BIODIVERSITY OF PANTEPUI

The Pristine "Lost World" of the Neotropical Guiana Highlands

---

Edited by

VALENTÍ RULL
Institute of Earth Sciences Jaume Almera (ICTJA-CSIC), Barcelona, Spain

TERESA VEGAS-VILARRÚBIA
Department of Evolutionary Biology, Ecology and Environmental Sciences, University of Barcelona, Barcelona, Spain

OTTO HUBER
Botanical Institute of Venezuela Foundation, Caracas, Venezuela

CELSA SEÑARIS
Center of Ecology, Venezuelan Institute for Scientific Research (IVIC), Caracas, Venezuela

ELSEVIER

ACADEMIC PRESS
An imprint of Elsevier

Notices
Knowledge and best practice in this field are constantly changing. As new research and experience broaden our understanding, changes in research methods, professional practices, or medical treatment may become necessary.

Practitioners and researchers must always rely on their own experience and knowledge in evaluating and using any information, methods, compounds, or experiments described herein. In using such information or methods they should be mindful of their own safety and the safety of others, including parties for whom they have a professional responsibility.

To the fullest extent of the law, neither the Publisher nor the authors, contributors, or editors, assume any liability for any injury and/or damage to persons or property as a matter of products liability, negligence or otherwise, or from any use or operation of any methods, products, instructions, or ideas contained in the material herein.

For Information on all Academic Press publications
visit our website at https://www.elsevier.com/books-and-journals

Working together
to grow libraries in
developing countries

www.elsevier.com • www.bookaid.org

Birds

Jorge L. Pérez-Emán[1,2], Miguel Lentino[2]
and Elisa Bonaccorso[3]

[1]Institute of Tropical Zoology and Ecology, Central University of Venezuela, Caracas,
Venezuela [2]Phelps Ornithological Collection, Caracas, Venezuela [3]Institute BIOSFERA and
Laboratory of Evolutionary Biology, University San Francisco de Quito, Quito, Ecuador

Introduction

The Pantepui biogeographical province lies on the Guiana Shield and represents a biogeographic province defined by the characteristic biota associated with the Guiana Highlands. These highlands are the result of a process of continuous erosion of ancient sandstone sediments (Precambrian age) that are hypothesized to have been initially uplifted during the opening of the tropical Atlantic in the Late Cretaceous (Ghosh, 1985; Sidder and Mendoza, 1991; Briceño and Schubert, 1990). Such a history of erosion has resulted in a unique landscape composed of a series of montane isolates (tepuis or cerros, hereafter included in the word tepui) that differ in elevation (from 800 to 3000 m a.s.l.) and degree of isolation and that are characterized by a localized biota with moderate-to-high endemism in different taxonomic groups (Mayr and Phelps, 1967; Steyermark, 1986; Berry et al., 1995; McDiarmid and Donnelly, 2005).

The ornithological exploration of the Guiana Highlands began almost 200 years ago. The Schomburgk brothers took the first steps to uncover the natural history of this region. Robert Schomburgk discovered Roraima-tepui on his first expedition (1838), and the first specimens were taken from that tepui by Richard Schomburgk on a follow-up expedition (1842). Additional exploration of this tepui and the neighboring area by Henry Whitely and others increased our knowledge of its avifauna, but it was only after the American Natural History Museum expeditions to Roraima-tepui and Cerro Duida, led by G. Tate in 1927 and 1928, that a first synthesis of the avifauna from this region was completed (i.e., Chapman, 1931). Accounts of exploration of the region have been given by Huber and Wurdack (1984), McDiarmid and Donnelly (2005), and others, but it is important to recognize the major contributions of William H. Phelps and W. H. Phelps Jr., who organized,

299

funded, and participated in a major regional exploration from 1937−1965, with some additional expeditions in later years. More recently, institutions such as the Foundation for the Development of Physical, Mathematical and Natural Sciences (FUDECI), Terramar Foundation, the American Museum of Natural History, and the Phelps Ornithological Collection organized further explorations in the 1980s and 1990s (Lentino and Bosque, 1989; Willard et al., 1991; Barrowclough and Escalante-Pliego, 1990; Barrowclough et al., 1995, 1997) and in 2000 (Pérez-Emán et al., 2003). Lately, an important number of expeditions have been conducted on different isolated mountains in Colombia, Guyana, and Suriname (Stiles et al., 1995; Barnett et al., 2002; Braun et al., 2003; Ridgely et al., 2005; Robbins et al., 2007; O'Shea et al., 2007; Zyskowski et al., 2011, among others), providing a better insight into the geographical area of the region characterized by the particular avifauna first described by Chapman (1931).

A definition of Pantepui

The history of the term Pantepui began by recognizing that the birds inhabiting the isolated mountains of the Guiana Highlands were unique to the region. The first bird descriptions from Schomburgk's collections (Cabanis, 1848) showed the distinctness of the avifauna from Roraima-tepui. However, major collections by Tate on both Roraima-tepui and Cerro Duida, large tepuis located almost 650 km away from each other, allowed ornithologists to realize that species described after Roraima collections were more widely distributed (Chapman, 1931). The American Museum of Natural History expedition to the Auyán-tepui, organized by Chapman and Phelps (Gilliard, 1941), and later expeditions, set the stage of knowledge needed to provide a thorough synthesis of the regional avifauna.

The term "Pantepui" (from the Greek *pan* = all; all tepuis) was first introduced by Mayr and Phelps (1955, 1967) to encompass the geographical location of the particular avifauna of the region. Their description was basically both geographical and geological ("the sandstone tabletop mountains in the Venezuelan Territorio Amazonas and Estado Bolivar and in the adjacent border regions of Brasil and Guyana") but did not incorporate the biotic component required for Pantepui to be recognized as a biogeographic region. However, apart from the definition itself, Mayr and Phelps included mountains of the Guiana Highlands based on faunistic grounds, particularly the endemic avifauna associated with the submontane and montane habitats found in the slopes and summits of the tepuis ("subtropical avifauna"), and in doing so, they included mountains not supported by their own definition (e.g., granitic mountains, non-tabletop mountains). The reference to a subtropical avifauna was rooted in Merriam's life zones concept, consistently applied by Chapman in his studies on bird distribution of the Neotropical montane regions (Merriam, 1892; Chapman, 1917; Vuilleumier, 2005), in which elevational distribution is thought to be primarily determined by climatic factors, mainly temperature. Consequently, establishing an elevational limit was included as an operational criteria for the definition of the Pantepui province and its biota. Mayr and Phelps (1967) used elevations of 1000 and 1500 m a.s.l. to estimate the area of Pantepui. Huber (1987) provided a currently accepted definition based on both geographical and biological terms (mountain ecosystems in summits and tepui slopes) and restricted the region to elevations from 1200/1500 to

3000 m a.s.l. Huber (1995) subsequently restricted it to above 1500 m (see Chapter 1: Definition and characterization of the Pantepui biogeographical province).

Establishing an elevational limit for the definition of the Pantepui province and the Pantepui biota are two different things. Species presence depends on a broad group of abiotic and biotic variables (e.g., temperature, precipitation, slope and slope orientation, soil type, resources, predators, competitors), as well as species' physiological characteristics, making areas of different elevations as environmentally suitable for the same species or assemblage of species. As such, the elevational distribution of Pantepui species is expected to fall above or below such elevation thresholds (see Chapman, 1931; Borges et al., 2018). However, use of such cutoff values allows the assembly of lists of birds occupying the particular elevational belt that includes the endemic Pantepui biota. On the other hand, using an elevational threshold to define a biogeographical region is not appropriate because such areas should be defined in terms of their unique biota (Cracraft, 1985). Thus rather than excluding lower-elevation tepuis (uplands *sensu* Huber, 1995; <1500 m a.s.l.), we include all regional tepuis if their known avifaunas are characterized by diagnostic elements of the Pantepui biogeographical province (e.g., Acary Mountains, Yapacana, Cerro El Negro, Tafelberg).

The geographical limits of the Pantepui province have changed as new information from bird distributions has become available. Major differences in the literature are related to establishing the eastern and westernmost tepuis included in biogeographical analyses. Early in geological history, the Roraima Formation extended from Suriname to the Sierra de la Macarena in Colombia (Gansser, 1954). However, the limits of the Pantepui province should be based on faunistic grounds. To the east, Mayr and Phelps (1967) included some mountains in Guyana close to the Venezuelan border and named them the "British Mountains." More recently, field work has shown that the avifauna of mountains such as Mount Ayanganna, Potaro Plateau, and Iwokrama and the Acary Mountains, among others in Guyana (Barnett et al., 2002; Braun et al., 2003; Ridgely et al., 2005; Robbins et al., 2007), and Tafelberg in Suriname (Zyskowski et al., 2011), have clear biogeographical affinities with Pantepui and, consequently, should be included in the Pantepui province, with Tafelberg representing its easternmost locality. The western limits, however, are not that clear. Borges et al. (2018) included both the Sierra La Macarena and Chiribiquete Mountains in Colombia, extending the westernmost limits of this biogeographical region substantially when compared to the previously considered Cerro Sipapo in Venezuela. Borges et al. (2018) identified only three endemic taxa associated with Pantepui for each of these localities. Other species included in their analyses (and present in these localities) are widespread in other Neotropical mountains (e.g., *Myioborus miniatus*, *Tangara gyrola*). A review of the three endemics used by Borges et al. (2018) to extend their western limit of Pantepui suggests that their affinities lie elsewhere. For Chiribiquete, *Chlorostilbon olivaresi* and *Hemitriccus margaritaceiventer chiribiquitensis* are likely more related to Magdalena Valley (Colombia) taxa than to Pantepui birds (Stiles et al., 1995; Stiles, 1996). Similarly, for Macarena, *Chlorospingus flavopectus* is clearly an Andean taxon, and *Xiphocolaptes promeropirhynchus macarenae* is also present in the Colombian Andes (Marantz et al., 2018). *Zonotrichia capensis roraimae*, recorded at both western localities and also present in the Guiana Highlands (Rising and Jaramillo, 2019), has a complex geographical variation. A phylogeographic molecular study of this species showed that the few samples

analyzed from Roraima and the Colombian Andes are not closely related (Lougheed et al., 2013). Thus biogeographical affinities of these taxa, together with broader avifauna and flora studies of the Chiribiquete and Macarena (Estrada and Fuertes, 1993; Stiles et al., 1995; Cortés-B et al., 1998; Giraldo-Cañas, 2001), indicate that these mountains share affinities with Andean, Amazonian, and Guianan regions rather than with Pantepui. Consequently, we do not include Macarena and Chiribiquete in our analysis of the Pantepui avifauna, and we consider Cerro Sipapo the western limit of Pantepui.

Patterns of diversity and endemism

The avifauna of Pantepui is characterized by a moderate diversity (richness) compared to the Andean region. We identified from the literature a total of at least 141 species occurring in the montane habitats of this region, including 45 tepuis from which some ornithological exploration has been conducted (Fig. 13.1). This number differs from previous publications (e.g., 98 spp. in Mayr and Phelps, 1967; 104 in Willard et al., 1991; 103 in Zyskowski et al., 2011; and 138 in Borges et al., 2018; Appendix I), mostly as a result of differences in species selection criteria. Mayr and Phelps (1967) included endemic species, adding taxa either from montane or lowland habitats with differentiated populations (e.g., *Glaucidium brasilianum duidae*). These authors also included montane species even in the absence of geographical differentiation (e.g., *Colibri delphinae*) or species occurring in lowland habitats but only recorded in montane habitats in the tepuis (e.g., *Phaethornis bourcieri*, *Elaenia ruficeps*, *T. gyrola*). Subsequent changes in bird lists are mostly associated with the addition of not previously recorded montane species and with the exclusion (or not) of species nonexclusive of montane habitats or without differentiated populations associated with highland habitats (Appendix I). Most recently, Borges et al. (2018) produced the most inclusive list, adding species with broad elevational distributions that occur in Pantepui habitats. We believe a more inclusive list is a better approach when assessing diversity of these montane assemblages, characterized by a mixture of lowland species with broad elevational distributions and highland species. In fact, a limited number of these broad elevational species are very characteristic of both summits and slopes of tepuis (e.g., *Myiarchus swainsoni phaeonotus*, *Coereba flaveola roraimae*). Additionally, a better review of the species present in these communities is required because some common elements in these habitats have not been included so far (e.g., *Tachyphonus phoenicius*, *Elaenia chiriquensis*, *Elanoides forficatus*).

