The LINNEAN SOCIETY of London BIOLOGICAL Journal of the Linnean Society

Biological Journal of the Linnean Society, 2016, **117**, 407–413. With 2 figures.

REVIEW

Neotropical bird evolution and 100 years of the enduring ideas of Frank M. Chapman

GUSTAVO H. KATTAN[1]*, SOFÍA A. TELLO[2], MANUEL GIRALDO[3] and C. D. CADENA[4]

[1]*Departamento de Ciencias Naturales y Matemáticas, Pontificia Universidad Javeriana Seccional Cali, Cali, Colombia*
[2]*Asociación para el Estudio y Conservación de las Aves Acuáticas en Colombia – Calidris, Cali, Colombia*
[3]*Departamento de Biología, Universidad del Valle, Cali, Colombia*
[4]*Laboratorio de Biología Evolutiva, Departamento de Ciencias Biológicas, Universidad de Los Andes, Bogotá, Colombia*

Received 26 July 2015; revised 11 October 2015; accepted for publication 12 October 2015

The processes of bird diversification in South America have long been a focus of evolutionary biologists and this paper partly acts as an introduction to a selection of such work published in the *Biological Journal of the Linnean Society* and collated into a Virtual Issue (http://wileyonlinelibrary.com/bij/neotropical-bird-evolution). At the beginning of the 20th century, Frank M. Chapman, curator of birds at the American Museum of Natural History, conducted a series of expeditions in Colombia and Ecuador to 'discover the geographic origins of South American bird-life'. The expeditions produced almost 30 000 specimens, obtained in a sampling scheme aimed at revealing the geographical and elevational distributions of birds. Chapman proposed a series of ideas about the evolutionary origins of the tropical Andean avifauna. Despite being nearly 100 years old, Chapman's evolutionary hypotheses on the role of the appearance of new environments and geographical barriers on speciation, have an enduring influence. With the development of molecular methods and tools for the study of the mechanisms and timing of speciation events, Chapman's hypotheses have seen a revival in the recent scientific literature. Recent work has provided support for some of Chapman's hypotheses, but has also revealed greatly complex processes of biotic differentiation in the Neotropics. What is remarkable is that with means that today seem precarious, Chapman envisioned evolutionary processes at a continental scale that remain valid, in fields that currently advance at an accelerated rhythm and soon render older ideas obsolete. © 2016 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **117**, 407–413.

ADDITIONAL KEYWORDS: American Museum – biological history – Colombia – Ecuador – evolutionary barriers.

INTRODUCTION

Understanding the origins and patterns of diversification of biotas at continental scales is a major challenge of biogeography. As one of the most biodiverse regions of the world, South America is a classical scenario for studying such phenomena (Turchetto-Zolet *et al.*, 2013). The evolutionary trajectory of this continent is marked by four main historical milestones related to orogenic events in the Pliocene/Miocene and climatic oscillations in the Pleistocene. First, unique lineages evolved in isolation as South America drifted apart from Gondwana (Poux *et al.*, 2006). Second, Andean uplift reconfigured the landscape at a continental scale, generating new montane environments and greatly influencing the evolution of Amazonian biota (Hoorn *et al.*, 2010). Third, the connection with North America opened the door to a biotic exchange that enriched South America's flora and fauna with new lineages (Barker *et al.*, 2015). Fourth, glacial cycles during the Pleistocene caused population contractions and speciation events (Turchetto-Zolet *et al.*, 2013).

*Corresponding author. E-mail: gustavokattan@gmail.com

Recent work based on molecular phylogenies has shed light on the processes of bird diversification in South America. Andean orogeny has long been identified as a major driver of lineage diversification and speciation, by isolating populations on both sides of the barrier. Based on a phylogenetic analysis of 27 bird lineages, Smith *et al.* (2014) found that cross-Andean differentiation of taxa was not a simple vicariant event, but rather a process mediated by differences among lineages in their ability to disperse across the barrier. With a 95% complete species-level phylogeny of the Emberizoidea, a highly diverse group of Neotropical songbirds, Barker *et al.* (2015) documented dispersal patterns between North and South America that started before the continents were connected by the Panama Isthmus, and subsequent diversification of several species-rich clades in South America, in which the Andes played a significant role.

