out on them have been vital to an understanding of the evolutionary history and ecological characteristics of the tepui biota (Chapman 1931; Mayr and Phelps 1967; Hernández and Lew 2001). Here, we provide a review of the species diversity and degree of endemism for birds in the Pantepui area of endemism to expand on previous efforts (Willard et al. 1991; Renjifo et al. 1997; Zyskowski et al. 2011).

There are a number of reasons for such a review. Continuing systematic and taxonomic revisions of South American birds refine our understanding of species identity of Pantepui birds (e.g., Weller 2000; Pérez-Emán 2005; Bonaccorso et al. 2011), while the number of field expeditions to tepuis in different countries has grown since the seminal synthesis of Mayr and Phelps (1967). Such initiatives allow quantitative analysis of bird assemblages at larger scales. Finally, the synthesis of tepui biodiversity is critical to define effective conservation strategies for this fragile ecosystem (Nogué et al. 2009; Señaris et al. 2009; Vegas-Vilarrúbia et al. 2012, Safont et al. 2014).

Several hypotheses have been proposed to explain the patterns of species diversity and endemism within the Pantepui. These hypothesis emphasize: (1) the geological antiquity of the Guyana Shield as a source of temporal and spatial isolation for the tepui biota (Maguire 1970); (2) vicariance events mediated by erosional processes of the Guyana Shield (Croizat 1976; Hoogmoed 1979; McDiarmid and Donnelly 2005); (3) long-distance dispersal from other mountain systems (Chapman 1931; Mayr and Phelps 1967), (4) speciation events involving ancestors from the Amazonian lowlands (Mayr and Phelps 1967; Hoogmoed 1979; Steyermark and Dunsterville 1980); and (5) past climate change affecting vegetation cover of tepuis, and promoting speciation and extinction along elevational gradients (Chapman 1931; Haffer 1970; Cook 1974; Rull 2005).

Most of these hypotheses assume the preponderance of some biogeographical processes affecting the current distributions of species forming the tepui biota. For example, Chapman (1931) suggested that past climate change caused bird population extinctions in intervening regions between the Andes and tepuis (see also Cook 1974 and Rull 2005). Other authors have emphasized that tepui birds are mostly derived from neighboring mountain regions, mainly the Andes and Venezuelan coastal mountains, through long-distance dispersal (Mayr and Phelps 1967). Evaluations of these alternative hypotheses need to consider the evolutionary/phylogenetic relationships among tepui birds (Pérez-Emán 2005; Bonaccorso and Guayasamin 2013) as well as the ecological and spatial distributions of the species concerned. The current study focuses on the latter approach.

Variability in elevational gradients, isolation between mountains and heterogeneity in vegetation cover have all been suggested as the main contemporaneous environmental variables affecting species diversity, compositional variability and endemism level in Pantepui plants and animals (Tate 1939; Cook 1974; Jaffe et al. 1993; Berry and Riina 2005, McDiarmid and Donnelly 2005; Nogué et al. 2013). In addition, the spatial arrangement and topographic attributes of the individual tepuis, coupled with variation in habitat requirements and dispersal abilities of birds, are factors likely to be relevant for a full understanding of large-scale variation in species assemblage composition and diversity across the Pantepui.

The present study is based on an extensive review of the literature used to build a database analyzed with the aim of identifying and testing distributional patterns of tepui bird assemblages. Our general proposals are to provide an updated baseline on Pantepui bird species diversity and endemism, identify patterns of species distribution within this area of endemism, and examine the influence of the physical

geography of tepuis on the diversity and taxonomic composition of bird assemblages.

The study was driven by the following questions:

Are there difference in altitudinal flexibility among endemic and non-endemic birds in tepui mountains? Some of the hypotheses cited above (e.g., Rull 2005) assume that populations of endemic species were isolated in the top of tepuis during climate change events. Therefore, it is expected that in current biological assemblages endemic species will occupy the higher parts of tepuis while non-endemic species will show more flexibility in their altitudinal distributions.

Is the Pantepui a homogeneous biogeographic unit, or it is possible to recognize different biogeographical subunits within this area of endemism? Mayr and Phelps (1967) proposed that the Pantepui could be divided into two major regions; we tested this proposal here with a more robust database than was available to Mayr and Phelps (1967).

Does distance from other mountain systems affect the nested arrangement, species richness and composition of bird assemblages of tepuis? Other montane systems have been indicated as faunal sources for the tepui avifauna (Chapman 1931, Mayr and Phelps 1967). In addition, Cook (1974) proposed that differential extinctions in regions near the Andes could isolate bird populations then occupying the eastern part of the tepui mountain range. We expected, therefore, that distance from these mountains would influence bird species composition at a large scale and the nested arrangement in the species distribution.

How do physical attributes of mountains, especially altitude, affect the diversity and composition of tepui bird assemblages? Tepui mountains have been described as sky islands (McCormack et al. 2009), with mountaintops isolated from each other by extensive areas of lowlands. The degree of isolation of each mountain and its altitude, however, are highly variable within the Pantepui complex, and bird diversity and composition are expected to be affected by the mountain attributes associated with high species richness and more differentiated avifaunas occurring on higher and more isolated mountains.

Methods

Study area

Tepuis are described in detail in the botanical and geological literature (Huber 1995; Berry and Riina 2005; McDiarmid and Donnelly 2005). Huber (1995) categorized the Guayana montane ecosystem into lowlands (0–500 m a.s.l.), uplands (500–2000 m a.s.l.) and highlands (> 2000 m a.s.l.); a high plant species turnover is observed along this altitudinal gradient (Steyermark 1986; Huber 2005, 2006). The slopes of the tepuis are generally dominated by forests of varying

canopy stature (Huber 2005). Shrubby, herbaceous vegetation and forest patches along streams are found on the summits of tepuis (Huber 2005, 2006).

The density of tepuis varies geographically, with these mountains being highly concentrated in eastern Venezuela (Fig. 1). The interstitial lowlands between the eastern tepuis are a mosaic of tropical forest and savanna (Huber 1995). Isolated tepuis in Guyana and Suriname are surrounded by lowland forests, with patches of savanna found in the piedmont of mountains such as the Tafelberg, Acary Mountains and the Potaro Plateau (Barnett et al. 2002; Zyskowski et al. 2011). In the western region, tepuis tend to be more eroded and isolated with vegetation in nearby lowland dominated by upland forest, with forests and non-forest vegetation growing on sandy soil (Anderson 1981; Willard et al. 1991; Estrada and Fuertes 1993; Stiles et al. 1995; Huber 2006).