Endemism in Pantepui and its geographical distribution

Endemism is high in Pantepui. If we consider endemic taxa, including both species and subspecies, the percentage of endemism is 75% (33% for species; 41 species; Appendix I). These high values (at the subspecific level) are comparable to the endemism levels shown by plants (Berry and Riina, 2005) and the herpetofauna (McDiarmid and Donnelly, 2005), groups in which the subspecies level was not considered. Endemism at the subspecific level includes 164 taxa, slightly differing from Borges et al. (2018) as a result of excluding
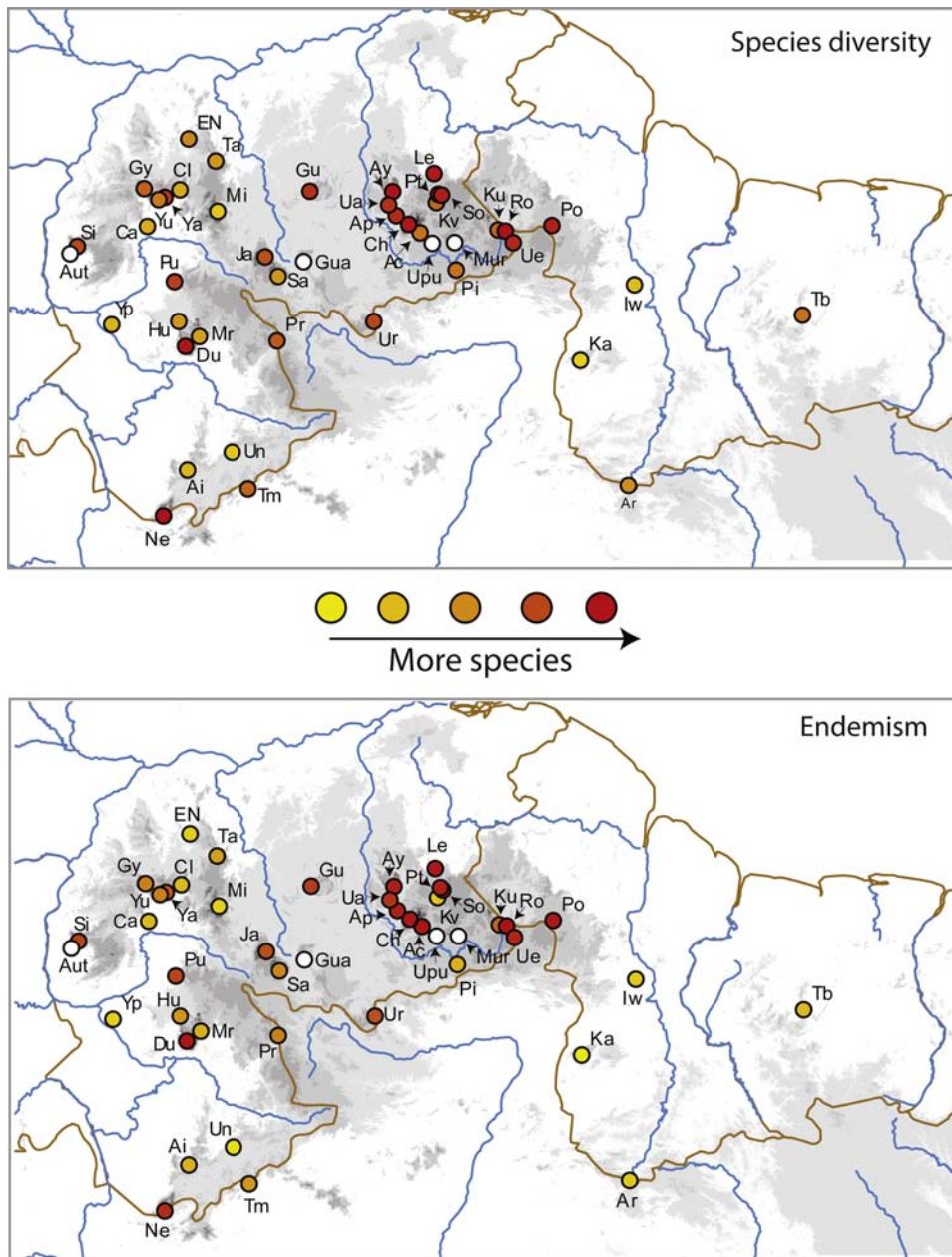
FIGURE 13.1 Species diversity and endemism by tepui in the Pantepui province. Tepui names are as follows (see Fig. 1.2 and Table 1.1 from Chapter 1): *Ar*, Acary Mountains; *Ac*, Akopán-tepui; *Ap*, Aprada-tepui; *Ai*, Cerro Arakamuni; *Ay*, Auyán-tepui; *Cl*, Cerro Calentura; *Ca*, Cerro Camani: *Ch*, Chimantá massif; *Du*, Cerro Duida; *EN*, Cerro El Negro; *Gu*, Cerro Guaiquinima; *Gy*, Cerro Guanay; *Hu*, Cerro Huachamakari; *Iw*, Iwokrama Mountains; *Ja*, Cerro Jaua; *Ka*, Kanuku Mountains; *Kv*, Kavanayén; *Ku*, Kukenán-tepui; *Le*, Sierra de Lema; *Mi*, Sierra de Maigualida; *Mr*, Cerro Marahuaka; *Ne*, Sierra de la Neblina; *Pr*, Sierra de Parima; *Pu*, Parú massif; *Pi*, Paurai-tepui; *Po*, Potaro Plateau; *Pt*, Ptari-tepui; *Ro*, Roraima-tepui; *Sa*, Cerro Sarisariñama; *Si*, Cerro Sipapo (Paraque); *So*, Sororopán-tepui; *Ta*, Cerro Tabaro; *Tb*, Tafelberg Mountains; *Tm*, Cerro Tamacuari; *Ua*, Uaipán-tepui; *Ue*, Uei-tepui; *Un*, Sierra Unturán; *Ur*, Cerro Urutani (Arutani, Marutaní); *Yp*, Cerro Yapacana; *Ya*, Cerro Yaví; *Yu*, Cerro Yutajé. Tepuis with very few information on bird species are represented by white circles and were not included in any analyses.

taxa from La Macarena and Chiribiquete and adding two overlooked subspecies described for Marahuaka (*Troglodytes rufulus marahuacae* and *Zonotrichia capensis perezchinchillae* (as opposed to *roraimae*) (Phelps and Aveledo, 1984). At the species level, endemism values have remained nearly unchanged since Mayr and Phelps' (1967) synthesis (Borges et al., 2018), a likely result of the combination of taxonomic changes resulting in elevating subspecies to the species category (e.g., *Schistocichla leucostigma saturata* vs *Myrmelastes saturatus*, Braun et al., 2005; Remsen et al., 2019; for more changes see Appendix II) and the increase in the number of taxa considered elements of the bird assemblage of the Pantepui avifauna. Most of this endemism (70%) is associated with montane species, whereas about 30% have affinities with lowland species with differentiated populations at higher elevations.

Elevational segregation in Pantepui is less common than in the Andes. There is only one case of montane-endemic species that segregate altitudinally (*M. miniatus* vs *Myioborus castaneocapilla* and *Myioborus albifacies*). In Pantepui, segregation normally occurs with regard to lowland species (e.g., *Trogon collaris* vs *Trogon personatus*) or it is absent as lowland species expand their range into higher elevations without replacement. In fact, nonendemic species present in Pantepui have elevational ranges averaging about 1700 m (Borges et al., 2018). However, some of these species include subspecies replacing lowland populations (e.g., *Xiphocolaptes promeropirhynchus neblinae*, *Glyphorynchus spirurus coronobscurus*, *Colaptes rubiginosus viridissimus*, *Ixothraupis xanthogastra phelpsi*), and studies based on morphological, distributional, and vocal analyses have shown that highland elevation populations likely represent different species. Such is the case of *Lepidothrix suavissima* and *Lepidothrix serena* (Prum, 1994) and of *Mionectes macconnelli* (subspecies *roraimae*), considered a different species (*Mionectes roraimae*; Hilty and Ascanio, 2014).

The number of endemics and species in general varies geographically within the region. Bird richness ranges from 7 to 97 species/tepui (in Kanuku Mountains and Roraima-tepui, respectively), whereas endemics range from 3 in Cerro Yapacana and Acary Mountains to 35 species in Roraima-tepui. Endemism and species diversity are strongly correlated ($R^2 = 0.923$) and show congruent spatial distribution patterns (Fig. 13.1). The percentage of endemism/tepui is approximately 40% or greater ($\sim$80% or greater if considering also endemic subspecies) in most but the lowest-elevation tepuis (values ranging from 10% to 20% for Tafelberg, Acary Mountains, and Yapacana).

Most of the avian species in Pantepui have widespread distributions. Twenty-seven endemic species (out of 41) are widely distributed across the region (14 in more than 20 tepuis), a similar pattern found for a large percentage of montane species with endemic subspecies (Borges et al., 2018). In contrast, some endemic species are found in just one tepui, *Emberizoides duidae* in Cerro Duida and *Myioborus cardonai* in Cerro Guaiquinima (Fig. 13.2), a pattern that is stronger at the subspecific level (approximately 30% of taxa in the region; 49 single-tepui endemics). The larger number of single-tepui endemics at the subspecies level are found in Sierra de la Neblina (13), Cerro Sipapo (5), Auyán-tepui (5), and Cerro Duida (4).

Major differences in diversity and species composition, and particularly in the distribution of endemics, have been found within the Pantepui province. A biogeographic subdivision was proposed by Mayr and Phelps (1967) regarding tepui placement in relation to the Caroní River. Cracraft (1985) also recognized two "subcenters" for his Pantepui center of endemism, the Gran Sabana and the Duida subcenters, suggesting that they
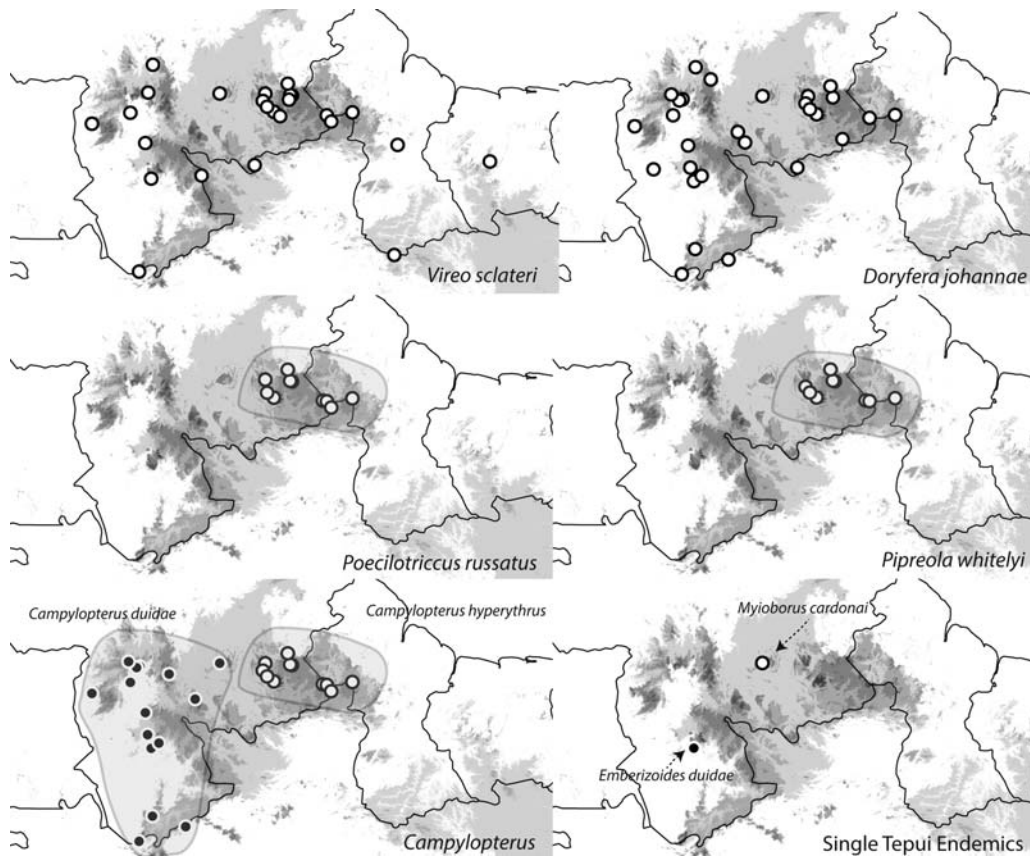
FIGURE. 13.2 Diversity of species geographic distributions in the Pantepui province. Some species are widely distributed, others are restricted to the eastern region, some sister taxa have complementary distributions in the region (*Campylopterus* spp.), and others are highly geographically restricted (i.e., *Myioborus cardonai* and *Emberizoides duidae*).

could be further subdivided with more information, particularly the Duida subcenter. Eastern tepuis are not only more diverse but also include most of the species known from the region (more than 85%; Appendix III). Exclusive taxa of the eastern tepuis are *Crypturellus ptaritepui*, *Myrmelastes saturatus*, *Grallaricula nana kukenamensis*, *Poecilotriccus russatus*, *Pipreola whitelyi*, *Lipaugus streptophorus*, *Cichlopsis leucogenys gularis*, and *Mitrospingus oleagineus* (Fig. 13.2). *Campylopterus hyperythrus* and *Diglossa major* are also exclusive of the eastern tepuis, but have their closest relative in the western tepuis (Mauck and Burns, 2009; McGuire et al., 2014). Some nonendemic species also occur exclusively in the eastern section of Pantepui, such as *Spinus magellanicus*, *Cistothorus platensis*, and *Piranga leucoptera*, some of them potentially associated with habitats available in these tepuis. In contrast, exclusive species for the western tepuis are few and, with the exception of *Emberizoides duidae* (Cerro Duida), are the closest relatives to species present in the eastern tepuis (*Diglossa duidae*, *Campylopterus duidae*, *M. albifacies*, and *M. cardonai*) (Barker et al., 2015; McGuire et al., 2014; Pérez-Emán, 2005).