Birds have been a classic model system for studies addressing questions about the processes involved in biotic diversification in tropical America. This is evident in a selection of 13 papers published in the *Biological Journal of the Linnean Society* over nearly 5 decades, that we have collated into a single Virtual Issue (http://wileyonlinelibrary.com/bij/neotropical-bird-evolution) to which this paper serves as an introduction. In the very first issue of the journal, Mayr (1969) pondered the extreme diversity of the tropical avifauna. In an attempt to explain the underlying causes of such diversity, he reviewed what he called the 'ecology of geographic speciation', with a focus on the different types of barriers promoting evolutionary divergence. Mayr saw no major differences in principle between avian speciation in the tropics and in the temperate zone (he believed speciation was always geographic, i.e. allopatric), but suggested that high tropical diversity resulted from ecological factors associated with the tropical environment, which led to the accumulation and persistence of a high number of species. He concluded, however, that linking speciation events to particular events in earth history was a highly speculative task and noted that rates of speciation could not be calculated given information available at the time.

The analytical difficulties noted by Mayr (1969) have been largely overcome with the rise of phylogenetic systematics and the use of molecular data. For example, the study by Bleiweiss (1998) using a phylogenetic hypothesis based on DNA–DNA hybridization data was an important step towards understanding the role of *in situ* diversification, colonization events, and extinction as drivers of the assembly of hummingbird faunas in mainland and island settings. The use of DNA sequence data to reconstruct time-calibrated phylogenies has further allowed researchers to examine temporal and spatial scenarios for the evolution of tropical birds more precisely. For example, Moyle (2005) rejected the hypothesis that the breakup of Gondwana was responsible for the divergence of major groups of Trogoniformes and favored a New World origin for the group, and Barker (2007) showed that the wren genus *Campylorhynchus* likely originated in North America and colonized South America at various times across the newly formed Isthmus of Panama.

Phylogenetic analyses indicate that other groups of tropical birds, like the flowerpiercers studied by Mauck & Burns (2009), originated in the Andes and dispersed to colonize montane regions of Central America and the Pantepui. These individual evolutionary histories contribute to overall patterns of area relationships such as those suggested by the work of Sánchez-González, Morrone & Navarro-Sigüenza (2008), who based on distributional data revealed a complex biotic history for tropical montane areas involving dispersal and vicariance events. Mauck & Burns (2009) further showed that bill morphology in flowerpiercers has been highly labile and argued that differences in ecomorphology, behaviour, and habitat use likely account for the local coexistence of several species in this group at tropical sites. The evolutionary lability of avian bills and its possible influence on diversification is revealed by detailed work at a microevolutionary scale on Darwin's finches (Grant, Grant & Petren, 2000) and in the furnariid *Spartonoica maluroides* (Cardoni *et al.*, 2013), which show divergence in bill morphology associated with adaptation to different food supplies and contrasting environments.

Such divergence may be a precursor to speciation in allopatry. Seddon & Tobias (2007) show that in *Myrmeciza* antbirds, communication signals diverge as a consequence of isolation in the periphery of a species range. Divergence also occurs in the presence of gene flow, but the work by Grant *et al.* (2000) shows that links between functional traits, traits involved in species recognition and mate selection (i.e. songs) and genetic differentiation are not always straightforward, and that one must exercise caution when examining trait variation for the purpose of delimiting species. The study by Cadena & Cuervo (2010) on the classification of *Arremon* brush-finches serves to illustrate that the true species-level diversity of Neotropical birds is still poorly understood and grossly underestimated, but also that geographic patterns of differentiation in ecology and various phenotypic traits are highly complex due to the diversity of environments and evolutionary processes to which tropical species are exposed.

Finally, phylogeographic studies on various groups (e.g. manakins, woodcreepers, sparrows) occupying a wide variety of environments and regions (Amazonia, the Atlantic forest, the Andes) have increased exponentially over recent years, leading to a much improved understanding of spatial patterns in population differentiation and of the role of geographic features (e.g. rivers, vegetation, or montane barriers) and of historical changes in the landscape (e.g. shifts and expansions/contractions of habitats associated with climatic fluctuations) as drivers of evolutionary divergence (Cabanne, Santos & Miyaki, 2007; Capurucho *et al.*, 2013; Campagna *et al.*, 2014).