Huber (1995) considers the Pantepui phytogeographic province to include only mountains with elevations above 1500 m a.s.l. In the current study we included mountains and hills that do not follow the Huber's criteria, such as the Sierras de Macarena and Chiribiquete in Colombia and some low tepuis in Venezuela (e.g., Cerro Yapacana). We include these mountains in the analysis due their phytogeographic similarities with the Pantepui (Estrada and Fuertes 1993; Cortés and Franco 1997), and because they are also part of the Roraima Formation (Galvis Vergara 1994), the main geological substrate of the Guayana Highlands.

Database

We used previously compiled species lists (Mayr and Phelps 1967; Willard et al. 1991; Zyskowski et al. 2011) to build a preliminary database, which was then standardized according to recent taxonomic studies (e.g., Weller 2000; Rheindt et al. 2008; Bonaccorso et al. 2011; Remsen et al. 2017). Our final list contains species with different degrees of association with tepuis, including endemic and non-endemic species (Supplementary Material 1). The list includes mainly montane birds with a few species with broader elevational distributions (e.g., *Pyrrhura picta* and *Tigrisoma fasciatum*). We evaluated whether these species showed geographical variation by assessing subspecies names by consulting the *Handbook of Birds of the World* (HBW) (del Hoyo et al. 1992, 1993, 1996, 1997,1999, 2001, 2002, 2003, 2004).

For each species, we gathered data on the minimum and maximum elevation records, trophic guilds, and habitat association taken from the literature (del Hoyo et al. 1992, 1993, 1996, 1997, 1999, 2001, 2002, 2003, 2004; Hilty and Brown 1986; Stotz et al. 1996; Hilty 2003; Restall et al. 2006, Supplementary Material 1). Also, birds were categorized as forest, forest edge, and non-forest species following habitat use descriptions found in Hilty (2003) and Restall et al. (2006).
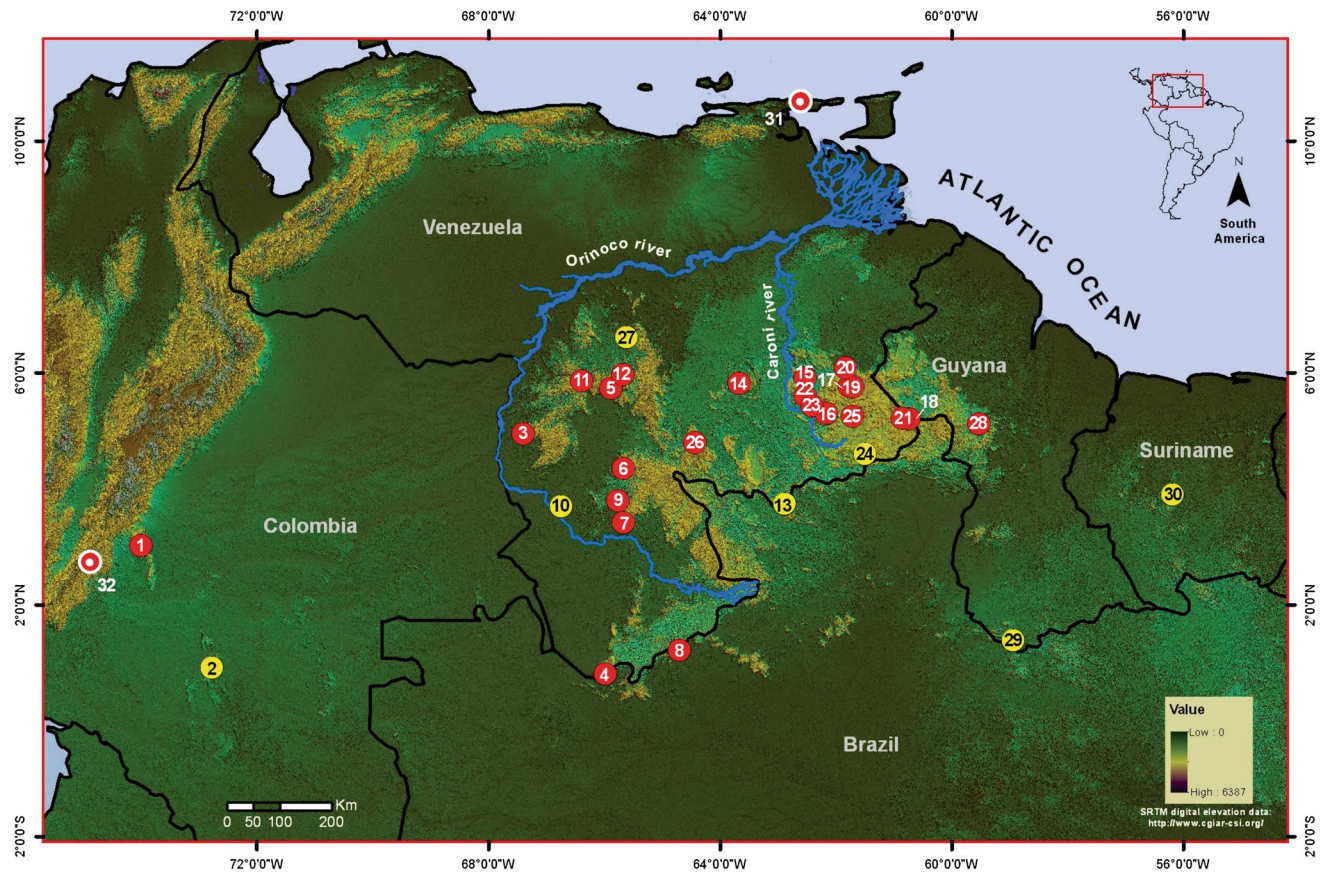
Fig. 1 Northern South America showing the geographical distribution of tepuis whose avifaunas were reviewed in this study. *Yellow circles* Mountains below 1500 m a.s.l., *red circles* mountains above 1500 m a.s.l. *1* Sierra Macarena (Ma), *2* Sierra Chiribiquete (Ch), *3* Cerro Sipapo (Si), *4* Cerro de la Neblina (Ne), *5* Cerro Yaví (Ya), *6* Serranía Paru (Pa), *7* Cerro Duida (Du), *8* Serrania Tapirapecó* (Tap), *9* Cerro Huachamacari (Hu), *10* Cerro Yapacana (Yp), *11* Cerro Guanay (Gy), *12* Cerro Calentura (Ca), *13* Cerro Urutani (Ur), *14* Cerro Guaiquinima (Gu), *15* Cerro Ayuán-tepui (Ay), *16* Cerro Chimantá-tepui (Ci), *17* Cerro Ptari-tepui (Pt), *18* Monte Roraima (Ro), *19* Sororopán-tepui (So), *20* Sierra de Lema (Le), *21* Cerro Cuquenán* (Cu), *22* Uaipán-tepui (Ua), *23* Aprada-tepui (At), *24* Paurai-tepui* (Pu), *25* Uei-tepui (Uei), 26 Cerro Jaua (Ju), *27* Cerro El Negro (Eg), *28* Potaro Plateau (Po), *29* Acary Mountains (Am), *30* Tafelberg (Ta). Cerro Humo (Hum; *31*) and Serranía Los Picachos (Pl; *32*) are reference sites for the Paria Peninsula and the Colombian Andes, respectively. *Asterisks* indicate tepuis with sparse bird sampling, excluded from the analysis