III. Animal Diversity

Biogeographical research in other groups has considered a finer division within the Pantepui province. In particular, Huber (1987) considered a Pantepui division based on both geographical (major drainages) and phytogeographical criteria. This author proposed a regionalization in five sectors, and posteriorly, Berry et al. (1995) refined such division considering just four sectors: Eastern District, Western District, Central District, and Southern District (see Chapter 1) (Fig. 13.3, Appendix III). The absence of some endemic species has a strong geographical component. In the southern sector *Roraimia adusta*, *Elaenia dayi*, *Xenopipo uniformis*, *Macroagelaius imthurni*, *Polytmus milleri*, and *Setopagis whitelyi* are missing. *P. milleri* and *S. whitelyi* are equally absent from the western tepuis. It should be assessed in the future if such absences are related to factors other than sampling biases. The Central District, on the other hand, has two exclusive endemics (*M. cardonai* and *E. duidae*), and Neblina (Southern District) has the major proportion of single-tepui endemics in the region (13, Borges et al., 2018). However, endemism in Sierra de la Neblina should be reconsidered as exploration of close tepuis such as Cerro Tamacuari and Sierra Unturán in the Tapirapicó massif, as well as Cerro Aracamuni, has shown that seven of these taxa are really endemics to this subregion rather than to Sierra de la Neblina. Additionally, species not recorded in Neblina have been collected in these newly explored mountains (e.g., *Lophornis pavoninus*, *Chlorophonia cyanea*, and *E. ruficeps*, Barrowclough and Escalante-Pliego, 1990; Barrowclough et al., 1995; Fig. 13.3), suggesting the relevance of exploring the biogeographic significance of these regional divisions for Pantepui birds.

Ecological and geographical factors correlated with patterns of diversity and endemism

The resemblance of the Pantepui landscape to an island archipelago has influenced analytical approaches to studying its diversity and endemism. The theory of island biogeography (MacArthur and Wilson, 1967) has been a major approach used to explain diversity differences among both tepuis and subregions in Pantepui (eastern vs western tepuis). Island biogeography, in its original form, evaluates the role of area and isolation on the diversity of species on an island habitat. Analyses of the Pantepui avifauna, using simple or multiple regression, have included variables such as tepui area (summit or a sum of the summit and slope areas), degree of isolation (distance to closest tepui or average distance to closest and/or largest tepuis), distance to a source of colonization, and elevation (Cook, 1974; Borges et al., 2018). A major weakness of this approach is to assume a unique source of colonists (Andes or Paria Peninsula) and a long-distance dispersal colonization mechanism, aspects that could be addressed more effectively through the study of historical and evolutionary patterns of the avifauna. In fact, distance to the colonization source showed an unexpected positive correlation (the greater the distance to the source, the higher the richness), contrary to island biogeography expectations (Cook, 1974; Borges et al., 2018). This last trend was even more pronounced in the most recent study (Borges et al., 2018), but excluding Sierra La Macarena and Chiribiquete from the analysis shows a clear lack of correlation with distance (Fig. 13.4).

Elevation has been the major factor explaining variation in tepui diversity and endemism. Higher tepuis are characterized by avifaunas with greater diversity and endemism,
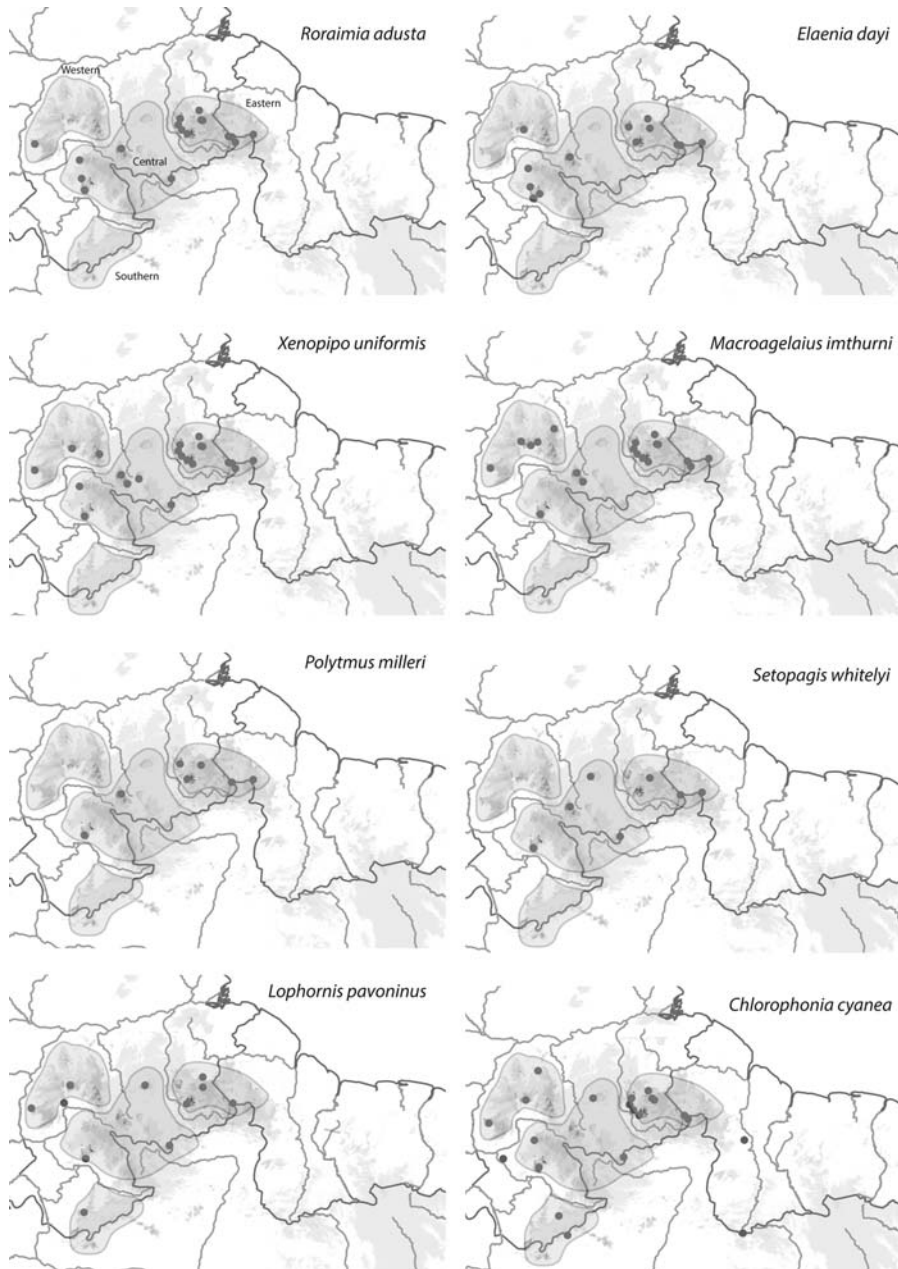
FIGURE 13.3 Distribution of some endemic species in Pantepui according to the finer biogeographical subdivision proposed by Berry et al. (1995) (see text for details). Some distributional gaps suggest potential biogeographic patterns requiring further studies or just sampling biases. For example, the last two species, *Lophornis pavoninus* and *Chlorophonia cyanea*, have not been recorded for Sierra de la Neblina but do occur in the Southern District.

III. Animal Diversity
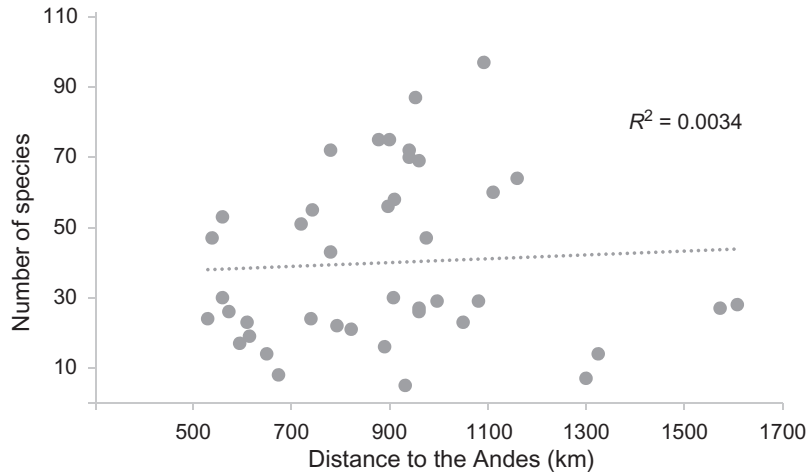
FIGURE 13.4   Linear regression between the minimum distance of each tepui to the Andes and its diversity in terms of number of species. Serrania Los Picachos, located in the Eastern Andes of Colombia, was used as the source of colonists based on Borges et al. (2018).
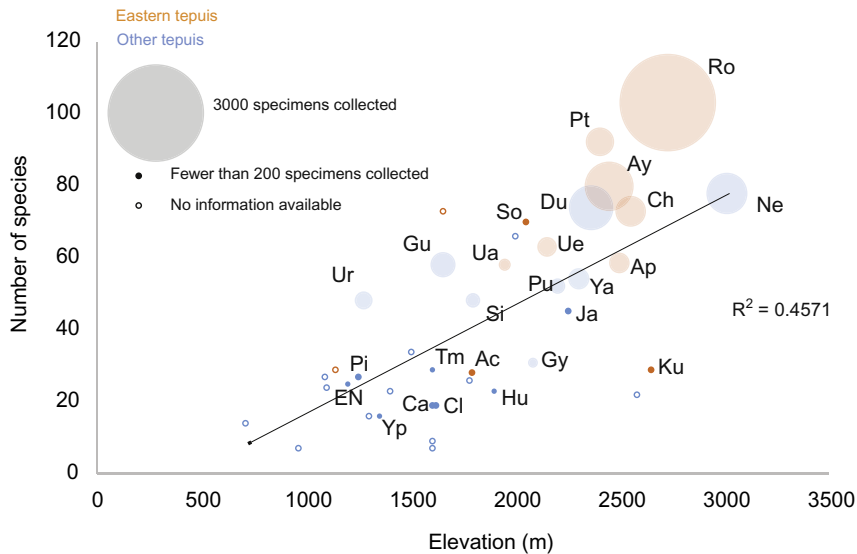
FIGURE 13.5   Linear regression between the elevation of each tepui and its diversity in terms of number of species. The size of symbols indicates the number of specimens collected to date on each mountain. Names for the most sampled mountains follows Fig. 13.1. Notice how some of the highest mountains, which also have the highest diversity, are among those with the best collection efforts; four of them (Roraima-tepui, Ptari-tepui, Auyán-tepui, and Chimantá massif) are tepuis from the Eastern District of Pantepui.

III. Animal Diversity

whereas area and isolation explained little variation in these variables (Cook, 1974; Borges et al., 2018). However, tepuis of similar elevation greatly differ in diversity and endemism; in the same way, tepuis of different elevations might be characterized by a similar avian diversity, which could be partially explained by sampling biases (see later, Fig. 13.5). Given these patterns, Cook (1974) realized that environmental heterogeneity or habitat diversity, as potentially correlated to elevation, does not satisfactorily explain the result and proposed that this pattern is a result of the greater degree of connectivity among the eastern tepuis, which are lying on a plateau of about 1000 m a.s.l. (Gran Sabana). In an ecological dynamics of colonization/extinction, as proposed by the island biogeography theory, such connectivity increases the probability of recolonization of locally extinct populations maintaining a higher diversity, a process that is less likely to occur in the more isolated western tepuis (Mayr and Phelps, 1967; Cook, 1974; Willard et al., 1991). Cook (1974) went further and proposed that this dynamic of extinction/colonization was associated with historical factors, in particular, habitat displacements resulting from climate changes during the Pleistocene Epoch (see also Haffer, 1974; Rull, 2004a,b).

The role of sampling biases in studying patterns of diversity and endemism

Understanding sampling biases helps to evaluate our knowledge on bird composition and distribution. Small tepuis (<1500 m a.s.l.) have a smaller number of species and endemics (fewer than 5 spp. in each tepui), a likely result of lower habitat availability (both area and heterogeneity). However, the patchy distribution of most species, especially on tepuis located west of the Caroní River, have resulted in a series of hypotheses concerning the dynamics of extinction/colonization that should be evaluated in light of potential collecting biases.