Hypotheses about the evolution and biogeography of Neotropical birds can be traced to Frank M. Chapman, an American ornithologist (1864–1945) who proposed several ideas based on work he conducted in Colombia and Ecuador at the beginning of the 20th century. The results of this work were presented in two monographs published in the *Bulletin of the American Museum of Natural History* (AMNH) in 1917 and 1926. Here we summarise Chapman's hypotheses and discuss how are they being addressed in the recent literature. To evaluate the influence of Chapman's ideas, we searched Google Scholar for citations of his Colombia (1917) and Ecuador (1926) monographs. We argue that Chapman's work represents an enduring legacy of relevance for evolutionary biology today, nearly a century after its original publication.

THE CHAPMAN EXPEDITIONS

As the curator of birds in the AMNH, Chapman (Fig. 1) organized a series of ornithological expeditions that criss-crossed the Colombian territory between 1910 and 1915, and Ecuador between 1913 and 1925. The objective of these expeditions was to 'discover the geographic origins of South American life' (Chapman, 1917). In Chapman's words, 'Colombia was selected as our first field of operations…because lying at the base of the Isthmus of Panama it is also at the crux of the problem of intercontinental relationships, and because it possesses more diverse physiographic and climatic conditions, combined with a greater variety of animal life, than any other part of South America of similar extent' (Chapman, 1917: 5).

Figure 1. Frank M. Chapman in the mountains of Quindío, Central Cordillera of the Andes of Colombia in 1911 (photo courtesy of Joel Cracraft, American Museum of Natural History).

Collecting stations were distributed throughout physiographic and climatic gradients, that were sampled with a rigorous design aimed at discovering which species were present at each locality. For Chapman, each specimen represented a concrete fact (presence of a species at a particular site) and common species were considered more valuable for revealing environmental influences on geographic distributions than rare species. The Colombian expeditions produced 15 775 bird specimens of 1285 species obtained from 74 localities. For Ecuador, Chapman had at his disposal 13 500 specimens of 1324 species.

CHAPMAN'S HYPOTHESES

In addition to his Colombian and Ecuadorean monographs (1917 and 1926), Chapman (1933) developed hypotheses about the biogeography and evolution of Andean birds in his autobiography and a wealth of papers in which he put forth important ideas about geographic variation and speciation in Neotropical birds (e.g. Chapman, 1923a,b, 1928, 1939, 1940). Central to his ideas was the differentiation of faunas that occurs along elevational gradients. Patterns of elevational distribution of Andean organisms had been described by Alexander von Humboldt in his *Essay on the Geography of Plants*, published in 1807. Based on his studies of glaciation, in 1888 the geographer Alfred Hettner defined four elevational zones for the eastern Andes of Colombia, and Theodor Wolf did the same for the Ecuadorean Andes in 1892, which he defined as Tropical, Subtropical, Subandine and Andine. Chapman, however, was the first to precisely characterize elevational zones (which he termed Tropical, Subtropical, Temperate and Páramo), by their distinctive bird faunas. He remarked, for example, that of the 360 species of birds collected in the Subtropical zone of Colombia, three-fifths were confined to this belt. He also noted that the limits of the elevational zones varied among mountain ranges and slopes, depending on climatic conditions. His main hypotheses can be summarized as follows.

1. When a new mountain system such as the tropical Andes is formed, the new areas are populated by: (i) latitudinal extension of the ranges of species from regions with similar climates, in this case from the south temperate zone; and (ii) species derived from ancestors from lower elevational zones (altitudinal extension).

