

Biogeography

## Defining the phylogeographic relationship between cis- and trans-Andean populations of *Dendrocincla fuliginosa* and *Xenops minutus* in Colombia

### *Definiendo las relaciones filogeográficas entre poblaciones cis- y trans- andinas de Dendrocincla fuliginosa y Xenops minutus en Colombia*

Enrique Arbeláez-Cortés \*

*Grupo de Estudios en Biodiversidad, Escuela de Biología, Facultad de Ciencias, Universidad Industrial de Santander, Carrera 27 Calle 9, Bucaramanga, Santander, Colombia*

\*Corresponding author: [enriquearbelaez@gmail.com](mailto:enriquearbelaez@gmail.com) (E. Arbeláez-Cortés)

Received: 8 March 2019; accepted: 18 September 2019

#### Abstract

Due to the position of Colombia between Central and South America, and the presence of several ecosystems in its territory, phylogeographic information from populations across this country is fundamental to understand the evolutionary history of widespread Neotropical species. The Andes have long been noted for their influence isolating lowland species into cis- and trans-Andean populations. However, detailed sampling across cis-Andean zones adjacent to the Andes (i.e., Orinoquia) has been lacking in avian phylogeographic studies. Information from DNA sequences, from 2 passerine birds: *Dendrocincla fuliginosa* and *Xenops minutus* is presented herein; to depict their phylogeographic patterns, focusing on the relationship between cis- and trans-Andean populations from Colombia. The analyses, regarding Colombian samples indicated that cis-Andean populations (i.e., Orinoquia and Amazon) are not closely related, rather the Orinoquia populations are more closely related to trans-Andean populations in both species. These relationships suggest that populations on both sides of the Andes were connected in the recent past (less than 1 myA). I propose that phylogeographic differentiation in lowland species in this region is not only explained by the presence of the Andean mountains, but also based on the ecological shifts between major ecosystems such as Amazonia and Orinoquia.

*Keywords:* Amazonia; Birds; Orinoquia; Lowlands; mtDNA; nDNA; South America

#### Resumen

Por su posición entre Centroamérica y Sudamérica, y por presentar varios ecosistemas, la información filogeográfica de poblaciones de Colombia es fundamental para entender la historia evolutiva de especies neotropicales ampliamente distribuidas. Los Andes se consideran como factor de separación de especies de tierras bajas en poblaciones cis- y trans-andinas. Pero un muestreo detallado de zonas cis-andinas adyacentes a los Andes (i.e., Orinoquia) ha estado ausente de los estudios filogeográficos con aves. Se presenta aquí información de secuencias de ADN de 2 aves paseriformes: *Dendrocincla fuliginosa* y *Xenops minutus*, para describir sus patrones filogeográficos, enfocando dicha

información en la relación entre poblaciones cis- y trans-andinas en Colombia. Los análisis indican que poblaciones cis-andinas (i.e., Orinoquía y Amazonía) no están estrechamente relacionadas entre sí, sino que las poblaciones de la Orinoquía están más relacionadas con poblaciones trans-andinas en ambas especies. Estas relaciones sugieren que las poblaciones en ambos lados de los Andes estuvieron conectadas en el pasado reciente (menos de 1 MA). Se propone que la diferenciación filogeográfica en especies de tierras bajas en esta región no puede explicarse solo por la presencia de las montañas andinas, sino también con base en cambios ecológicos entre ecosistemas mayores como la Amazonía y la Orinoquía.

*Palabras clave:* Amazonía; Aves; Orinoquía; Tierras bajas; ADNmt; ADNn; Sudamérica