Collecting effort should provide a way to evaluate how complete our knowledge is from the tepui region. Mayr and Phelps (1967) assumed good sampling for most of the tepuis they included in their analyses, though the effort was quite variable among those tepuis. The number of expeditions, collected individuals, and collecting days and seasons differ among tepuis. Based on literature and collectors field notes, we chose the number of collected individuals (highly correlated to number of expeditions) to explore the completeness of avifauna knowledge on four of these tepuis: Sierra de la Neblina, Cerro Guaiquinima, Auyán-tepui, and Cerro Guanay. For Neblina, 19 new montane species, 14 of which are known to occur in the western tepuis (Willard et al., 1991), were recorded in three new expeditions. Two new Guaiquinima expeditions, one in 1990 and another in 2000, added 27 and 20 extra species, respectively, for a total of 47 new species (Pérez-Emán et al., 2003). Auyán-tepui, with two new expeditions, increased its known summit avifauna by 21 species (Barrowclough et al., 1997) and, for Cerro Guanay, an additional expedition of just 10 days increased its known avifauna by 16 new species, 9 of which were Pantepui endemics. Thus although by the late 1960s more than 10,000 specimens had been collected from Pantepui (Dickerman and Phelps, 1982), knowledge of its avifauna is far from complete. Perhaps the best-known avifaunas are those from Roraima-tepui, Cerro Duida, and Ptari-tepui. Based on the distribution of Pantepui endemics (considering the eastern and western division and their exclusive species), the number of expected endemics is 36 for Eastern tepuis and 30 for western tepuis (Appendix III). Roraima-tepui and

Ptari-tepui are represented by 35 and 34 endemics, respectively. Roraima is missing only *C. ptaritepui*, which is absent from the eastern-chain tepuis (Roraima, Kukenan, and Uei) and Potaro Mountains in Guyana, whereas *Megascops roraimae* and *Streptoprocne phelpsi* are missing from Ptaritepui but are likely to be recorded with new visits to this tepui. Similarly, all potential endemic species for the western tepuis have been recorded in Cerro Duida. Such knowledge is likely a result of the number of expeditions (eight for Roraima), long field work (an American Natural History Museum expedition spent 3–4 months in Cerro Duida), and time of the year of the expedition or seasonality effect (Ptari-tepui was visited three times in the same year in 1944). Additionally, collecting locality (sampled habitats and percentage of area surveyed; see O'Shea et al. (2007) for a comparison of species found in Kopinang Mountains and Roraima in Guyana) and type of collecting/recording (shotguns, mistnets, visual and aural records) should explain a large part of the variation observed in species composition in different tepuis. Consequently, among other biogeographical inferences, the role of extinction to explain the lower diversity in the western tepuis (such as Neblina, Cook, 1974) should be reevaluated in light of these results.

Historical explanations for diversity and endemism in Pantepui

The role of potential barriers, as well as the impact of climatic factors and their association with the landscape, are major historical factors shaping bird distributions. Understanding the role of these factors requires knowledge of the evolutionary history of the taxa included in the analysis (e.g., Smith et al., 2014). Lack of phylogenetic hypotheses requires the assumption that taxonomic categories convey information on the distinctness and time of differentiation among populations of a particular species or sister taxon relationships. Mayr and Phelps (1967), for example, claimed that the presence of endemic genera, species, and subspecies in Pantepui testified to the continuous and long period of avian colonization of the region. Fortunately, a burst of phylogenetic information has contributed to an increased knowledge of genealogical relationships among taxa. For example, a pattern of paraphyletic or polyphyletic relationships has resulted in recognizing previous Pantepui differentiated populations of widespread species as endemic to the region [e.g., *Aulacorhynchus whitelianus* (Bonaccorso et al., 2011), *Elaenia olivina* (Rheindt et al., 2009), *Myioborus castaneocapilla* (Pérez-Emán 2005), *Megascops roraimae* (Dantas et al., 2016), and *Hydropsalis roraimae* (Sigurðsson and Cracraft 2014; but see Remsen et al., 2019)] or recognizing unexpected phylogenetic relationships [e.g., *Myrmelastes saturatus* (Braun et al., 2005), *Vireo sclateri* (Slager et al., 2014)]. Such knowledge of evolutionary relationships provides us with better insights into the historical scenario associated with the building or maintenance of the Pantepui avifauna.

Geographical differentiation and diversification within Pantepui

Has the Pantepui province, with its "island archipelago" landscape, promoted speciation within the region? An exploratory initial approach to assess geographical differentiation within Pantepui is through taxonomy. Distribution of endemic species shows very idiosyncratic patterns, but one that is found in many species is the break associated with the potential barrier represented by the valley carved by the Caroní River (Figs. 13.2 and 13.6),
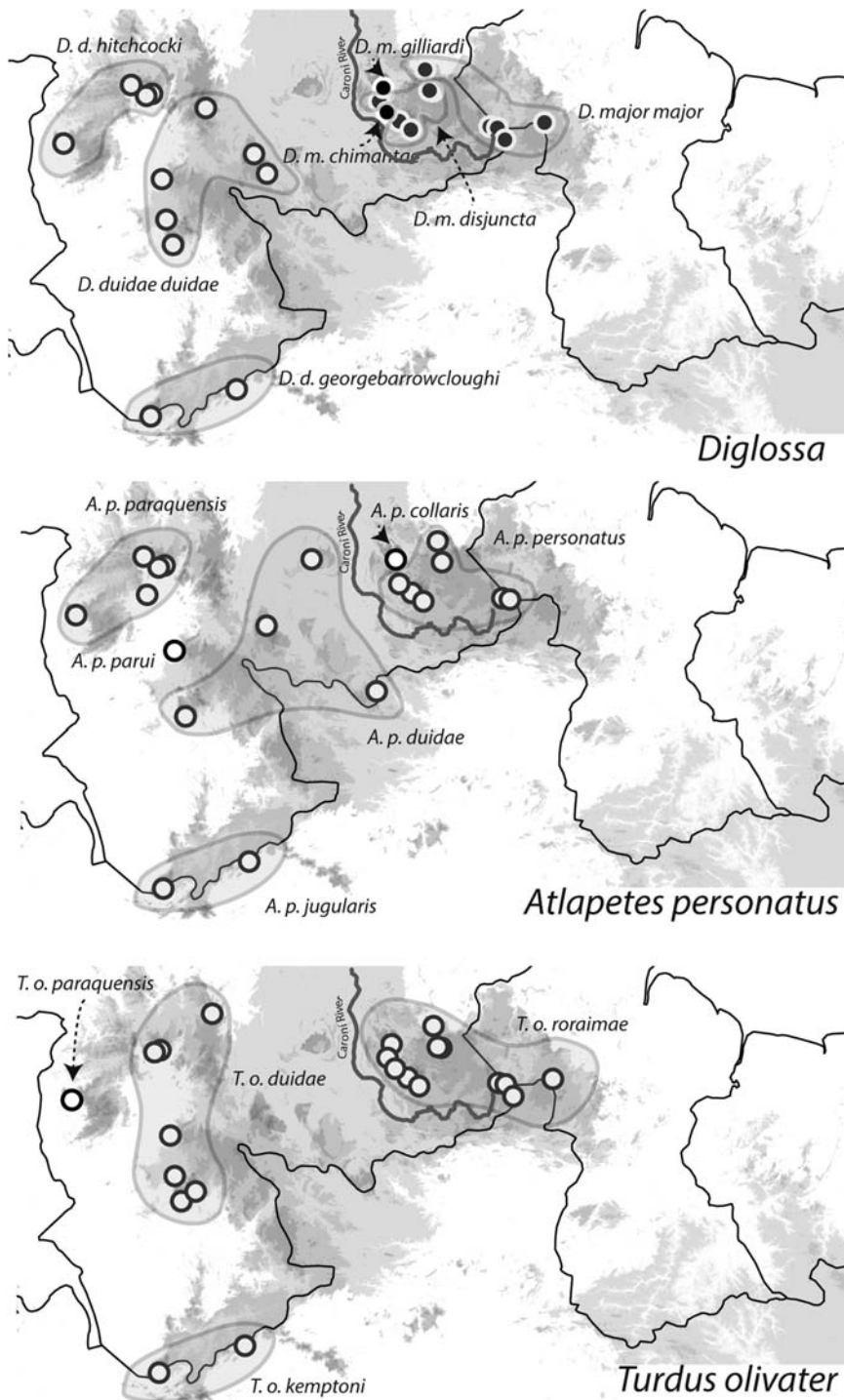
FIGURE 13.6 Some extreme patterns of differentiation in the Pantepui province. Some genera, such as *Diglossa*, have two endemic species, each of them with multiple sub species. *Atlapetes personatus*, an endemic species, and *Turdus olivater*, a nonendemic species, also show large geographic differentiation within Pantepui. Notice the taxonomic break at both sides of the Caroní River and the pattern of larger differentiation (more subspecies) in the western section compared to the eastern group of tepuis for the last two species.

a pattern also documented in plants (Maguire, 1979; Steyermark, 1986; Berry et al., 1995) but not as strongly in amphibians and reptiles (McDiarmid and Donnelly, 2005). At the subspecific level, 24 out of the 41 endemic species (59%) have differentiated into two or more subspecies (up to 6 in the case of *Troglodytes rufulus* and *Atlapetes personatus*, Fig. 13.6). For nonendemic taxa, more than one subspecies is found in 33% of species, with a larger differentiation in montane nonendemic taxa than in lowland taxa with differentiated highland populations (39% vs. 24%). In the first case, the largest differentiated taxa with four subspecies are *Amazilia viridigaster*, *Colaptes rubiginosus*, *Chamaeza campanisona*, *Turdus olivater*, and *Zonotrichia capensis* (Fig. 13.6). In the second case, with three subspecies, are *Hemitriccus margaritaceiventer* and *Platyrinchus mystaceus*.

Molecular phylogenetic studies provide information about evolutionary processes. Pairs or groups of closely related species in Pantepui conform to monophyletic groups for the genera *Campylopterus* and *Myioborus* (McGuire et al., 2014; Pérez-Emán, 2005). This pattern is suggested but not as strongly in the genus *Diglossa* (Mauck and Burns, 2009; Barker et al., 2015), in which both species in Pantepui were long suspected to be associated with different lineages (Vuilleumier, 1969; Graves, 1982). These results suggest diversification within Pantepui and identify the valley of the Caroní River as an important barrier associated with taxonomic breaks and limits of distributions, as also shown by *Trogon personatus* eastern and western populations (Cuervo, 2013).

Molecular studies on *Myioborus* redstarts provide information about diversification and the role of historical factors in geographic differentiation in the region. *M. castaneocapilla* occurs on both sides of the Caroní River, and its populations are traditionally classified into three subspecies (Phelps and Phelps, 1963): *M. c. castaneocapilla*, occurring in the eastern tepuis; *M. c. duidae*, of the Central tepuis; and *M. c. maguirei*, endemic to Cerro La Neblina. *M. cardonai* is endemic to Guaiquinima, and *M. albifacies* is found in the northwestern tepuis (Cerros Sipapo, Camani, Guanay, Yavi, and Yutajé). A molecular phylogenetic study based on mitochondrial DNA recovered three lineages of Pantepui *Myioborus*: (1) *M. albifacies*, distributed in the western region and represented by the populations from Yutajé and Guanay; (2) *M. castaneocapilla maguirei* and *M. cardonai*, from Sierra de la Neblina and Cerro Guaiquinima, respectively; and (3) *M. c. castaneocapilla*, from the eastern region: Auyán-tepui, La Escalera, and Roraima-tepui (Pérez-Emán 2002, 2005, Fig. 13.7). The close relationship between *M. castaneocapilla maguirei* and *M. cardonai*, rendering *M. castaneocapilla* a paraphyletic species, suggests that current species limits do not reflect phylogenetic relationships among populations and species, a pattern equally supported by a study using both mitochondrial and nuclear genes (Lovette et al., 2010). *Myioborus* populations at either side of the Caroní River showed a large nucleotide divergence ($>3\%$) compared with shallow divergences among haplotypes within each region. This result is surprising because populations as far away as 600 km (*M. c. maguirei* and *M. cardonai*) were genetically more closely related than populations separated by less than 200 km (*M. cardonai* and *M. c. castaneocapilla* from Auyán-tepui) across the Caroní River. This study also showed that the extent of geographical differentiation in the western tepuis (as compared to the eastern tepuis) is clearly larger than that found among populations from the eastern section. Given the larger geographical extent of the western region and the larger geographical distances among populations (Fig. 13.7), greater genetic structure is not
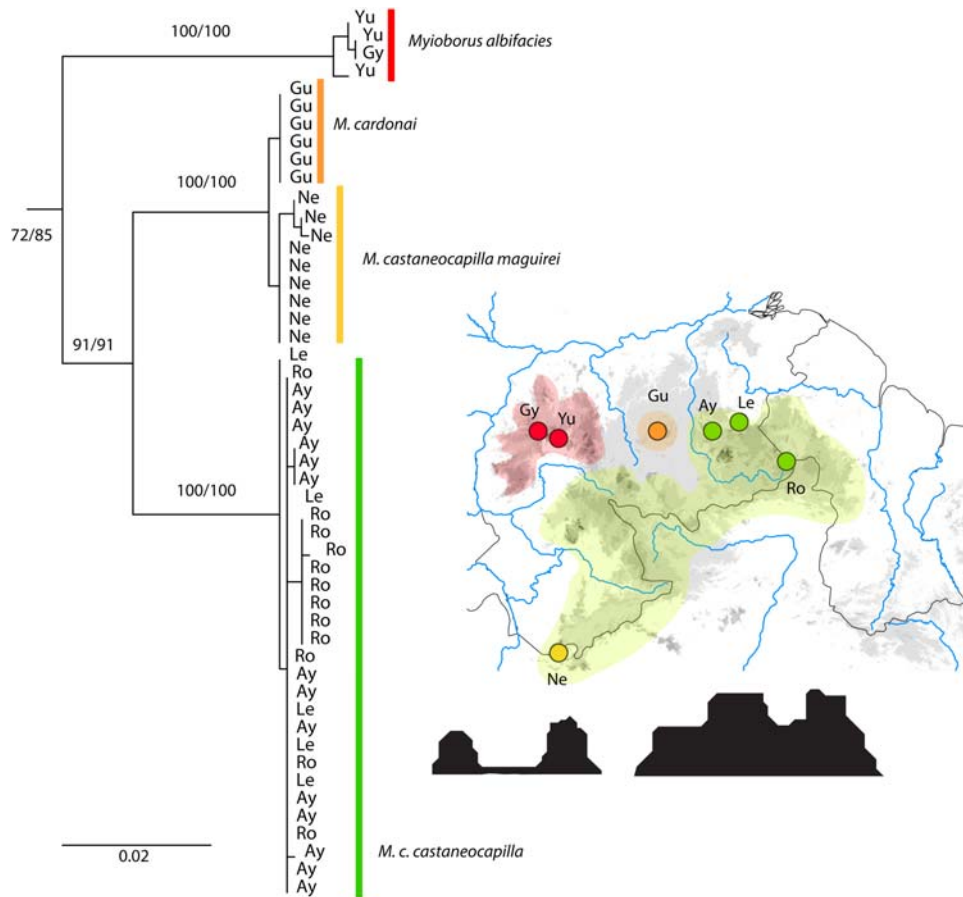
FIGURE 13.7   Molecular phylogeny of Pantepui *Myioborus* showing their geographic distribution. Notice that *Myioborus castaneocapilla* is not monophyletic, with *Myioborus c. maguirei*, from Serranía de la Neblina (yellow), being more related to *M. cardonai*, from Cerro Guaiquinima (orange). The largest genetic break is between *Myioborus albifacies* and the other taxa, whereas populations from the eastern region show a shallow genetic divergence. Silhouettes represent the general topography of the western and eastern section of the Pantepui province. Tepui names follow Fig. 13.1. Numbers refer to node support values: Maximum Likelihood bootstrap and Bayesian Inference posterior probabilities based on Pérez-Emán (2002).