2. (i) The birds of the Subtropical and Temperate elevational zones are mostly derived from ancestors in the zones immediately below them, in successive steps of colonization and differentiation; (ii) the birds of the Páramo zone (the high-elevation biome composed of shrublands and open habitats above treeline) are mostly derived from ancestors from low elevations with similar climates in the south of the continent.
3. Among species of the Temperate (elevational) zone, those derived from ancestors in the lower elevational zones show more differentiation than species derived from ancestors in the southern temperate zone; the differences are more a consequence of environmental conditions than of time or distance.
4. The emergence of the Andes caused the differentiation of *cis*-Andean (Amazonian) and *trans*-Andean (Pacific) faunas; among Andean species, some exhibit uniformity throughout the Colombian and Ecuadorian ranges, whereas other show differentiation between the western (Pacific) and eastern (Amazonian) slopes.
5. The Subtropical zone extends in the Andes from Bolivia northward, and is continuous in Central American mountain systems from Costa Rica to Mexico, with practically the same species composition; there is a hiatus in the lowlands of Panama (a 'zoological fault'), and a former connection is postulated between the Andes and the mountains of Costa Rica.

CHAPMAN'S THINKING IN THE CURRENT LITERATURE

We found more than 400 papers that cited Chapman (1917, 1926), but in 90 papers one or more of Chapman's hypotheses were explicitly central to the study's main theme. Only one paper cited Chapman before the 1960s (Fig. 2), on the biogeography of Africa's flora and fauna (Moreau, 1933). Beginning in 1967, a steady increase in citations is observed that continues to the present, with 16 papers in the period 2010–2013. The lack of older citations may be due to their absence in electronic databases, but it is unlikely that many exist. Almost half of the recent papers use molecular techniques, and nearly 10% apply distribution models and use geographic information systems. Thus, after 100 years Chapman's ideas have not lost currency, and new technological developments are allowing the testing of these ideas with modern, rigorous tools.

At the beginning of the 20th century, knowledge about the geological history of the northern Andes was very sketchy, but it was known that current elevations were attained in the latter part of the Tertiary, less than 20 Mya. Therefore, it could be inferred that the Andean avifauna was relatively young. In addition, from Hettner's work it was known that glaciations in the recent geological past had affected the elevational distribution of vegetation (Chapman, 1917). A few geological studies were conducted in the 1920s, but large-scale geological explorations that allowed an understanding of northern Andean orogeny did not begin until the 1960s (Irving, 1975).

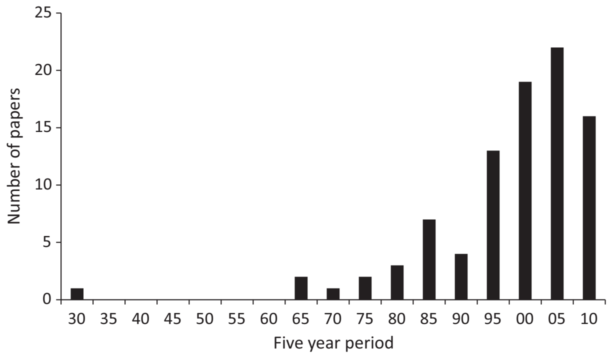

Figure 2. Numbers of papers published in 5-year periods beginning in 1930, that test and elaborate Chapman's hypotheses. The sample includes papers ($N = 90$) that cite Chapman (1917, 1926) and were found in Google Scholar up until 2013.

In spite of the limited geological knowledge, Chapman recognized the importance of Andean uplift for the diversification of the Neotropical biota, as a phenomenon that isolated populations on both sides of the mountain range, and created new montane environments that opened up opportunities for colonization and diversification. Biotic differentiation across the mountain range had already been noted by Darwin during his travels in the southern Andes, but Chapman presented a detailed description of this phenomenon based on taxonomic relationships of species on both sides of the range. He also assigned great importance to the role of biogeographical barriers for the evolution of birds, but recognized that some species may exhibit great powers of dispersal (Chapman, 1917, 1926).

For 4 decades after Chapman's work, the study of Neotropical birds continued at a slow pace, mostly from taxonomic and distributional points of view, and there were no major advancements in our understanding of their evolution. Starting in the 1970s, a rise in biogeographical studies led to a resurgence of Chapman's ideas, but with the additional consideration of Pleistocene climatic cycles as a major force in the evolution of the South American biota (Vuilleumier, 1969; Cracraft, 1985; Haffer, 1985). During this resurgence period, authors also stressed the importance of barriers such as large Amazonian rivers, but recognized the possibility of ecological interactions delimiting ranges, rather than the inability of birds to cross barriers (Haffer, 1985). New analyses of the origin of high-elevation tropical birds showed that many species indeed had their origins in the southern latitudes, but found that a large fraction had evolved *in situ* (Vuilleumier, 1986).