After compiling the final species list, we searched species and subspecies records on individual tepuis, compiling data from Venezuela (25 tepuis), Colombia (2), Guyana (2) and Suriname (1). We exclude three sites (Serrania Tapirapecó, Paurai Tepui and Cuquenan Tepui) from the analysis as local inventories were too sparse to characterize the avifauna of these mountains. Subspecies were only considered if the consulted literature explicitly mentioned this taxonomic category, except for subspecies known to be widespread distributed through tepuis (e.g., *Aeronautes montivagus tatei*, *Patagioenas fasciata roraimae*).

The option to consider subspecies in the analysis opens up the possibility of including taxa that are not appropriate evolutionary entities, as several such bird subspecies were not evaluated in recent taxonomic revisions. On the other hand, to ignore the numerous subspecies cited in the tepui ornithological literature could underestimate the true extent of avian diversity in the region (see "Discussion" section). Consequently, we opted to maintain separate analysis based on subspecies and species.

Species or subspecies whose ranges were poorly described in the literature were not included in the analysis. We consulted nearly 40 publications including taxonomic monographs and local inventories (Supplementary Material 2), and the final database represents a significant improvement on the compilations of Willard et al. (1991) and Zyskowski et al. (2011).

Although our intention was to summarize bird distributions for specific tepui, we recognize that our databases (Supplementary Material 3, 4) are likely affected by false absences due to the fact that some tepuis are better sampled than others. Although the sampling efforts on individual tepui remain difficult to quantify, we believe that

the data compiled here represent the best available on bird species occurrence at the site level.

The biogeographic affinities of tepui avifauna were investigated by means of a distributional analysis of non-endemic birds across the principal montane regions of the Neotropics broadly defined as the Northern Andes, Central Andes, Central Highlands (mostly in Costa Rica and Panama), mountains in Coastal Venezuela, and montane regions in eastern Brazil. We assumed that numbers of species shared among montane regions are good proxies for their biogeographical relationships. We examined species distribution using HBW volumes as the main sources (del Hoyo et al. 1992, 1993, 1996, 1997,1999, 2001, 2002, 2003, 2004).

Ecological and biogeographic analysis

We adopted the deconstruction approach suggested by Marquet et al. (2004) in which the total species diversity is broken down into smaller subsets of species that share a particular attribute. The main attributes used to decompose the studied avifauna were biogeographic (endemic vs. non-endemic), taxonomic (species vs. subspecies), and ecological (feeding guilds and habitat association).

Bands of 250 m were used as comparative units to examine the influence of elevation on the bird species diversity. Records of maximum and minimum altitude for each species taken from the literature were used, assuming that the species occur between these limits (Patterson et al. 1998).

We collected data on the following physical and geographic characteristics for 23 tepuis: (1) maximum elevation (meters a.s.l.), (2) summit area (squared kilometers), (3) linear distance from Andes (kilometers in a straight line), (4) linear distance from the Paria Peninsula (kilometers in a straight line), and (5) distance to the closest tepui (kilometers in a straight line). Summit area was not available for the Cerro Urutani, Sororopán-tepui, Sierra de Lema, or Acary Mountains, therefore, we excluded these mountains from the analysis. The main data source for maximum elevation and summit area was Huber (1995), complemented by Stiles et al. (1995), Bottia et al. (2005), and Nogué et al. (2009). Geographic coordinates for each tepui were taken from the literature and used to calculate distance among tepuis and between tepuis and Cerro Humo in the Paria Peninsula (northern Venezuela) and Serrania de los Picachos in the Colombian Andes (Fig. 1). These montane localities were chosen as reference sites due to their proximity to tepuis and availability of bird inventories or general accounts of their avifaunas (Bohórquez 2002; Hilty 2003).

The relationships between number of species and physical characteristics of tepuis were tested using multiple regressions. Dependent variables in the regression models were: total number of species; number of endemic species; number of non-endemic species; number of endemic taxa (species plus subspecies); number of forest, forest edge and non-forest bird species. Physiographic data described above (Supplementary Material 5) were used as independent variables in the regression models.

The Akaike information criterion (AIC) was used to choose the best-fitted regression models among the combination of predictor variables for each dependent variable. Multiple regressions were performed with both independent and dependent variables log transformed (log $10 + 1$). We used AIC weights to estimate the relative importance of each predictor variable in the competing models (Burnham and Anderson 1998). The regressions and multi-model inference were performed in SAM 4.0 (Rangel et al. 2010).

Species distribution patterns were examined through non-metric multidimensional scaling with Jaccard indices as a similarity measure and cluster analysis with Jaccard indices and the unweighted pair group method with arithmetic mean as the linkage strategy. Mayr and Phelps (1967) proposed two main biogeographic units within the Pantepui (eastern and western tepuis) delimited by the Rio Caroni (Fig. 1). In addition, bird species diversity is affected by maximum elevation of individual tepuis (Cook 1974). Analyses of similarity with a two-way crossed design (Clarke and Warwick 2006) were used for testing effects of geographic location and elevation on the bird species composition. Following the definition of Huber (1995), elevation categories were defined as above and below 1500 m a.s.l. We also evaluated the degree of concordance of site ordinations based on biotic composition (total species and endemic taxa) and physiographic data using the BIOENV approach described in Clarke et al. (2008).