unexpected. In fact, at the subspecies level, the number of endemics is larger in the western tepuis (as a region) than the eastern tepuis (116 vs 102 taxa, Fig. 13.6), a similar pattern found for amphibians and reptiles (McDiarmid and Donnelly, 2005). Moreover, the deep molecular divergence shown by *M. albifacies* compared to the rest of *Myioborus* populations (greater than 5%) is indicative of a long history of independent evolution. In fact, cerros Guanay and Yutajé are similar in species composition to other western tepuis such as cerros Camani, Yaví, and Sipapo (consistent with the idea of considering biogeographic divisions), and we can find taxonomic differences (endemism at the subspecific level) in many

species found in these tepuis (*Synallaxis cabanisi yavii*, *Roraimia adusta obscurodorsalis*, *Syndactyla roraimae paraquensis*, *Thamnophilus insignis nigrofrontalis*, *Chamaeza campanisona yavii*, *Knipolegus poecilurus paraquensis*, *Troglodytes rufulus yavii*, *Atlapetes personatus paraquensis*, and *Diglossa duidae hitchcocki*; Phelps and Phelps, 1963).

The lack of a strong geographic structure in haplotype distribution among *Myioborus* populations from the eastern part of Pantepui suggests that the Gran Sabana plays (or played) an important role in connecting populations throughout the eastern range. Paleoecological data (lack of deposition of organic material, peats) suggest drier conditions in the region before 8000−10,000 years ago (Schubert et al., 1992, 1994; Zink et al., 2011), potentially rejecting hypotheses of climate stability (although peat removal during wet conditions is another possibility, Rull et al., 2013). Moreover, floristics and palynological records indicate the presence of high-tepui flora elements in the Gran Sabana during the Late Pleistocene, suggesting elevational movements of species with changing climatic phases (Rull et al., 2013; Huber 1988, 1995), which might have also occurred during the Holocene (Rull and Montoya, 2017) (see Chapter 2: Climatic and ecological history of Pantepui and surrounding areas). This evidence indicates that elevational belts of vegetation descended during glacial periods, possibly connecting populations from peripheral tepuis to the Gran Sabana (Rull, 2005; Rull and Nogué, 2007), a pattern that supports the scenario of greater connectivity proposed for Mayr and Phelps (1967) and Cook (1974) to explain the greater diversity (origin and maintenance) of the eastern tepuis.

Origin of Pantepui birds

Different hypotheses have been proposed to explain the origin and diversification of the Pantepui avifauna (see Chapter 4: Origin and evolution of the Pantepui biota). Chapman (1931) and Mayr and Phelps (1967) provided up to five hypotheses, which differ in the relative role of vicariance and dispersal on the origin and differentiation of the Pantepui avifauna. From these, the habitat specialization hypothesis refers to available habitat in the region. As such, it is not an historical hypothesis but an ecological one. Habitat specialists include cliff dwellers, such as the swifts, swallows, and *Hirundinea ferruginea* (Appendix I), which have high dispersal abilities and use habitats not restricted to montane habitats (Robbins et al., 2007). Similarly, *Steatornis caripensis* could be assigned to this group, as it is not restricted to the region, but their specific habitat requirements for living and reproduction is provided by the tepuis. The other four hypotheses are the plateau, the distance dispersal, the cool climate, and the habitat shift hypothesis. The first one is a vicariance hypothesis and the other three are hypotheses emphasizing the role of bird movement (dispersal or displacement) to explain the current composition of the Pantepui avifauna, suggesting the origin of Pantepui avifauna was in other areas, either montane regions or areas at lower elevations.

The plateau hypothesis, or more recently named "Lost World" hypothesis (Rull 2004a, 2004b), claimed that differentiation occurred as a result of vicariance due to erosion of a formerly continuous area and isolation of population of birds widely distributed in the region (Chapman, 1931; Tate, 1938; Croizat-Chaley, 1976). Available phylogenetic information (and divergence times) indicate that geographic differentiation is younger than the origin

of the current landscape of the region. For example, in *Aulacorhynchus whitelianus*, modest plumage and body size differentiation among populations within Pantepui is not reflected by any degree of mitochondrial differentiation (Bonaccorso et al., 2011), suggesting that such morphological differentiation, if indicative of isolation, is relatively recent. Similar results were found in an analysis of *Mecocerculus leucophrys*, where no genetic differentiation was found among recognized Pantepui subspecies, and even between these and the Andean populations (Cuervo, 2013). Moreover, recent studies on tepui amphibian populations, some of them "summit specialists" or highly divergent in morphology among tepuis, have revealed astonishingly low levels of genetic differentiation, suggesting their relatively young age, as well as a pattern of recent (or even active) dispersal among summits (Kok et al., 2012; Salerno et al., 2012, 2015). Similar patterns were found in phylogenetic studies of characteristic Pantepui plant genera in the families Rapateaceae and Bromeliaceae, such as *Stegolepis* and *Brocchinia* (Givnish et al., 1997, 2000, 2011).

   The dispersal hypothesis focuses on colonization of Pantepui by birds from other montane regions either by long-distance or stepping-stone dispersal mechanisms. It was supported by Mayr and Phelps (1967), who suggested that about 50% of the Pantepui avifauna had its origins in the Andes or northern coastal ranges. Alternative scenarios suggest dispersal from Pantepui to the Andes (Prum, 1988) or using the northern Cordilleras of South America as a corridor (Marin, 2010; Marín-Espinoza et al., 2014). This last author claims that presence of Guianan species in the Paria Peninsula and Turimiquire mountains is positive evidence for this hypothesis. However, most of this species are from the lowlands or records are doubtful [one captured but not collected individual of *Campylopterus duidae* in a mangrove habitat in northeastern Venezuela (Lefebvre et al., 1994), an unlikely finding for a montane species distributed at high elevations in Pantepui]. There is no evidence clearly supporting the dispersal hypothesis or its mechanism; however, there are few tepuian species with great dispersal capacity, among them *Streptoprocne phelpsi*, a species that has been recorded in the Cordillera de la Costa (one specimen collected at Rancho Grande, Aragua; Hilty, 2003), and *Nannopsittaca panychlora*, which is able to fly over lowlands and away from the tepuian walls and is a normal resident at the Turimiquire region and the Paria Peninsula (Hilty, 2003).

   The climate hypothesis proposes a similar dispersal scenario as the previous hypothesis but associated with changes in climate conditions. Climate change is proposed to connect and fragment bird distributions, causing the closest related taxa to show disjunct distributions (Chapman, 1931; Tate, 1938). Haffer (1974) added that low-elevation mountains or hills, present between the Andean region and Pantepui, acted as resources aiding in a stepping-stone dispersal process. Most of these climate changes are associated with Pleistocene glacial and interglacial periods, and Mayr and Phelps (1967) criticized the hypothesis on the grounds that it did not explain the continuous colonization of Pantepui. However, these authors thought of a unique recent period without considering that such climate changes have occurred at multiple times throughout Earth's history (Haffer, 2008). More recently, a more regional perspective of this hypothesis was based on floristic and palynological grounds. Both Steyermark and Dunsterville (1980) and Huber (1988) argued that floristic similarities between highland and lowland vegetation in Pantepui is a consequence of a lack of effective isolation resulting in current vertical migration of species through valleys and gentle slopes and, additionally, shifts in vegetation associated with

cold−warm cycles during the Pleistocene. Rull (2004a,b, 2005) proposed a diversification hypothesis based on connectivity phases (glacials), promoting gene flow between isolated populations of similar species or hybridization between species, and isolation phases (interglacials), particularly in the highlands, promoting diversification through vicariance. Displacement of environmentally sensitive species causing mixing of biotas (transient communities) and adaptation to new environments are important elements of this hypothesis, as proposed in the disturbance-vicariance hypothesis (Bush and Colinvaux, 1990; Bush, 1994).

Recent molecular studies allow for evaluation of both the dispersal and climate hypotheses. These studies have shown that lineages present in Pantepui have their closest relatives in the Andes (e.g., Pantepui subspecies of *Trogon personatus*, Da Costa and Klicka, 2008; Cuervo, 2013; *Myiothlypis bivittata roraimae*, Lovette et al., 2010; *Aulacorhynchus whitelianus*, Bonaccorso and Guayasamin, 2013; *Megascops roraimae*, Dantas et al., 2016) or low-lying hills adjacent to the Andes (e.g., *Thamnophilus insignis*, Brumfield and Edwards, 2007). Just one study has shown that Pantepui species are closely related to Paria species (e.g., *Myioborus*, Pérez-Emán, 2005), but it found no clear phylogenetic relationship of this monophyletic group with any other *Myioborus* species. Moreover, timing of divergence varies among species, but in general, results suggest nonsynchronous colonization dynamics, as shown in Amazonian ecosystems (Smith et al., 2014; Naka and Brumfield, 2018). Indeed, a hummingbird study showed that of the three species of mangoes (Trochilidae) present in Pantepui, each diverged from its closest Andean relative at different times, two of them (*Colibri delphinae, C. coruscans*) less than half a million years ago and the other (*Doryfera johannae*) at almost 3 million years ago (Quintero and Perktas, 2018). In summary, molecular evidence mainly supports a hypothesis of colonization from the Andes in an asynchronous temporal pattern. Such results, however, do not rule out dispersal hypotheses based on individual species mechanisms or dispersal mediated by climate changes.

The final hypothesis, the habitat shift, focuses on the importance of elevational speciation in the origin of the Pantepui avifauna. Mayr and Phelps (1967) proposed that populations differentiate through time at higher elevations due to benign environmental conditions compared to adjacent lowlands. However, contrary to this view, Bush and Colinvaux (1990) and Bush (1994) argued that mountain slopes have greater opportunities to hold transient communities (largest disturbance) and, as such, increase the likelihood of isolation and speciation promoted by abiotic and biotic factors. Regardless of the mechanisms associated with differentiation, some of the assumed parapatric or elevationally segregated sister taxon relationships given by Mayr and Phelps (1967) to support this hypothesis have proved to be incorrect (*S. whitelyi* is not closely related to *Nyctipolus nigrescens*, Sigurðsson and Cracraft, 2014; *Hylophilus sclateri* is no longer an *Hylophilus* but a *Vireo*, Slager et al., 2014; *Herpsilochmus roraimae* is not the closest relative of *Herpsilochmus dorsimaculatus*, G. Bravo, pers. comm.; *Thamnophilus insignis* is closer to *Thamnophilus divisorius* than to *Thamnophilus amazonicus*, Brumfield and Edwards, 2007, and *Myrmelastes saturatus* was found to be a different species and potentially unrelated to its parapatric neighbor in the Pantepui province *Myrmelastes leucostigma*, Braun et al., 2005). On the other hand, recent phylogenetic data have also shown that a number of Pantepui endemics (species or subspecies) are sisters to widely distributed lowland taxa

(e.g., *Megascops choliba duidae*, Dantas et al., 2016; *Lipaugus streptophorus* and *L. vociferans*, Berv and Prum, 2014; *Myrmothera campanisona* vs *Myrmothera simplex*, Carneiro et al., 2018; *Mionectes macconnelli* vs *M. roraimae*, Hilty and Ascanio, 2014). Thus, how lowland taxa, which undoubtedly have broad elevational ranges (Borges et al., 2018), differentiate into highland endemics is a fertile ground in the understanding of the processes that generate Pantepui diversity and endemism.