Molecular tools in the last couple of decades have provided evidence that support some of Chapman's ideas about the evolution of Neotropical birds, but have also revealed a much more intricate history than previously realized. In general, studies have confirmed the role of the Andes in the diversification of bird lineages, both by causing vicariance and by creating new environments. Evidence that Andean uplift fragmented ancestral populations and generated cis-Andean and trans-Andean lineages has been found for birds as varied as toucans, parrots, potoos and treecreepers (Brumfield, Swofford & Braun, 1997; Bates *et al.*, 2008; Weir & Price, 2011; Lutz *et al.*, 2013; Quintero, Ribas & Cracraft, 2013). For example, based on a phylogeny constructed from mitochondrial and nuclear DNA sequences, Lutz *et al.* (2013) found that the divergence between *Selenidera* and *Andigena* toucans is consistent with the uplift of the northern Andes, but diversification within *Andigena* occurred in relation to the fragmentation of montane habitats caused by Pleistocene climatic oscillations. Recent work, however, suggests that the uplift of the Andes did not affect all lineages equally, and that cross-Andean differentiation was often spurred by post-uplift dispersal events which occurred more frequently in older lineages and led to increased diversification in groups with poorer dispersal abilities (Smith *et al.*, 2014).

Molecular data have also revealed evidence consistent with the hypothesis of diversification of lineages along elevational gradients. In the flycatcher genus *Leptopogon*, which has four species along the eastern slope of the Andes, a pattern of species relations consistent with a process of diversification into successively higher elevations was documented (Bates & Zink, 1994). The lowland species is sister to the rest of the clade, and the upper elevation species is the sister taxon of the two mid-elevation species. Similar patterns have been documented for some species of jays, woodcreepers and antshrikes (Brumfield & Edwards, 2007; Bonaccorso, 2009; Arbeláez-Cortés, Navarro-Sigüenza & García-Moreno, 2012). However, in some cases parapatric altitudinal taxa are not each other's closest relatives (Ribas *et al.*, 2007), and these patterns may not reflect divergence associated with elevational gradients but rather secondary contact between populations originally diverging in allopatry (Caro *et al.*, 2013). Recent evidence also indicates that high-elevation birds in the tropical Andes are derived from ancestors in the southern latitudes (Chesser, 2000, 2004).

Molecular studies have helped to disentangle the phylogeographic relationships of many Neotropical bird lineages, but have also revealed great complexities and convoluted evolutionary histories in this rich avifauna, concomitant with the complex physiographical and environmental history of the continent (Bates *et al.*, 2008; Smith *et al.*, 2014). It is not rare to find that several factors have acted on a lineage over evolutionary time to generate intricate phylogeographic patterns. For example, patterns of genetic structure in different lineages indicate that Andean uplift resulted in diversification along elevational gradients or in disjunct distributions on both sides of the mountain range, but subsequent vicariance related to vegetation shifts, as well as range expansions, dispersal and extinction events across the Andes acting at different spatial and temporal scales, have produced complicated distribution patterns of sister taxa (Cheviron, Hackett & Capparella, 2005; Brumfield & Edwards, 2007; Miller *et al.*, 2008). Additionally, many species-rich taxa such as hummingbirds and tanagers have profusely radiated within the Andes (Sedano & Burns, 2010; McGuire *et al.*, 2014).

CONCLUDING REMARKS

Chapman's work was well ahead of his time and transcended the field of ornithology. His hypotheses have been used as a conceptual framework for the study of diverse organisms including plants, insects, amphibians, reptiles and mammals. Likewise, one-third of the studies citing Chapman focus on the tropical Andes, but the other two-thirds refer to broader geographic realms or different regions. Chapman had clear biogeographical and evolutionary questions in his mind when he organized the Colombian and Ecuadorean expeditions, at a time when these disciplines were in their infancy. His data collection scheme (specimens collected at specific stations along environmental gradients throughout a geographical realm) followed a careful design, in spite of the logistical limitations inherent to the time and place, to obtain the information required to test his ideas. With the limited tools he had available, he was able to infer large-scale patterns of biogeographical relationships of the Neotropical biota based on careful analyses of morphology and distributional patterns. In addition, Chapman's data-rich specimens have allowed for recent examination of his ideas using tools developed well after his time (Cadena, Cheviron & Funk, 2011).