Patterns of β-diversity in the bird assemblage were investigated using the analytical method of Podani and Schmera (2011) in which the β-diversity is partitioned into three components: shared species similarity (S), differences in species richness (D) and species replacement (R). Three coefficients (S_{Jac}, D_{rel} and R_{rel}) (formulas in Podani and Schmera 2011) were calculated and represented as percentages allowing evaluation of the relative contribution of each component to the β-diversity pattern. The analysis was run in the computer program SDRSimplex (downloaded from http://ramet.elte.hu/~podani).

We tested the hypothesis that bird species composition of individual tepuis is nested within each other through the nestedness metric based on overlap and decreasing fill (NODF) whose values range from 0 to 100, with larger numbers indicating increased nestedness (Almeida-Neto et al. 2008; Ulrich et al. 2009). To investigate how the patterns of species nestedness are influenced by tepuis attributes, presence/absence matrices were ordered by: (1) maximum altitude, (2) eastern-western sequence of tepuis, (3) western-eastern sequence of tepuis, (4) isolation metric 1 (distance of the target tepui to the nearest tepui), and (5) isolation

metric 2 (average distance of the target tepui to the five nearest tepuis). The statistical significance of the NODF indices was assessed by means a shuffled columns null model that randomizes the order of columns in the matrix and tests if a particular order of the columns leads to a higher degree of nestedness than expected by chance. NODF analysis were performed using the free web application Nestedness for Dummies developed by Strona et al. (2014).

Results

Bird species diversity of the Pantepui

The core tepui avifauna is composed of 138 bird species (43 endemic and 95 non-endemic) distributed in 34 families (Supplementary Material 6). Sixteen non-endemic species have at least one endemic subspecies within the Pantepui. The taxonomic distinctiveness of the tepuis avifauna is most obvious at the subspecies level, with 167 subspecies being endemic to these mountains (Supplementary Material 6).

Forest species are the dominant component of the tepuis avifauna (84 species, 61% of avifauna), while the contribution of forest edge and non-forest species is 25% (34 species) and 14% (20 species), respectively. Endemic and non-endemic species are distributed in similar proportions among the habitat categories ($\chi^2 = 0.04$, $df = 2$, $P = 0.86$).

Most birds are insectivores, both in endemic (46.5% of species) and non-endemic (45%) components. Omnivores (19.5%) and frugivores (16.5%) have a similar contribution to the tepuis avifauna. Nectarivores, especially hummingbirds (Trochilidae), contribute disproportionately to the endemic (21% of species), as opposed to non-endemic (10.5%), component. Few carnivorous (three species) and granivorous (three species) birds are known from the tepuis.

A small number of non-endemic bird species (19%) occur in all five broadly defined Neotropical montane regions, with most non-endemic birds shared with the Northern (85%) and Central Andes (80%). A smaller proportion of species is shared with mountains in coastal Venezuela (64% of species), the Central Highlands (46%) and montane regions in eastern Brazil (41%).

Elevational patterns

Total bird species richness increases with altitude, peaking at 1251–1500 m a.s.l. and then gradually decreases (Fig. 2). Endemic birds are most diverse between a broad band of 1251–2000 m a.s.l, while the highest number of non-endemic species is found at a range of 751–1000 m a.s.l. (Fig. 2). The highest numbers of forest species are found from 751 to 1500 m a.s.l., while forest edge and non-forest birds are most species diverse from 1251 to 1750 m a.s.l. (Fig. 2).

Endemic birds tend to occupy higher elevations than non-endemic (median mid-point = 1475 vs. 1200 m, respectively) (Fig. S1). For example, only eight endemic species occur below 500, m while 62 non-endemic species are distributed below this altitudinal limit (Fig. S1).

Compositional variability

The average number of bird species per tepui is 50.52 (range 14–97 species; Table 1). The number of endemic species varies from 0 (Sierra Macarena) to 36 (Monte Roraima) (Table 1). The proportion of endemic species is higher than 40% for almost half of the analyzed tepuis. In contrast, less than 60% of the avifauna is composed of endemic taxa (species plus subspecies) on only four tepuis (Sierra Macarena, Sierra Chiribiquete, Acary Mountains and Tafelberg). The proportions of endemic species ($F = 14.99$, r^2 adjusted = 0.35, $P = 0.001$) and endemic taxa ($F = 9.22$, r^2 adjusted = 0.24, $P = 0.005$) are positively correlated with the maximum altitude of tepuis.

Most species are widely distributed across the tepuis (Fig. 3), although a few are apparently restricted to one or two mountains, such as *Chlorostilbon olivaresi* (Cerro Chiribiquete), *Phyllomyias burmeisteri* (Cerro Chimantá), *Myioborus cardonai* (Cerro Guaiquinima), *Emberizoides duidae* (Cerro Duida), and *Euchrepomis callinota* (Acary Mountains and Tafelberg). Geographical restriction is more evident among endemic taxa, for which nearly 28% are found on a single mountain in our sample (Fig. 3). Cerro Neblina (3014 m a.s.l.) is the tepui with the highest number of single-mountain-endemic taxa (13), followed by Cerro Ayuán-tepui (2450 m a.s.l.) and Cerro Sipapo (1800 m a.s.l.) with five endemic taxa each.

Bird species assemblage composition is more homogeneous on tepuis located east of the Rio Caroni than western ones, except for non-endemic species (Fig. 4). Mountains located at both extremes of the tepuis range (Tafelberg, Acary Mountains, Sierra Chiribiquete and Sierra Macarena) had the lowest similarity in bird composition (Fig. 4).

Cerro Yapacana has a distinctive species composition compared to other tepuis, likely due to its low species diversity (Fig. 5). The non-Venezuelan tepuis, with the exception of the Potaro Plateau, also form a distinctive group (Fig. 5). Non-endemic birds reveal no clear pattern of site grouping (Fig. 5).