Future prospects and conservation

Current knowledge of the Pantepui avifauna has come a long way since the first biogeographical analyses were published. As our knowledge of the current distribution of its avifauna improves (as more basic surveys are done) and their phylogenetic relationships become available, more thorough and informative analyses could be done. Global evaluation of the origin of the Pantepui avifauna, including an assessment of potential mechanisms of dispersal, the description of patterns of elevational segregation in the Pantepui avifauna and further testing of different evolutionary hypotheses about its origin are just some of the questions that need to be addressed in the future. The last question has the potential to evaluate the likelihood of parapatric speciation or secondary contact in explaining such population replacements, a process associated with the buildup of biodiversity in montane ecosystems (Cadena et al., 2019).

Ecological studies in Pantepui have largely been neglected. These studies should range from ecosystem-level studies, assessing ecological services provided by birds (e.g., dispersal, pollination, prey regulation), to community-level studies that focus on the spatial and temporal dynamics of avian communities or assemblages. Migration studies are lacking and could include the likelihood of species altitudinal migration, the importance of these habitats/ecosystems to latitudinal migrants, and short-range migratory behavior (from northern Cordilleras to the tepuis). Nearctic−Neotropical migratory birds occur in low abundance on Pantepui, but the high number of observed species suggests that the region is an important area for migrants that has yet to be evaluated.

Population-level studies that provide details on the demography and natural history of the species are of vital importance to understand the vulnerability (or not) of these ecosystems. There is sparse information on the phenology of molt and reproduction published as a result of specimen collection, but only Willard et al. (1991) provided some analyses. Moreover, available information is biased temporally, as most tepui expeditions have been conducted during the dry season. An interesting pattern has been observed in lowland species distributed at different elevations on the tepui slopes. Individuals of *Xiphorhynchus pardalotus* that inhabit the lowlands start molting a month later than individuals at higher elevations, potentially in response to regional rainfall patterns. Questions such as how general these patterns are, what the association could be with differential responses of species to climate change, and what factors are associated with differentiation along elevation ranges are only some of the topics that could be addressed with these studies. Even in the face of all potential limitations to studying these ecosystems, a clear key to success is the logistics necessary to conduct ecological studies in the area,

particularly in the eastern region, due to the availability of roads, their easy accessibility, and the large regional area crossed by them.

The conservation status of the Pantepui avifauna needs to be evaluated. The avifauna of the region is distributed in areas that are not currently threatened by human influence (though tourism activity might require some evaluation). However, the impact of mining and habitat degradation in the lowlands (and lower slopes) adjacent to the tepuis might have an effect on the ecological dynamics of these birds. Additionally, an important conservation aspect to consider is the impact of climate change on Pantepui bird populations. Careful evaluation and descriptions of avian distribution along elevational gradients, spatial connectivity in the region, and the potential impact of climate changes could identify threatened populations and/or species and highlight critical aspects to consider for the conservation and management of these ecosystems (Rull and Nogué, 2007; Nogué et al., 2013).

Acknowledgments

References

Barker, F.K., Burns, K.J., Klicka, J., Lanyon, S.M., Lovette, I.J., 2015. New insights into New World biogeography: an integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. Auk 132, 333−348.

Barnett, A., Shapley, R., Benjamin, P., Henry, E., Garrell, M., 2002. Birds of the Potaro Plateau, with eight new species for Guyana. Cotinga 18, 19−36.

Barrowclough, G.F., Escalante-Pliego, P., 1990. Notes on the birds of the Sierra de Unturán, southern Venezuela. Bull. Br. Ornithol. Club 110, 167−169.

Barrowclough, G.F., Escalante-Pliego, P., Aveledo-Hostos, R., Pérez-Chinchilla, L., 1995. An annotated list of the birds of the Cerro Tamacuarí region, Serranía de Tapirapecó, Federal Territory of Amazonas, Venezuela. Bull. Br. Ornithol. Club 115, 211−219.

Barrowclough, G.F., Lentino, M.R., Sweet, P.R., 1997. New records of birds from Auyán-tepui, Estado Bolívar, Venezuela. Bull. Br. Ornithol. Club 117, 194−198.

Berry, P.E., Huber, O., Holst, B.K., 1995. Floristic analysis and phytogeography. In: Steyermark, J.A., Berry, P.E., Holst, B.K. (Eds.), Flora of the Venezuelan Guayana. Introduction, vol. 1. Timber Press, Oregon, pp. 161−191.

Berry, P.E., Riina, R., 2005. Insights into the diversity of the Pantepui flora and the biogeographic complexity of the Guayana Shield. Biol. Skr. 55, 145−167.

Berv, J.S., Prum, R.O., 2014. A comprehensive multilocus phylogeny of the Neotropical cotingas (Cotingidae, Aves) with a comparative evolutionary analysis of breeding system and plumage dimorphism and a revised phylogenetic classification. Mol. Phyl. Evol. 81, 120−136.

Bonaccorso, E., Guayasamin, J.M., Peterson, A.T., Navarro-Sigüenza, A.G., 2011. Molecular phylogeny and systematics of Neotropical toucanets in the genus *Aulacorhynchus* (Aves, Ramphastidae). Zool. Scr. 40, 336−349.

Bonaccorso, E., Guayasamin, J.M., 2013. On the origin of Pantepui montane biotas: a perspective based on the phylogeny of *Aulacorhynchus* toucanets. PLoS One 8, e67321. Available from: https://doi.org/10.1371/journal.pone.0067321.

Borges, S.H., Dantas Santos, M.P., Moreira, M., Baccaro, F., Capurucho, J.M.G., Ribas, C., 2018. Dissecting bird diversity in the Pantepui area of endemism, northern South America. J. Ornithol. 159, 1073–1086.

Braun, M.J., Robbins, M.B., Milensky, C.M., O'Shea, B.J., Barber, B.R., Hinds, W., et al., 2003. New birds for Guyana from Mts Roraima and Ayangganna. Bull. Br. Ornithol. Club 123, 24–33.

Braun, M.J., Isler, M.L., Isler, P.R., Bates, J.M., Robbins, M.B., 2005. Avian speciation in the Pantepui: the case of the Roraiman Antbird (*Percnostola* [*Schistocichla*] *"leucostigma" saturata*). Condor 107, 327–341.

Briceño, H.O., Schubert, C., 1990. Geomorphology of the Gran Sabana, Guayana Shield, southeastern Venezuela. Geomorphology 3, 125–141.

Brumfield, R.T., Edwards, S.V., 2007. Evolution into and out of the Andes: a Bayesian analysis of historical diversification in *Thamnophilus* antshrikes. Evolution 61, 346–367.

Bush, M.B., 1994. Amazonian speciation: a necessarily complex model. J. Biogeogr. 21, 5–17.

Bush, M.B., Colinvaux, P.A., 1990. A long climatic and vegetation record from lowland Panama. J. Veg. Sci. 1, 105–118.

Cabanis, J.V., 1848. In: Schomburg, R. (Ed.), Reisen in Britisch-Guiana in den Jahren 1840–1844, vol. 3. J. J. Weber, Leipzig, pp. 662–765.

Cadena, C.D., Pérez-Emán, J.L., Cuervo, A.M., Céspedes, L.N., Epperly, K.L., Klicka, J.T., 2019. Extreme genetic structure and dynamic range evolution in a montane passerine bird: implications for tropical diversification. Biol. J. Linn. Soc. 126, 487–506.

Carneiro, L., Bravo, G.A., Aristizábal, N., Cuervo, A.M., Aleixo, A., 2018. Molecular systematics and biogeography of lowland antpittas (Aves, Grallariidae): the role of vicariance and dispersal in the diversification of a widespread Neotropical lineage. Mol. Phyl. Evol. 120, 375–389.

Chapman, R.M., 1917. The distribution of bird-life in Colombia. A contribution to a biological survey in South America. Bull. Am. Mus. Nat. Hist. 36, 1–729.

Chapman, R.M., 1931. The upper zonal bird-life of Mts. Roraima and Duida. Bull. Am. Mus. Nat. Hist. 63, 1–135.

Cook, R.E., 1974. Origin of the highland avifauna of southern Venezuela. Syst. Zool. 23, 257–264.

Cortés-B, R., Franco-R, P., Rangel-C, J.O., 1998. La flora vascular de la Sierra de Chiribiquete, Colombia. Caldasia 20, 103–141.

Cracraft, J., 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. Ornithol. Monogr. 36, 49–84.

Croizat-Chaley, L., 1976. Biogeografía analítica y sintética ("Panbiogeografía") de las Américas. Academia de Ciencias Físicas. Matemáticas y Naturales, Caracas.

Cuervo, A.M., 2013. Evolutionary Assembly of the Neotropical Montane Avifauna (Ph.D. dissertation). Louisiana State University, 125 pp.

Da Costa, J.M., Klicka, J., 2008. The Great American Interchange in birds: a phylogenetic perspective with the genus *Trogon*. Mol. Ecol. 17, 1328–1343.

Dantas, S.M., Weckstein, J.D., Bates, J.M., Krabbe, N.K., Cadena, C.D., Robbins, M.B., et al., 2016. Molecular systematics of the new world screech-owls (*Megascops*: Aves, Strigidae): biogeographic and taxonomic implications. Mol. Phyl. Evol. 94, 626–634.

Dickerman, R.W., Phelps Jr., W.H., 1982. An annotated list of the birds of Cerro Urutaní on the border of Estado Bolívar, Venezuela, and Territorio Roraima, Brazil. Am. Mus. Novit. 2732, 1–20.

Estrada, J., Fuertes, J., 1993. Estudios botánicos en la Guayana colombiana: 4. Notas sobre la vegetación y la flora de la Sierra de Chiribiquete. Revista de la Academia Colombiana de Ciencias Exactas Físicas y Naturales 18, 483–497.

Gansser, A., 1954. The Guiana Shield (South America). Eclogae Geol. Helv. 47, 77–117.

Ghosh, S., 1985. Geology of the Roraima Group and its implications. Boletín de Geología (Venezuela), Publicación Especial 10, 33–50.

Gilliard, E.T., 1941. The birds of Mt. Auyan-tepui, Venezuela. Bull. Am. Mus. Nat. Hist. 67, 439–508.

Giraldo-Cañas, D., 2001. Relaciones fitogeográficas de las sierras y afloramientos rocosos de la Guayana colombiana: un estudio preliminar. Revista Chilena de Historia Natural 74, 353–364.

Givnish, T.J., Evans, T.M., Pires, J.C., Sytsma, K.J., 1997. Molecular evolution and adaptive radiation in *Brocchinia* (Bromeliaceae: Pitcairnioideae) atop the tepuis of the Guayana Shield. In: Givnish, T.J., Sytsma, K. J. (Eds.), Molecular Evolution and Adaptive Radiation. Cambridge University Press, Cambridge, pp. 259–311.

III. Animal Diversity

Givnish, T.J., Evans, T.M., Zjhra, M.L., Patterson, T.B., Berry, P.E., Sytsma, K.J., 2000. Molecular evolution, adaptive radiation, and geographic diversification in the amphiatlantic family Rapateaceae: evidence from *ndh* F sequences and morphology. Evolution 54, 1915—1937.

Givnish, T.J., Barfuss, M.H.J., van Ee, B., Riina, R., Schulte, K., Horres, R., et al., 2011. Phylogeny, adaptive radiation, and historical biogeography in Bromeliaceae: insights from an eight-locus plastid phylogeny. Am. J. Bot. 98, 872—895.

Graves, G., 1982. Speciation in the Carbonated Flower-Piercer (*Diglossa carbonaria*) complex of the Andes. Condor 84, 1—14.

Haffer, J., 1974. Avian speciation in tropical South America. Pub. Nuttall Ornithol. Club 14, 1—390.

Haffer, J., 2008. Hypotheses to explain the origin of species in Amazonia. Braz. J. Biol. 68 (Suppl), 917—947.

Hilty, S.L., 2003. Birds of Venezuela., second ed. Princeton University Press, Princeton, USA.

Hilty, S.L., Ascanio, D., 2014. McConnell's Flycatcher *Mionectes macconnelli* is more than one species. Bull. Br. Ornithol. Club 134, 270—279.

Huber, O., 1987. Consideraciones sobre el concepto de Pantepui. Pantepui 2, 2—10.

Huber, O., 1988. Guayana highlands versus Guayana lowlands, a reappraisal. Taxon 37, 595—614.

Huber, O., 1995. Geographical and physical features. In: Steyermark, J.A., Berry, P.E., Holst, B.K. (Eds.), Flora of the Venezuelan Guayana. Introduction., vol. 1. Timber Press, Oregon, pp. 1—61.

Huber, O., Wurdack, J.J., 1984. History of botanical exploration in Territorio Federal Amazonas, Venezuela. Smithsonian Contrib. Bot. 56, 1—83.

Kok, P.J.R., MacCulloch, R.D., Means, D.B., Roelants, K., van Bocxlaer, I., Bossuyt, F., 2012. Curr. Biol. 22, R587—R589.

Lefebvre, G., Poulin, B., McNeill, R., 1994. Temporal dynamics of mangrove bird communities in Venezuela with special reference to migrant warblers. Auk 111, 405—415.

Lentino, M., Bosque, C., 1989. Avifauna preliminar de Marahuaca, T.F. Amazonas, Venezuela. Acta Terramaris 1, 65—70.

Lougheed, S.C., Campagna, L., Dávila, J.A., Tubaro, P.L., Lijtmaer, D.A., Handford, P., 2013. Continental phylogeography of an ecologically and morphologically diverse Neotropical songbird, *Zonotrichia capensis*. BMC Evol. Biol. 13, 58.