## Introduction

Phylogeographic studies of widespread lowland Neotropical birds usually have indicated a strong genetic differentiation among allopatric populations (Cheviron et al., 2005; Fernandes et al., 2014; Harvey & Brumfield, 2015; Marks et al., 2002; Miller et al., 2008; Nyári, 2007; Rheindt et al., 2009). For lowland species, these studies have usually considered the Andes mountains as a barrier to gene flow between populations to the West (trans-Andean) and to the East (cis-Andean). For species such as *Automolus ochrolaemus*, *A. subulatus* (Schultz et al., 2017), *Hylophylax naevius*/*H. naevioides* (Fernandes et al., 2014), *Lepidothrix coronata* (Cheviron et al., 2005), and *Myiopagis viridicata* (Rheindt et al., 2009), a clear phylogeographic differentiation between cis- and trans-Andean populations has been found. However, other species such as *Glyphorynchus spirurus* (Marks et al., 2002), *Schiffornis turdina* (Nyári, 2007), and *Mionectes oleagineus* (Miller et al., 2008), exhibit a lower degree of genetic differentiation between trans- and cis-Andean populations. Therefore, recent dispersion (or population connection) across (or around) the Andes, originally proposed by Haffer (1967), has been considered to explain such phylogeographic relationships between cis- and trans-Andean populations. Results of these single-species studies, agree with those studies including several lowland bird species (Smith, Harvey et al., 2014; Smith, McCormack et al., 2014), indicating that phylogeographic relationships among populations in Neotropical lowlands are complex. Connection across the Andes as a cause underlying the actual patterns of species distributions has also been analyzed using geographic models of potential ranges of bird species, and there is evidence of historic ecological continuity across low-lying passes that could promote population connectivity between cis- and trans-Andean regions (Cadena et al., 2016).

Despite advances in the knowledge of the evolution of lowland Neotropical birds, phylogeographic patterns of these lineages have been derived mainly from information from Mexico, Central America, and Brazil; but a gap often exists in phylogeographic information from Colombia.

Given the geographic location of Colombia between Central and South America, their complex landscape, and the dynamic history of their environment (Cadena et al., 2007, 2016; Flantua et al., 2007; Haffer, 1967; Nores, 2004); more taxon and geographic sampling across this country is crucial to reconstruct the evolutionary history of Neotropical organisms (Avendaño et al., 2017). To test if Colombian populations adhere to the established cis/trans Andean dichotomy, phylogeographic patterns of 2 widespread lowland species that range on both sides of the Andes and inhabit forests were analyzed: *Dendrocincla fuliginosa* and *Xenops minutus* (Furnariidae).

*Dendrocincla fuliginosa* (Vieillot, 1818) ranges from southeastern Honduras to eastern Brazil, mainly below 1,300 m asl, but occasionally up to 2,000 m asl. This species inhabits humid and savanna forests in lowlands and foothills, generally in mature forests, but it also tolerates secondary vegetation and plantations. *Dendrocincla fuliginosa* forages for invertebrates and small vertebrates on vertical trunks at low- and mid-levels, usually alone but also follows ant swarms (as facultative) and mixed-species flocks (Del Hoyo et al., 2003; Restall et al., 2006). This species comprises 11 subspecies; 4 of which occur in Colombia (Gill & Donsker, 2018). Molecular information indicated that the diversification of *D. fuliginosa* began around 4 myA (Derryberry et al., 2011; Weir & Price, 2011).

*Xenops minutus* (Sparman, 1788) ranges from southern Mexico to southeastern South America (below 1,000 m asl, but locally up to 1,500 m asl), and inhabits tropical lowland forests where it forages for arthropods, usually alone or in mixed-species flocks, climbing along branches and woody vines in low- to mid-level vegetation (Del Hoyo et al., 2003; Restall et al., 2006). This species comprises 10 subspecies; 5 of which occur in Colombia (Gill & Donsker, 2018). Molecular information suggests that the split of *X. minutus* from its sister species occurred around 10 myA (Derryberry et al., 2011). Harvey & Brumfield (2015) used genome-wide single nucleotide polymorphisms to investigate the phylogeography of this taxon, and found the presence of at least 3 deeply divergent clades that seem to represent different species.

For both species, the Andes have been considered as a barrier involved in their diversification (Harvey & Brumfield, 2015; Weir & Price, 2011), but these studies lack Colombian samples. Smith et al. (2014) included Colombian samples of *Xenops minutus* and *D. fuliginosa* in a phylogeographic study, but analyzed general patterns across multiple species. The aim here is to depict the phylogeographic patterns of both species, focusing on defining relationships among cis- and trans-Andean populations from Colombia.