When all species and endemic ones are compared, most tepuis fall into two major groups with Rio Caroni as the geographic limit between them (Fig. 5). Site distribution, when considering endemic taxa, in contrast, shows a more complex pattern, although it was possible to identify two major groups at 25% similarity level, with the exceptions

Fig. 2a, b Number of bird species distributed among biogeographic and ecological groups along the elevation gradient
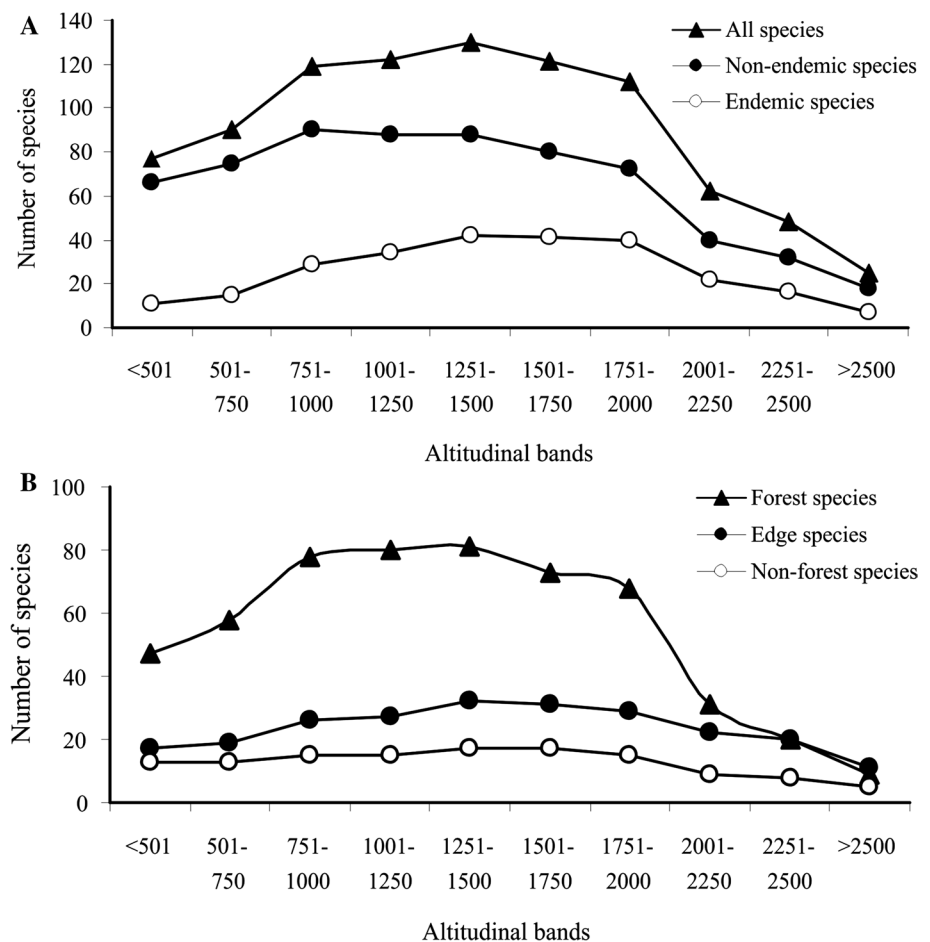
of the Cerros Guaiquinima and Urutani, which are western tepuis that group with ones east of the Rio Caroni (Fig. 5).

Bird species composition is affected by geographic position relative to the Rio Caroni and tepuis altitudes. Differences in species composition are more affected by elevation than geographic position when considering all species and non-endemic species (Table 2). The influences of geographic position and elevation on species composition are more similar when considering endemic species and subspecies (Table 2).

Physical geography of tepuis and species diversity and composition

Maximum elevation was the variable that best predicted the number of species in all bird groups tested (Supplementary Material 7). For endemic taxa, distance from the Andes and maximum elevation contributed similarly to the regression models (Fig. S2). In addition, distance from the nearest tepui and summit area influenced the number of non-forest bird species, although the average of coefficients of determination in the tested models was low (Fig. S2).

Bird species composition is also affected by the physical and geographic characteristics of tepuis, both for total species (global BEST test, $r = 0.636$, $P < 0.001$, 999 permutations), and for endemic taxa (global BEST test, $r = 0.76$, $P < 0.001$, 999 permutations). Maximum altitude and distance from the Andes were the variables that best correlated with total species composition ($r = 0.636$). For endemic taxa only, the best correlating variable was distance from Andes ($r = 0.76$).

Components of β-diversity and nestedness

For all species and non-endemic species, composition similarity, richness difference, and species replacement contributed similarly to patterns of β-diversity (Fig. S3). Richness difference was the dominant component of β-diversity for endemic species and endemic taxa (Fig. S3). In addition, for endemic taxa, species replacement made a major contribution to β-diversity compared with endemic species (Fig. S3).

Difference criteria applied to order matrices returned significant patterns of nestedness in species composition, except for the western-eastern gradient of tepuis distribution (Table 3). Patterns of nestedness are more evident for

Table 1 Summary of bird species diversity of tepuis analyzed in this study

Tepuis	Maximum elevation	Total species	Endemic species	Endemic taxa
Sierra Macarena (Ma)	1600	28	0 (0.00)	3 (10.7)
Sierra Chiribiquete (Ch)	1000	16	1 (6.2)	3 (18.7)
Acary Mountains (Am)	1100	28	4 (14.3)	12 (42.9)
Cerro El Negro (Eg)	1200	26	4 (15.4)	22 (84.6)
Tafelberg (Ta)	1090	29	5 (17.2)	14 (48.3)
Cerro Yapacana (Yp)	1300	14	3 (21.4)	9 (64.3)
Cerro de la Neblina (Ne)	3014	77	23 (29.9)	59 (76.6)
Cerro Calentura (Ca)	1617	18	6 (33.3)	16 (88.9)
Cerro Yaví (Ya)	2300	51	17 (33.3)	43 (84.3)
Cerro Guanay (Gy)	2080	26	9 (34.6)	20 (76.9)
Cerro Ayuán-tepui (Ay)	2450	75	27 (36.0)	60 (80.0)
Monte Roraima (Ro)	2732	97	36 (37.1)	78 (80.4)
Cerro Guaiquinima (Gu)	1650	55	21 (38.2)	43 (78.2)
Sierra de Lema (Le)	1650	72	28 (38.9)	54 (75.0)
Sororopán-tepui (So)	2050	70	28 (40.0)	56 (80.0)
Cerro Ptari-tepui (Pt)	2400	87	35 (40.2)	69 (79.3)
Uaipán-tepui (Ua)	1950	57	23 (40.3)	49 (85.9)
Cerro Urutani (Ur)	1270	47	19 (40.4)	40 (85.1)
Serranía Paru (Pa)	2200	51	21 (41.9)	43 (84.3)
Cerro Huachamacari (Hu)	1900	24	10 (41.7)	20 (83.3)
Cerro Duida (Du)	2358	72	31 (43.1)	62 (86.1)
Potaro Plateau (Po)	2000	65	28 (43.1)	48 (73.8)
Cerro Chimantá-tepui (Ci)	2550	72	32 (44.4)	57 (79.2)
Cerro Sipapo (Si)	1800	47	21 (44.7)	42 (89.4)
Uei-tepui (Uei)	2150	59	27 (45.8)	49 (83.0)
Cerro Jaua (Ju)	2250	43	20 (46.5)	40 (93.0)
Aprada-tepui (At)	2500	58	28 (48.3)	53 (91.4)