Modern researchers have an impressive set of tools and techniques at their disposal to address complex questions. With sophisticated statistical techniques, we can determine the likelihood of different scenarios that take into account multiple variables. Molecular tools provide a window into the past that allow researchers to discern phylogeographic patterns with a confidence that is not possible with morphological characters such as plumage. In the 1990s researchers used techniques such as isozyme electrophoresis and DNA–DNA hybridization to reveal patterns of population differentiation and species spatial relationships that provided a test of Chapman's hypotheses. In the last 15 years, studies have moved on to the use of sequence data from mitochondrial and nuclear genes to discern lineage relationships and phylogeographic patterns. Molecular dating permits testing hypotheses that put the timing of evolutionary events in the context of geological and other historical milestones, such as Andean uplift and Pleistocene climatic fluctuations. We have detailed global and local maps at our fingertips and can locate sites with extraordinary precision using space age technology, and electronic tools help us organize and analyse large datasets.

With means that today seem precarious, Chapman was able to discern differentiation patterns at various spatial scales, from local to continental. Chapman's ideas remain current 100 years after they were formulated in vibrant fields that advance at an accelerated rate and render most older ideas obsolete.

ACKNOWLEDGEMENTS

We would like to thank two anonymous reviewers for constructive comments and J. A. Allen for support in preparing the Virtual Issue.

REFERENCES

Arbeláez-Cortés E, Navarro-Sigüenza AG, García-Moreno J. 2012. Phylogeny of woodcreepers of the genus *Lepidocolaptes* (Aves, Furnariidae), a widespread Neotropical taxon. *Zoologica Scripta* **41:** 363–373.

Barker FK. 2007. Avifaunal interchange across the Panamanian isthmus: insights from *Campylorhynchus* wrens. *Biological Journal of the Linnean Society* **90:** 687–702.

Barker FK, Burns KJ, Klicka J, Lanyon SM, Lovette IJ. 2015. New insights into New World biogeography: an integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. *The Auk Ornithological Advances* **132:** 333–348.

Bates JM, Zink RM. 1994. Evolution into the Andes: molecular evidence for species relationships in the genus *Leptopogon*. *The Auk* **111:** 507–515.

Bates JM, Cadena CD, Tello JG, Brumfield RT. 2008. Diversification in the Neotropics: phylogenetic patterns and historical processes. *Ornitologia Neotropical* **19**(Suppl.)**:** 427–432.

Bleiweiss R. 1998. Origin of hummingbird faunas. *Biological Journal of the Linnean Society* **65:** 77–97.

Bonaccorso E. 2009. Historical biogeography and speciation in the Neotropical highlands: molecular phylogenetics of the jay genus *Cyanolyca*. *Molecular Phylogenetics and Evolution* **50:** 618–632.

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

Brumfield RT, Swofford DL, Braun MJ. 1997. Evolutionary relationships among the potoos (Nyctibiidae) based on isozymes. In: Remsen JV, ed. *Studies in Neotropical Ornithology Honoring Ted Parker*. Ornithological Monographs 48. Washington, DC: American Ornithologists' Union, 129–146.

Cabanne GS, Santos FR, Miyaki CY. 2007. Phylogeography of *Xiphorhynchus fuscus* (Passeriformes, Dendrocolaptidae): vicariance and recent demographic expansion in southern Atlantic forest. *Biological Journal of the Linnean Society* **91:** 73–84.

Cadena CD, Cuervo AM. 2010. Molecules, ecology, morphology, and songs in concert: how many species is *Arremon torquatus* (Aves: Emberizidae)? *Biological Journal of the Linnean Society* **99:** 152–176.

Cadena CD, Cheviron ZA, Funk WC. 2011. Testing the molecular and evolutionary causes of a 'leapfrog' pattern of geographical variation in coloration. *Journal of Evolutionary Biology* **24:** 402–414.