Lovette, I.J., Pérez-Emán, J.L., Sullivan, J.P., Banks, R.C., Fiorentino, I., Córdoba-Córdoba, S., et al., 2010. A comprehensive multilocus phylogeny for the wood-warblers and a revised classification of the Parulidae (Aves). Mol. Phyl. Evol. 57, 753—770.

MacArthur, R.H., Wilson, E.O., 1967. The Theory of Island Biogeography. Princeton University Press, Princeton.

Maguire, B., 1979. Guayana, Region of the Roraima Sandstone Formation. In: Larsen, K., Holm-Nielsen, L.B. (Eds.), Tropical Botany. Academic Press, London, pp. 185—221.

Marantz, C.A., Aleixo, A., Bevier, L., Patten, M.A., 2018. Strong-billed Woodcreeper (Xiphocolaptes promeropirhynchus. In: del Hoyo, J., Elliott, A., Sargatal, J.J., Christie, D.A., de Juana, E. (Eds.), Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona, Retrieved from: https://www.hbw.com/node/56609 (10.09.18).

Marin, G., 2010. Acerca del origen y biogeografía de la avifauna del Pantepuy o Croizat versus Mayr: una revisión crítica. Biologist (Perú) 8, 79—108.

Marín-Espinoza, G., González-Bruzual, L.G., Navarro-Rodríguez, R., 2014. *Elaenia ruficeps* (Aves: Tyrannidae, Elaeniinae): nuevo indicio de la interconexión biogeográfica de las avifaunas del Macizo Guayanés y la Cordillera Nororiental de Venezuela. Biologist 12, 1—7.

Mauck III, W.M., Burns, K.J., 2009. Phylogeny, biogeography, and recurrent evolution of divergent bill types in the nectar-stealing flowerpiercers (Thraupini: *Diglossa* and *Diglossopis*). Biol. J. Linn. Soc. 98, 14—28.

Mayr, E., Phelps Jr., W.H., 1955. Origin of the bird fauna of Pantepui. In: Portman, A., Sutter, E. (Eds.), Acta Xl Congressus Internationalis Omithologici. XI International Ornithological Congress, Basel, pp. 399—400.

Mayr, E., Phelps Jr., W.H., 1967. The origin of the bird fauna of the South Venezuelan Highlands. Bull. Am. Mus. Nat. Hist. 136, 269—328.

McDiarmid, R.W., Donnelly, M.A., 2005. The herpetofauna of the Guayana Highlands: amphibians and reptiles of the Lost World. In: Donnelly, M.A., Crother, B.I., Guyer, C., Wake, M.H., White, M.E. (Eds.), Ecology and Evolution in the Tropics: A Herpetological Perspective. University of Chicago Press, Chicago, Illinois, pp. 461—560.

McGuire, J.A., Witt, C.C., Remsen Jr., J.V., Corl, A., Rabosky, D.L., et al., 2014. Molecular phylogenetics and the diversification of hummingbirds. Curr. Biol. 24, 910–916.

Merriam, C.H., 1892. The geographic distribution of life in North America with special reference to the Mammalia. Proc. Biol. Soc. Wash. 7, 1–64.

Naka, L.N., Brumfield, R.T., 2018. The dual role of Amazonian rivers in the generation and maintenance of avian diversity. Sci. Adv. 4, eaar8575.

Nogué, S., Rull, V., Vegas-Vilarrúbia, T., 2013. Elevational gradients in the neotropical table mountains: patterns of endemism and implications for conservation. Divers. Distrib. 19, 676–687.

O'Shea, B.J., Milensky, C.M., Claramunt, S., Schmidt, B.K., Gebhard, C.A., Schmitt, C.G., et al., 2007. New records for Guyana, with description of the voice of Roraiman Nightjar *Caprimulgus whitelyi*. Bull. Br. Ornithol. Club 127, 118–128.

Pérez-Emán, J., 2002. Molecular systematics, biogeography, and population history of the genus *Myioborus* (Aves, Parulinae) (Ph.D. dissertation). University of Missouri-St. Louis, 132 pp.

Pérez-Emán, J.L., 2005. Molecular phylogenetics and biogeography of the Neotropical redstarts (*Myioborus*; Aves, Parulinae). Mol. Phyl. Evol. 37, 511–528.

Pérez-Emán, J., Sharpe, C.J., Lentino, M., Prum, R.O., Carreño F, I.J., 2003. New records of birds from the summit of Cerro Guaiquinima, Estado Bolívar, Venezuela. Bull. Br. Ornithol. Club 123, 78–90.

Phelps Jr., W.H., Aveledo, R.H., 1984. Dos nuevas subespecies de aves (Troglodytidae, Fringillidae) del Cerro Marahuaka, Territorio Amazonas, Venezuela. Boletín de la Sociedad Venezolana de Ciencias Naturales 39, 5–10.

Phelps, W.H., Phelps Jr., W.H., 1963. Lista de las aves de Venezuela con su distribución. Segunda edición. Volumen 1, Parte 2, Passeriformes. Boletín de la Sociedad Venezolana de Ciencias Naturales 24 (104, 106), 1–479 pp.

Quintero, E., Perktas, U., 2018. Phylogeny and biogeography of a subclade of mangoes (Aves, Trochilidae). J. Ornithol. 159, 29–46.

Prum, R.O., 1994. Species status of the White-fronted Manakin, *Lepidothrix serena* (Pipridae), with comments on conservation biology. Condor 96, 692–702.

Prum, R.O., 1988. Historical relationships among avian forest areas of endemism in the Neotropics. In: Quellet, H. (Ed.), Acta XIX Congressus Internationalis Ornithologici. XIX International Ornithological Congress, Ottawa, pp. 2562–2572.

Remsen Jr., J.V., Areta, J.I., Cadena, C.D., Claramunt, S., Jaramillo, A., Pacheco, J.F., et al., 2019. A classification of the bird species of South America. American Ornithologists' Union. Available from: http://www.museum.lsu.edu/~Remsen/SACCBaseline.html.

Rheindt, F.E., Christidis, L., Norman, J.A., 2009. Genetic introgression, incomplete lineage sorting and faulty taxonomy create multiple polyphyly in a montane clade of *Elaenia* flycatchers. Zool. Scr. 38, 143–153.

Ridgely, R.S., Agro, D., Joseph, L., 2005. Birds of Iwokrama Forest. Proc. Acad. Nat. Sci. Philadelphia 154, 109–121.

Rising, J., Jaramillo, A., 2019. Rufous-collared Sparrow (*Zonotrichia capensis*). In: del Hoyo, J., Elliott, A., Sargatal, J., Christie, D.A., de Juana, E. (Eds.), Handbook of the Birds of the World Alive. Lynx Edicions, Barcelona, Retrieved from: https://www.hbw.com/node/61910 (04.02.19).

Robbins, M.B., Braun, M.B., Milensky, C.M., Schmidt, B.K., Prince, W., Rice, N.H., et al., 2007. Avifauna of the Upper Essequibo River and Acary Mountains, southern Guyana. Ornitol. Neotrop. 18, 339–368.

Rull, V., 2004a. Biogeography of the "Lost World": a palaeoecological perspective. Earth-Sci. Rev. 67, 125–137.

Rull, V., 2004b. Is the Lost World really lost? Palaeoecological insights into the origin of the peculiar flora of the Guayana Highlands. Naturwissenschaften 91, 139–142.

Rull, V., 2005. Biotic diversification in the Guayana Highlands: a proposal. J. Biogeogr. 32, 921–927.

Rull, V., Montoya, E., 2017. Holocene vegetation dynamics on the Apakará summit of the neotropical Guayana Highlands and potential environmental drivers. Rev. Palaeobot. Palynol. 240, 22–32.

Rull, V., Nogué, S., 2007. Potential migration routes and barriers for vascular plants of the Neotropical Guyana Highlands during the Quaternary. J. Biogeogr. 34, 1327–1341.

Rull, V., Montoya, E., Nogué, S., Vegas-Vilarrúbia, T., Safont, E., 2013. Ecological palaeoecology in the Neotropical Gran Sabana region: long-term records of vegetation dynamics as a basis for ecological hypothesis testing. Perspect. Plant Ecol. Evol. Syst. 15, 338–359.

III. Animal Diversity

Schubert, C., Fritz, P., Aravena, R., 1992. Investigaciones paleoambientales: resultados preliminares. In: Huber, O. (Ed.), Chimantá. Escudo de Guayana, Venezuela. Un ensayo ecológico tepuyano. Oscar Todtmann Editores, C. A., Caracas, Venezuela, pp. 97—110.

Schubert, C., Fritz, P., Aravena, R., 1994. Late Quaternary paleoenvironmental studies in the Gran Sabana (Venezuelan Guayana Shield). Quat. Int. 21, 81—90.

Salerno, P.E., Ron, S.R., Señaris, C., Rojas-Runjaic, F.J.M., Noonan, B.P., Cannatella, D.C., 2012. Ancient tepui summits harbor young rather than old lineages of endemic frogs. Evolution 66, 3000—3013.

Salerno, P.E., Señaris, J.C., Rojas-Runjaic, F.J.M., Cannatella, D.C., 2015. Recent evolutionary history of Lost World endemics: population genetics, species delimitation, and phylogeography of sky-island treefrogs. Mol. Phyl. Evol. 82, 314—323.

Sidder, G.B. and S.V. Mendoza. 1991. Geology of the Venezuelan Guayana Shield and its Relation to the entire Guayana Shield. U.S. Geological Survey Open File Report, 91—141.

Sigurðsson, S., Cracraft, J., 2014. Deciphering the diversity and history of New World nightjars (Aves: Caprimulgidae) using molecular phylogenetics. Zool. J. Linn. Soc. 170, 506—545.

Slager, D.L., Battey, C.J., Bryson Jr., R.W., Voelker, G., Klicka, J., 2014. A multilocus phylogeny of a major New World avian radiation: the Vireonidae. Mol. Phyl. Evol. 80, 95—104.

Smith, B.T., McCormack, J.E., Cuervo, A.M., Hickerson, M.J., Aleixo, A., Cadena, C.D., et al., 2014. The drivers of tropical speciation. Nature 515, 406—409.

Steyermark, J.A., 1986. Speciation and endemism in the flora of the Venezuelan tepuis. In: Vuilleumier, F., Monasterio, M. (Eds.), High Altitude Tropical Biogeography. Oxford University Press, New York, pp. 317—373.

Steyermark, J.A., Dunsterville, G.C.K., 1980. The lowland floral element on the summit of Cerro Guaiquinima and other cerros of the Guayana highland of Venezuela. J. Biogeogr. 7, 283—303.

Stiles, F.G., Tellería, J.L., Díaz, M., 1995. Observaciones sobre la composición, ecología y zoogeografía de la avifauna de la Sierra de Chiribiquete, Caquetá, Colombia. Caldasia 17, 481—500.

Stiles, F.G., 1996. A new species of Emerald hummingbird (Trochilidae, *Chlorostibon*) from the Sierra de Chiribiquete, southeastern Colombia, with a review of the *C. mellisugus* complex. Wilson Bull. 108, 1—27.

Tate, G.H.H., 1938. Notes on the Phelps Venezuelan Expedition. Geograph. Rev. 28, 452—474.

Vuilleumier, F., 1969. Pleistocene speciation in birds living in the high Andes. Nature 223, 1179—1180.

Vuilleumier, F., 2005. Dean of American ornithologists: the multiple legacies of Frank M. Chapman of the American Museum of Natural History. Auk 122, 389—402.

Willard, D.E., Foster, M.S., Barrowclough, G.F., Dickerman, R.W., Cannell, P.F., Coats, S.L., et al., 1991. The birds of Cerro de la Neblina, Territorio Federal Amazonas, Venezuela. Fieldiana. Zoology 65, 1—80.

Zink, J.A., García, P., van de Plicht, J., 2011. Tepui peatlands: age record and environmental changes. In: Zink, J. A., Huber, O. (Eds.), Peatlands of the Western Guayana Highlands, Venezuela. Springer, Heidelberg, pp. 189—236.

Zyskowski, K., Mittermeier, J.C., Ottema, O., Rakovic, M., O'Shea, B.J., Lai, J.E., et al., 2011. Avifauna of the easternmost tepui, Tafelberg in Central Suriname. Bull. Peabody Mus. Nat. Hist. 52, 153—180.