Mountains are ordered by percentage of endemic species. *Numbers in parentheses* represent percentages of total species on each mountain

Fig. 3 Number of bird species and endemic taxa (species plus subspecies) distributed between the tepuis analyzed here
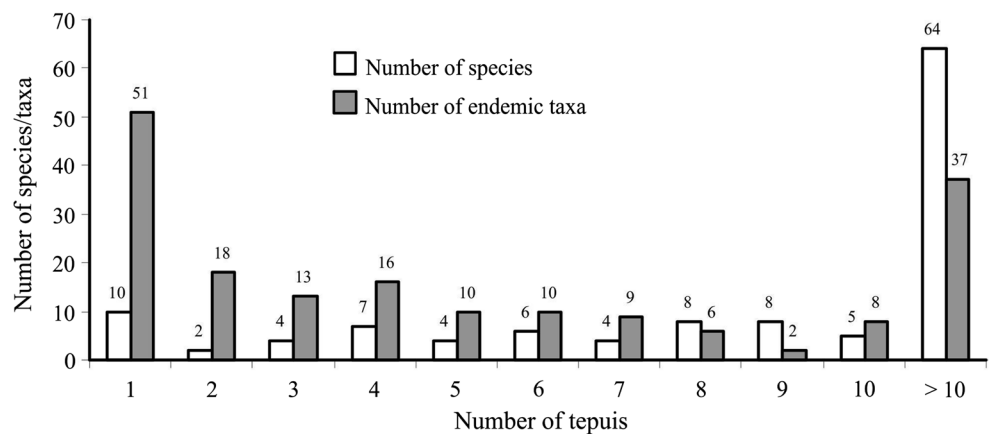
total species than endemic taxa, with NODF values being consistently lower in the latter. Tepuis with a lower number of all species and endemic taxa are a subset of species-richer ones (Table 3). Also species and endemic taxa composition of lower tepuis are a subset of those with higher elevations (Table 3).

Nested analysis suggests a general loss of species in tepuis along a geographic gradient from east to west but not
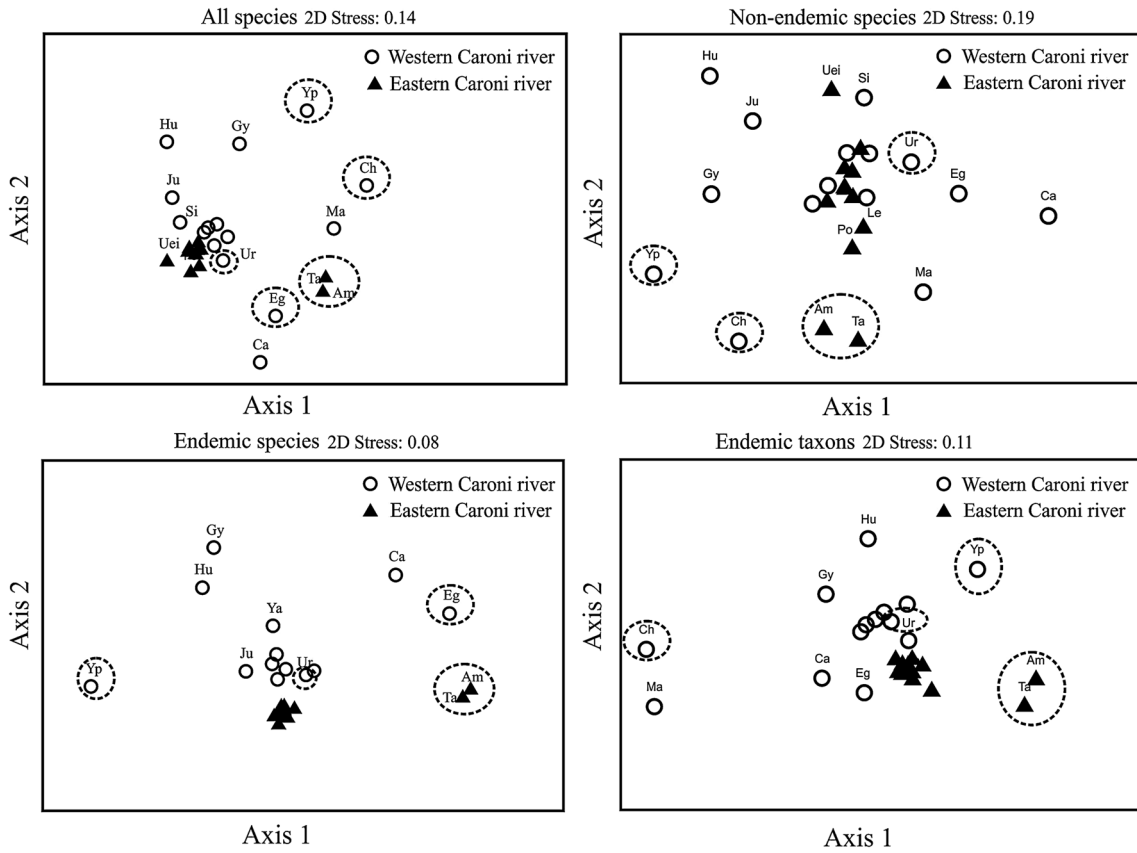
Fig. 4 Plots of non-metric multidimensional scaling ordinations of 27 tepuis using different databases. *Dotted circles* indicate tepuis lower than 1500 m a.s.l. For abbreviations, see Fig. 1