Campagna L, Kopuchian C, Tubaro PL, Lougheed SC. 2014. Secondary contact followed by gene flow between divergent mitochondrial lineages of a widespread Neotropical songbird (*Zonotrichia capensis*). *Biological Journal of the Linnean Society* **111:** 863–868.

Capurucho JMG, Cornelius C, Borges SH, Cohn-Haft M, Aleixo A, Metzger JP, Ribas CC. 2013. Combining phylogeography and landscape genetics *of Xenopipo atronitens* (Aves: Pipridae), a white sand campina specialist, to understand Pleistocene landscape evolution in Amazonia. *Biological Journal of the Linnean Society* **110:** 60–76.

Cardoni DA, Greenberg R, Maldonado JE, Isacch JP. 2013. Morphological adaptation to coastal marshes in spite of limited genetic structure in the Neotropical passerine *Spartonoica maluroides* (Aves: Furnariidae). *Biological Journal of the Linnean Society* **109:** 78–91.

Caro LM, Caycedo-Rosales PC, Bowie RCK, Slabbekoorn H, Cadena CD. 2013. Ecological speciation along an elevational gradient in a tropical passerine bird? *Journal of Evolutionary Biology* **26:** 357–374.

Chapman FM. 1917. The distribution of bird-life in Colombia: a contribution to a biological survey of South America. *Bulletin of the American Museum of Natural History* **36:** 1–729.

Chapman FM. 1923a. The distribution of the motmots of the genus *Momotus*. *Bulletin of the American Museum of Natural History* **48:** 27–59.

Chapman FM. 1923b. Mutation among birds in the genus *Buarremon*. *Bulletin of the American Museum of Natural History* **48:** 243–278.

Chapman FM. 1926. The distribution of bird-life in Ecuador: a contribution to a study of the origin of Andean bird-life. *Bulletin of the American Museum of Natural History* **55:** 1–784.

Chapman FM. 1928. Mutation in *Capito auratus*. *American Museum Novitates* **335:** 1–21.

Chapman FM. 1933. *Autobiography of a bird-lover*. New York, NY: D. Appleton-Century Company.

Chapman FM. 1939. The riddle of *Oxyruncus*. *American Museum Novitates* **1047:** 1–4.

Chapman FM. 1940. The post-glacial history of *Zonotrichia capensis*. *Bulletin of the American Museum of Natural History* **77:** 381–438.

Chesser RT. 2000. Evolution in the high Andes: the phylogenetics of *Muscisaxicola* ground-tyrants. *Molecular Phylogenetics and Evolution* **15:** 369–380.

Chesser RT. 2004. Systematics, evolution, and biogeography of the South American ovenbird genus *Cinclodes*. *The Auk* **121:** 752–766.

Cheviron ZA, Hackett SJ, Capparella AP. 2005. Complex evolutionary history of a Neotropical forest bird (*Lepidothrix coronata*) and its implications for historical hypotheses of the origin of Neotropical avian diversity. *Molecular Phylogenetics and Evolution* **36:** 338–357.

Cracraft J. 1985. Historical biogeography and patterns of differentiation within the South American avifauna: areas of endemism. In: Buckley PA, Foster MS, Morton ES, Ridgely RS, Buckley FG, eds. *Neotropical ornithology*. . Ornithological Monographs 36. Washington DC: American Ornithologists' Union, 49–84.

Grant PR, Grant BR, Petren K. 2000. The allopatric phase of speciation: the sharp-beaked ground finch (*Geospiza difficilis*) on the Galápagos islands. *Biological Journal of the Linnean Society* **69:** 287–317.

Haffer J. 1985. Avian zoogeography of the Neotropical lowlands. In: Buckley PA, Foster MS, Morton ES, Ridgely RS, Buckley FG, eds. *Neotropical Ornithology*. Ornithological Monographs 36. Washington, DC: American Ornithologists' Union, 113–146.

Hoorn C, Wesselingh FP, ter Steege H, Bermudez MA, Mora A, Sevink J, Sanmartín I, Sanchez-Meseguer A, Anderson CL, Figuereido JP, Jaramillo C, Riff D, Negri FR, Hooghiemstra H, Lundberg J, Stadler T, Sarkinen T, Antonelli A. 2010. Amazonia through time: Andean uplift, climate change, landscape evolution, and biodiversity. *Science* **330:** 927–931.