Appendix I List of the 141 species included in previous analyses of Pantepui avifauna and this study. Category: PE, Pantepui endemic; MSUB, species with montane subspecies; LSUB, lowland species with highland differentiated populations (subspecies); M, montane species; L, lowland species; H, habitat specialist; B, species with broad distribution and high dispersal abilities

Species	Category	Mayr and Phelps (1967)	Willard et al. (1991)	Zyskowski et al. (2011)	Borges et al. (2018)	This study
Crypturellus ptaritepui	PE	X	X	X	X	X
Tigrisoma fasciatum	M		X	X	X	X
Buteogallus solitarius	B		X	X	X	X
Geranoaetus melanoleucus	B		X	X	X	X
Patagioenas fasciata	MSUB	X	X	X	X	X
Megascops choliba	LSUB	X	X	X	X	X
Megascops roraimae	PE	X	X	X	X	X
Glaucidium brasilianum	LSUB	X	X	X	X	X
Aegolius harrisii	M		X	X	X	X
Steatornis caripensis	H		X		X	X
Hydropsalis roraimae	PE	X	X	X	X	X
Setopagis whitelyi	PE	X	X	X	X	X
Streptoprocne phelpsi	PE	X	X	X	X	X
Streptoprocne zonaris	H				X	X
Chaetura cinereiventris	H	X	X	X		X
Aeronautes montivagus	MSUB	X	X	X	X	X
Cypseloides cryptus	H				X	X
Phaethornis augusti	LSUB	X	X	X	X	X
Phaethornis bourcieri	L	X	X			X
Phaethornis griseogularis	M		X	X	X	X
Doryfera johannae	MSUB	X	X	X	X	X
	PE	X	X	X	X	X

(*Continued*)

III. Animal Diversity

(Continued)

Species	Category	Mayr and Phelps (1967)	Willard et al. (1991)	Zyskowski et al. (2011)	Borges et al. (2018)	This study
Campylopterus hyperythrus						
Campylopterus duidae	PE	X	X	X	X	X
Colibri coruscans	MSUB	X	X	X	X	X
Colibri delphinae	M		X	X	X	X
Lophornis pavoninus	PE	X	X	X	X	X
Lophornis ornatus	L				X	X
Polytmus milleri	PE	X	X	X	X	X
Heliodoxa xanthogonys	PE	X	X	X	X	X
Amazilia viridigaster	MSUB	X	X	X	X	X
Amazilia lactea	LSUB				X	X
Amazilia versicolor	L				X	X
Amazilia tobaci	L				X	X
Chlorostilbon mellisugus	LSUB				X	X
Trogon personatus	MSUB	X	X	X	X	X
Trogon collaris	L				X	X
Aulacorhynchus whitelianus	PE	X	X	X	X	X
Veniliornis kirkii	MSUB	X	X	X	X	X
Colaptes rubiginosus	MSUB	X	X	X	X	X
Falco deiroleucus	L				X	X
Pyrrhura egregia	PE	X	X	X	X	X
Pyrrhura picta	L				X	X
Nannopsittaca panychlora	M	X	X	X	X	X
Amazona dufresniana	L				X	X
Taraba major	LSUB	X	X	X	X	X
Thamnophilus insignis	PE	X	X	X	X	X

(*Continued*)

(Continued)

Species	Category	Mayr and Phelps (1967)	Willard et al. (1991)	Zyskowski et al. (2011)	Borges et al. (2018)	This study
Dysithamnus mentalis	MSUB	X	X	X	X	X
Dysithamnus leucostictus	M			X	X	X
Myrmotherula behni	MSUB	X	X	X	X	X
Herpsilochmus roraimae	PE	X	X	X	X	X
Euchrepomis callinota	MSUB				X	X
Myrmelastes saturatus	PE	X	X	X	X	X
Myrmelastes caurensis	L			X	X	X
Grallaria guatimalensis	MSUB	X	X	X	X	X
Grallaricula nana	MSUB	X	X	X	X	X
Myrmothera simplex	PE	X	X	X	X	X
Chamaeza campanisona	MSUB	X	X	X	X	X
Synallaxis macconnelli	MSUB	X	X	X	X	X
Cranioleuca demissa	PE	X	X	X	X	X
Philydor rufum	MSUB				X	X
Roraimia adusta	PE	X	X	X	X	X
Automolus subulatus	LSUB				X	X
Clibanornis rubiginosus	MSUB				X	X
Syndactyla roraimae	PE	X	X	X	X	X
Sclerurus mexicanus	L				X	X
Lochmias nematura	MSUB	X	X	X	X	X
Xiphocolaptes promeropirhynchus	LSUB	X	X	X	X	X
Glyphorynchus spirurus	LSUB				X	X
Xiphorhynchus pardalotus	L				X	X

(*Continued*)

III. Animal Diversity

(Continued)

Species	Category	Mayr and Phelps (1967)	Willard et al. (1991)	Zyskowski et al. (2011)	Borges et al. (2018)	This study
Phyllomyias burmeisteri	MSUB	X		X	X	X
Leptopogon amaurocephalus	LSUB		X		X	X
Elaenia cristata	LSUB				X	X
Elaenia dayi	PE	X	X	X	X	X
Elaenia olivina	PE	X	X	X	X	X
Elaenia ruficeps	L	X				X
Mecocerculus leucophrys	MSUB	X	X	X	X	X
Pogonotriccus chapmani	PE	X	X	X	X	X
Phylloscartes nigrifrons	PE	X	X	X	X	X
Mionectes macconnelli	MSUB	X	X	X	X	X
Mionectes oleagineus	LSUB				X	X
Myiophobus roraimae	MSUB	X	X	X	X	X
Hemitriccus margaritaceiventer	LSUB	X	X	X	X	X
Poecilotriccus russatus	PE	X	X	X	X	X
Platyrinchus mystaceus	LSUB	X	X	X	X	X
Hirundinea ferruginea	H	X	X	X	X	X
Contopus fumigatus	MSUB	X	X	X	X	X
Contopus nigrescens	M				X	X
Knipolegus poecilurus	MSUB	X	X	X	X	X
Myiarchus swainsoni	L				X	X
Oxyruncus cristatus	MSUB	X	X	X	X	X
Pipreola whitelyi	PE	X	X	X	X	X
Lipaugus streptophorus	PE	X	X	X	X	X
Rupicola rupicola	L		X		X	X

(*Continued*)

(Continued)

Species	Category	Mayr and Phelps (1967)	Willard et al. (1991)	Zyskowski et al. (2011)	Borges et al. (2018)	This study
Procnias albus	M				X	X
Procnias averano	M				X	X
Lepidothrix suavissima	PE	X	X	X	X	X
Xenopipo uniformis	PE	X	X	X	X	X
Ceratopipra cornuta	PE	X	X	X	X	X
Pachyramphus castaneus	LSUB	X	X	X	X	X
Vireo sclateri	PE	X	X	X	X	X
Pygochelidon cyanoleuca	H	X	X		X	X
Alopochelidon fucata	H				X	X
Cistothorus platensis	M	X	X	X	X	X
Henicorhina leucosticta	L				X	X
Coereba flaveola	L					X
Pheugopedius coraya	LSUB	X		X	X	X
Troglodytes rufulus	PE	X	X	X	X	X
Microcerculus ustulatus	PE	X	X	X	X	X
Cichlopsis leucogenys	MSUB	X	X	X	X	X
Turdus flavipes	MSUB	X	X	X	X	X
Turdus leucops	M	X	X	X	X	X
Turdus olivater	MSUB	X	X	X	X	X
Turdus ignobilis	LSUB	X	X	X	X	X
Pipraeidea melanonota	M	X	X	X	X	X
Ixothraupis xanthogastra	LSUB	X	X	X	X	X
Ixothraupis punctata	L		X			X
Ixothraupis guttata	MSUB	X	X	X	X	X
Tangara gyrola	L	X			X	X
Stilpnia cyanoptera	MSUB	X	X	X	X	X

(Continued)

III. Animal Diversity

(Continued)

Species	Category	Mayr and Phelps (1967)	Willard et al. (1991)	Zyskowski et al. (2011)	Borges et al. (2018)	This study
Cyanerpes caeruleus	LSUB				X	X
Hemithraupis guira	LSUB				X	X
Diglossa duidae	PE	X	X	X	X	X
Diglossa major	PE	X	X	X	X	X
Haplospiza rustica	MSUB	X	X	X	X	X
Emberizoides duidae	PE	X	X	X	X	X
Catamenia homochroa	MSUB	X	X	X	X	X
Mitrospingus oleagineus	PE	X	X	X	X	X
Zonotrichia capensis	MSUB	X	X	X	X	X
Atlapetes personatus	PE	X	X	X	X	X
Piranga flava	MSUB	X	X	X	X	X
Piranga leucoptera	M		X	X	X	X
Setophaga pitiayumi	L	X	X	X	X	X
Myioborus miniatus	M	X	X	X	X	X
Myioborus castaneocapilla	PE	X	X	X	X	X
Myioborus cardonai	PE	X	X	X	X	X
Myioborus albifacies	PE	X	X	X	X	X
Myiothlypis bivittata	MSUB	X	X	X	X	X
Basileuterus culicivorus	LSUB				X	X
Macroagelaius imthurni	PE	X	X	X	X	X
Chlorophonia cyanea	MSUB	X	X	X	X	X
Spinus magellanicus	M	X		X	X	X
Total number of species		98	104	103	136	141

Appendix II Changes in the taxonomy of Pantepui birds since Mayr and Phelps (1967). Current names are based on the South American Classification Committee (Remsen et al., 2019)

Previous name(s)	Current name
Harpyhaliaetus solitarius	*Buteogallus solitarius*
Otus guatemalae	*Megascops roraimae*
Megascops guatemalae	
Megascops vermiculatus roraimae	
Caprimulgus longirostris	*Systellura longirostris*
Hydropsalis roraimae	
Caprimulgus whitelyi	*Setopagis whitelyi*
Hydropsalis whitelyi	
Cypseloides phelpsi	*Streptoprocne phelpsi*
Aulacorhynchus derbianus	*Aulacorhynchus whitelianus*
Piculus rubiginosus	*Colaptes rubiginosus*
Schistocichla caurensis	*Myrmelastes caurensis*
Percnostola leucostigma	*Myrmelastes leucostigma*
	Myrmelastes saturatus
Margarornis adusta	*Roraimia adusta*
Synallaxis moesta	*S. macconnelli*
Cranioleuca curtata demissa	*C. demissa*
Philydor hylobius	Not valid (described from juvenile males of *Syndactyla roraimae*)
Automolus roraimae	*S. roraimae*
Acrochordopus zeledoni	*Phyllomyias burmeisteri*
Pipromorpha macconnelli	*Mionectes macconnelli*
Todirostrum mystaceus	*Platyrinchus mystaceus*
Idioptilon margaritaceiventer	*Hemitriccus margaritaceiventer*
Todirostrum russatum	*Poecilotriccus russatus*
Chloropipo uniformis	*Xenopipo uniformis*
Pipra cornuta	*Ceratopipra cornuta*
Hylophilus sclateri	*Vireo sclateri*
Notiochelidon cyanoleuca	*Pygochelidon cyanoleuca*
Atticora cyanoleuca	

(Continued)

(Continued)

Previous name(s)	Current name
Thryothorus coraya	*Pheugopedius coraya*
Platycichla flavipes	*Turdus flavipes*
Tangara xanthogastra	*Ixothraupis xanthogastra*
Tangara chrysophrys	*Ixothraupis guttata*
Tangara guttata	
Tangara punctata	*Ixothraupis punctata*
Tangara cyanoptera	*Stilpnia cyanoptera*
Spodiornis rusticus	*Haplospiza rustica*
Emberizoides herbicola duidae	*Emberizoides duidae*
Parula pitiayumi	*Setophaga pitiayumi*
Basileuterus bivittatus	*Myiothlypis bivittata*
Carduelis magellanica	*S. magellanicus*
Sporagra magellanica	

Appendix III Endemic species from Pantepui and its distribution based on biogeographic sectors as defined by Berry et al. (1995)

Species	Eastern district	Western district	Central district	Southern district
Crypturellus ptaritepui	1	0	0	0
Megascops roraimae	1	1	1	1
Hydropsalis roraimae	1	1	1	1
Setopagis whitelyi	1	0	1	0
Myrmelastes saturatus	1	0	0	0
Campylopterus hyperythrus	1	0	0	0
Campylopterus duidae	0	1	1	1
Lophornis pavoninus	1	1	1	1
Poecilotriccus russatus	1	0	0	0
Heliodoxa xanthogonys	1	1	1	1
Aulacorhynchus whitelianus	1	1	1	1
Polytmus milleri	1	0	1	0
Syndactyla roraimae	1	1	1	1
Herpsilochmus roraimae	1	0	1	1
R.oraimia adusta	1	1	1	0
Myrmothera simplex	1	1	1	1
Cranioleuca demissa	1	1	1	1
Pyrrhura egregia	1	0	1	0
Streptoprocne phelpsi	1	1	1	1
Elaenia dayi	1	1	1	0
Elaenia olivina	1	1	1	1
Pipreola whitelyi	1	0	0	0
Phylloscartes nigrifrons	1	1	1	1
Phylloscartes chapmani	1	1	1	1
Lipaugus streptophorus	1	0	0	0
Lepidothrix suavissima	1	1	1	1
Xenopipo uniformis	1	1	1	0
Vireo sclateri	1	1	1	1
Ceratopipra cornuta	1	1	1	1

(Continued)

III. Animal Diversity

(Continued)

Species	Eastern district	Western district	Central district	Southern district
Troglodytes rufulus	1	1	1	1
Thamnophilus insignis	1	1	1	1
Microcerculus ustulatus	1	1	1	1
Diglossa duidae	0	1	1	1
Diglossa major	1	0	0	0
Emberizoides duidae	0	0	1	0
Mitrospingus oleagineus	1	0	0	0
Atlapetes personatus	1	1	1	1
Myioborus castaneocapilla	1	0	1	1
Myioborus cardonai	0	0	1	0
Myioborus albifacies	0	1	0	0
Macroagelaius imthurni	1	1	1	0
Total per district	36	26	32	23