Fig. 5 Cluster analysis of bird communities of 27 tepuis from different databases. For abbreviations, see Fig. 1
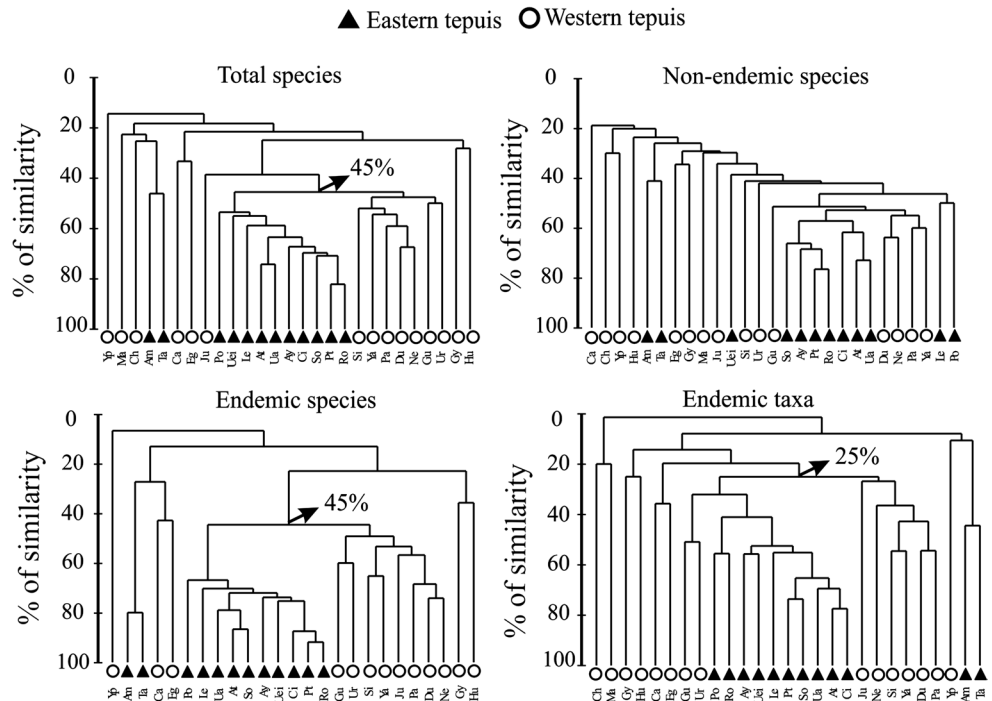
Table 2 Results of two-way analysis of similarity contrasting two treatments: geographic position relative to Rio Caroni (eastern or western) and altitudinal categories (uplands or highlands)

Taxonomic level	Groups	Global R-value	p-value
Total species	Rio Caroni	0.32	0.001
	Altitudinal categories	0.64	0.001
Non-endemic species	Rio Caroni	0.16	0.004
	Altitudinal categories	0.58	0.002
Endemic species	Rio Caroni	0.51	0.001
	Altitudinal categories	0.72	0.001
Endemic taxa	Rio Caroni	0.51	0.001
	Altitudinal categories	0.56	0.002

Highlands and uplands include tepuis above and below 1500 m a.s.l., respectively

The number of permutation were 999 for all comparisons

Table 3 Values of nestedness metric based on overlap and decreasing fill for presence/absence of bird species in 27 tepuis ordered by different criteria

Matrices ordered by	Total species	Endemic taxa
Number of species	65.7*	45.9*
Maximum altitude	52.9*	37.7*
Eastern–western sequence	45.0**	30.3***
Western–eastern sequence	20.9 NS	15.9 NS
Isolation 1 (distance from the nearest tepui)	46.5**	34.0*
Isolation 2 (average distance from the five nearest tepuis)	45.0**	32.4**

NS Not significant, *$P < 0.001$, **$P < 0.01$, ***$P < 0.05$

Discussion

Biogeographic uniqueness of tepuis

The Pantepui area of endemism harbors a unique and distinctive biodiversity, although it occupies a modest area of 5.000–10.000 km^2 (Berry and Riina 2005; McDiarmid and Donnelly 2005; Jaffe et al. 1993; Pyrcz 2005; Marmels 2007; Voss et al. 2013). Mayr and Phelps (1967) list 96 bird species as typical of tepuis in Venezuela, with 29 (30%)

endemic to these mountains. Here we list 138 bird species, of which 43 (31%) are endemic to the Pantepui. The difference in the total species number is explained by different criteria used to select species as the core tepui avifauna (Mayr and Phelps 1967). The total number of species in the tepui avifauna reported here is, however, consistent with other studies (Stotz et al. 1996; Renjifo et al. 1997; Zyskowski et al. 2011).

Despite the changes in taxonomy, the proportion of endemic bird species remains similar to that reported in Mayr and Phelps (1967). Taxonomic changes have occurred widely across taxonomic groups including hummingbirds (*Amazilia cupreicauda*), toucanets (*Aulacorhynchus whitelianus*), flycatchers (*Elaenia olivina*), nightjars (*Hydropsalis roraimae*), and owls (*Megascops roraimae*) where taxa formerly considered subspecies have been elevated to full species level (Weller 2000; Rheindt et al. 2008; Bonaccorso et al. 2011; Danta et al. 2016; Sigurdsson and Cracraft 2014).

It is important, however, to emphasize that our analyses are likely biased by an incomplete taxonomic treatment of bird subspecies. Despite recent scientific advances, the majority of subspecies in the tepuis avifauna have not been formally analyzed from the perspective of species limit, which may have exaggerated the degree of endemism within Pantepui by considering as unique taxa those that do not represent distinct evolutionary lineages. This situation highlights the need for systematic studies to fully appreciate the taxonomic distinctiveness and degree of endemism of the Pantepui avifauna. Nevertheless, even the more conservative species-level estimate of endemism highlights the great importance of tepuis to Neotropical bird diversity (Renjifo et al. 1997; Sánchez-González et al. 2008).

Ecological distribution of tepuis birds

The Pantepui avifauna is composed of a heterogeneous mix of species with diversified habitats, food requirements, and biogeographic affinities. Indeed, the deconstruction approach used in this study reveals different facets of bird species distribution across the Pantepui. For example, a difference in species richness between tepuis is a prominent characteristic of endemic components of tepuis birds, which likely reflects the insular nature of these mountains. In addition, endemic taxa reveal a discernible geographic pattern of species replacement along a longitudinal gradient, a pattern not observed among the non-endemic species.