Irving EM. 1975. Structural evolution of the northernmost Andes, Colombia. US Geological Survey Professional Paper 846.

Lutz HL, Weckstein JD, Patané JSL, Bates JM, Aleixo A. 2013. Biogeography and spatio-temporal diversification of *Selenidera* and *Andigena* toucans (Aves: Ramphastidae). *Molecular Phylogenetics and Evolution* **69:** 873–883.

Mauck WM, Burns KJ. 2009. Phylogeny, biogeography, and recurrent evolution of divergent bill types in the nectar-stealing flowerpiercers (Thraupini: *Diglossa* and *Diglossopis*). *Biological Journal of the Linnean Society* **98:** 14–28.

Mayr E. 1969. Bird speciation in the tropics. *Biological Journal of the Linnean Society* **1:** 1–17.

McGuire JA, Witt CC, Remsen JV Jr, Cori A, Rabosky DL, Altshuler DL, Dudley R. 2014. Molecular phylogenetics and the diversification of hummingbirds. *Current Biology* **24:** 910–916.

Miller MJ, Bermingham E, Klicka J, Escalante P, do Amaral FSR, Weir JT, Winker K. 2008. Out of Amazonia again and again: episodic crossing of the Andes promotes diversification in a lowland forest flycatcher. *Proceedings of the Royal Society B* **275:** 1133–1142.

Moreau RE. 1933. Pleistocene climatic changes and the distribution of life in East Africa. *Journal of Ecology* **21:** 415–435.

Moyle RG. 2005. Phylogeny and biogeographical history of Trogoniformes, a pantropical bird order. *Biological Journal of the Linnean Society* **84:** 725–738.

Poux C, Chevret P, Huchon D, de Jong WW, Douzery EJP. 2006. Arrival and diversification of Caviomorph rodents and Platyrrhine primates in South America. *Systematic Biology* **55:** 228–244.

Quintero E, Ribas CC, Cracraft J. 2013. The Andean *Hapalopsittaca* parrots (Psittacidae: Aves): an example of montane-tropical lowland vicariance. *Zoologica Scripta* **42:** 28–43.

Ribas CR, Moyle RG, Miyaki CY, Cracraft J. 2007. The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in *Pionus* parrots. *Proceedings of the Royal Society B* **274:** 2399–2408.

Sánchez-González LA, Morrone JJ, Navarro-Sigüenza AG. 2008. Distributional patterns of the Neotropical humid montane forest avifaunas. *Biological Journal of the Linnean Society* **94:** 175–194.

Sedano RE, Burns KJ. 2010. Are the northern Andes a species pump for Neotropical birds? Phylogenetics and biogeography of a clade of Neotropical tanagers (Aves: Thraupini). *Journal of Biogeography* **37:** 325–343.

Seddon N, Tobias JA. 2007. Song divergence at the edge of Amazonia: an empirical test of the peripatric speciation model. *Biological Journal of the Linnean Society* **90:** 173–188.

Smith BT, McCormack JE, Cuervo AM, Hickerson MJ, Aleixo A, Cadena CD, Pérez-Emán J, Burney CW, Sie X, Harvey MG, Faircloth BC, Glenn TC, Derryberry EP, Prejean J, Fields S, Brumfield RT. 2014. The drivers of tropical speciation. *Nature* **515:** 406–409.

Turchetto-Zolet AC, Pinheiro F, Salgueiro F, Palma-Silva C. 2013. Phylogeographical patterns shed light on evolutionary process in South America. *Molecular Ecology* **22:** 1193–1213.

Vuilleumier F. 1969. Pleistocene speciation in birds living in the high Andes. *Nature* **223:** 1179–1180.

Vuilleumier F. 1986. Origins of the tropical avifaunas of the high Andes. In: Vuilleumier F, Monasterio M, eds. *High altitude tropical biogeography*. Oxford: Oxford University Press, 586–622.

Weir JT, Price M. 2011. Andean uplift promotes lowland speciation through vicariance and dispersal in *Dendrocincla* woodcreepers. *Molecular Ecology* **20:** 4550–4563.