Maximum altitude of tepuis is the physiographic variable that best explains the variation in bird species diversity and composition (see also Cook 1974; Jaffe et al. 1993). Higher tepuis tend to have greater slope areas, which are generally occupied by forests with variable physiognomies (Tate 1939; Huber 1995, 1988). In this sense, maximum altitude could

in the opposite direction (Table 3). Finally, the two metrics of tepuis isolation indicate that bird assemblages of the more isolated mountains are nested within those of the more connected ones (Table 3). Although results were significant, it is important to emphasize that the NODF values were relatively low (< 0.50) indicating that several tepuis have idiosyncratic species/taxa compositions.

be considered a proxy for tepuis vegetation heterogeneity, which in turn affects the bird species diversity (Huber 1988; McDiarmid and Donnelly 2005). Details of this relationship, however, require further field studies.

The summit area or total area of tepuis are not among the variables that explain bird diversity and composition, confirming analysis of Cook (1974). However, summit area is apparently relevant for non-forest birds. The top of most tepuis is characterized by different types of open and herbaceous vegetation growing in wet, dry, or stony soils (Huber 2005, 2006; Rull 2004; Safont et al. 2014). The diversity of open vegetation types at the top of tepuis is directly proportional to the extent of the summit area (Huber 2006). Therefore, tepuis summit area is likely to be a suitable proxy for the habitats available to non-forest birds.

Non-endemic montane birds are more frequent along the lower parts of tepuis, while endemic species are found at higher elevations, a pattern shared with plants (Nogué et al. 2013). This pattern of altitudinal distribution, however, could be affected by differential sampling effort in distinct altitudinal bands (Lomolino 2001). Unfortunately, no study has evaluated bird distributions along vertical gradients of tepuis together with controlled sampling effort, as has been done in other Neotropical montane systems (e.g., Herzog et al. 2005; Forero-Medina et al. 2011; Cavarzere and Silveira 2012).

Tepuis as islands of biodiversity

The tepuis are isolated from each other by contrasting vegetation between the mountain slopes and lowland valleys, making the concept of "sky islands" appropriate to describe this ecosystem (McCormack et al. 2009). Such a geographic context has prompted the analysis of tepuis species distributions using as a premise theories of island biogeography (Whittaker and Fernandez-Palacios 2007; Safont et al. 2014).

However, the interstitial lowland habitats between tepuis are not analogous to oceans in a true oceanic island context, since such habitats represent different environmental filters or barriers depending on the bird species group considered. Indeed, bird species exhibit altitudinal flexibility, which may facilitate movements among and between tepuis and lowlands (see Steyermark and Dunsterville 1980; Kok et al. 2012; Salerno et al. 2012; Nogué et al. 2013 for examples of altitudinal flexibility in plants and frog species).

While the dispersal capabilities of birds are favored by altitudinal flexibility, this is not sufficient to homogenize overall bird distribution within the Pantepui. In fact, our analysis confirms the major division between the eastern and western tepuis first noted by Mayr and Phelps (1967). In addition, the high proportion of single-tepui-endemic

species and taxa suggests isolation between bird populations, although such drastic spatial restriction could be an artifact of poor taxonomic resolution, as discussed above.

In this sense, the isolation of tepuis could favor the speciation processes within the Pantepui. Isolation in the biological sense is a variable which is difficult to measure, and distance from the nearest tepui used in this study may not provide a good measure of it. Maximum altitude of tepuis, however, affected bird species diversity and could be also interpreted as a measure of the degree of isolation of a mountain.

Extinction events and differential colonization have also been proposed as important mechanisms affecting the large-scale patterns of bird distribution within the Pantepui (Chapman 1931; Cook 1974). Bird assemblages on lower mountains are subsets of those on higher ones, suggesting a selective loss of species along elevational gradients. In other montane systems such nested patterns in bird distribution have been interpreted as evidence of selective extinction (Atmar and Patterson 1993; Brown 1971; Barrantes et al. 2011). The nested patterns reported here, however, are also consistent with the absence, on lower mountains, of habitats adequate to sustain species populations with specific requirements.

Distance from faunal source is another key component of the equilibrium theory of island biogeography (MacArthur and Wilson 1967). Although the evolutionary relationships between the faunas of tepuis and other Neotropical mountains have yet to be settled (Sánchez-González et al. 2008), the Andes have been identified as an important source of many components of the Pantepui avifauna (Mayr and Phelps 1967; Bonaccorso and Guayasamin 2013). Indeed, the non-endemic component of tepui avifauna shows high species similarity with that of the Northern and Southern Andes. However, contrary to the expectation that mountains near the Andes have higher species diversity, the eastern tepui tend to host a more diverse and differentiated avifauna (Cook 1974). In addition, nested analysis suggests a general ordered loss of species from eastern to western tepuis, but not in the opposite direction.

The most obvious explanation for these patterns is that western tepuis are more isolated from each other, making colonization events rarer and favoring extinctions, leading to a decrease in local species diversity (Cook 1974; Willard et al. 1991). In contrast, the eastern tepuis occupy larger and more connected areas, which presumably increase habitat availability with consequent increases in species diversity (Mayr and Phelps 1967).

In addition to the influence of contemporaneous geography and environment on species distribution, bird assemblages in tepuis were likely affected by past geological and climatic events (Briceño and Schubert 1990; Edmond et al.

1995; Rull 2004; D'Apolito et al. 2013; Mecchia et al. 2014). Innumerable historical hypotheses have been proposed to explain the patterns of endemism and diversity across the Pantepui (Chapman 1931; Mayr and Phelps 1967; Maguire 1970; Hernández and Lew 2001; Rull 2005). Recent molecular phylogenies with different taxa including plants, birds, frogs and mammals (Givnish et al. 2000, 2004; Pérez-Emán 2005; Salerno et al. 2012; Bonaccorso and Guayasamin 2013; Leite et al. 2015; Kok et al. 2012, 2017) have important implications for the testing these hypotheses, although a detailed discussion of these studies is beyond the scope of this paper and will be addressed elsewhere.

Conclusion

Bird diversity and species compositions of tepuis are unique to the Neotropical region, and the species assemblages of these mountains were likely structured through the spatial distribution of these mountains, habitat diversity, and complex historical events. Details of these ecological and historical drivers, however, remain poorly investigated in the field due to the difficulty of accessing most tepuis. Advances in the investigation of diversity and evolution in the Pantepui birds require well-designed ecological studies and systematic revisions of bird species and subspecies. This latter challenge needs an expansion of modern bird collecting from specific mountains, including those located at the extremes of the Guayana Shield. In addition, the protection and detailed investigation of unique and fragile tepui ecosystems need to be prioritized by governments, the academic community and other relevant stakeholders (Nogué et al. 2009; Rull et al. 2016).

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