## Materials and methods

Eighteen tissue samples of *D. fuliginosa* (17 localities from 8 Colombian departments) and 13 tissue samples of *X. minutus* (12 localities from 9 Colombian departments), covering their main distribution ranges in Colombia (Appendix 1) were used. DNA was isolated from frozen tissues using Qiagen DNeasy™ kit (Qiagen Inc., Valencia, CA, USA), following the manufacturer protocol. I amplified the mitochondrial (mtDNA) gene subunit 2 of the nicotinamide adenine dinucleotide dehydrogenase (ND2), using primers H1056U and L5215U (H. Vázquez-Miranda in litt.) and the nuclear (nDNA) locus 20454 using primers 20454F and 20454R (Backström et al., 2008). All PCR trials were performed in a final volume of 15 µl, containing 1x PCR buffer, 1.5 mM MgCl<sub>2</sub>, 0.2 mM each dNTP, 0.4-0.5 µM each primer, 1-2 unit DNA polymerase, and around 50-100 ng of DNA. PCR conditions were the same used for those loci in Arbeláez-Cortés et al. (2014).

PCR products were purified using Exo-SAP-IT™ (GE Healthcare Bio-Sciences Corp. Piscataway, NJ, USA), and the sequences were obtained by ABI Prism BigDye™ v3.1 (Qiagen Inc., Valencia, CA, USA) terminator chemistry in an ABI 3730XL automated sequencer located in an overseas facility (University of Washington, USA). All PCR products were exported from Colombia under the respective permission of Colombian authorities (see Acknowledgments). Sequences were edited and manually aligned using BioEdit (Hall, 1999). For sequences of nDNA, I inspected chromatograms to detect double peaks, which were edited by coding them following a standard IUPAC ambiguity code. Double peaks were scanned across all individuals to check for accuracy and consistency in their identification. The allele phase of the nDNA locus was resolved using a coalescent-based Bayesian method of the Phase algorithm (Stephens & Donnelly, 2003; Stephens et al., 2001) in DNAsp v.5 (Librado & Rozas, 2009) employing default settings. The resulting highest-probability haplotypes for further analyses were used. All sequences are deposited in GenBank (MN486096-MN486154).

For the mtDNA locus ND2, additional sequences of other countries from GenBank were obtained. For *D. fuliginosa*, 17 sequences from Brazil, 3 from Suriname, 2 from Peru, 2 from Venezuela, 2 from Panama, 1 from Ecuador, and 1 from Trinidad and Tobago were obtained (Claramunt et al., 2010; Naka et al., 2012; Weir et al., 2009). For *X. minutus*, 21 sequences were obtained from Guyana, 10 from Belize, 9 from Panama, 8 from Brazil, 2 from Venezuela, 1 from Ecuador, and 1 from Paraguay (Derryberry et al., 2011; Naka et al., 2012, M.J. Miller, 2008 unpublished). For each of these GenBank sequences, I obtained the geographical information available either from: their metadata, the database of the biological collection which harbors the sample, the supplementary material of the cited papers, or from other papers in which several of these individuals have been included (C.W. Burney, 2009 unpublished; Smith et al., 2014). Only GenBank sequences for which there was at least country information were included. I georeferenced localities without information using GeoNames (GeoNames, 2013) or Google Earth (Google, 2010). In the cases where only the information for the country or state was available, I used central geographic coordinates to depict their position on a map only for illustrative purposes. I included ND2 sequences from closest congeneric species, *Xenops rutilans* and *Dendrocincla anabantina* (Derryberry et al., 2011) as outgroups. A list of samples with GenBank accession numbers is provided in appendix 1. Because the size of the sequences obtained and the ones available from GenBank varied, I trimmed the ND2 alignments to 625 bp, for *D. fuliginosa*, and to 622 bp for *X. minutus*. For the nDNA locus 20454 I aligned 285 bp for *D. fuliginosa* and 381 bp for *X. minutus*. However, full sequences were deposited in GenBank.

It should be noted that Weir and Price (2011) indicated that *D. fuliginosa* is paraphyletic. These authors found that the eastern South American populations are distantly related from the western populations. For this reason, I analyzed both the whole set of sequences available for *D. fuliginosa* and a subset from its western range, but I focus my results and discussion on the latter. Here, I refer to these populations as *D. fuliginosa*, even though the information in Weir and Price (2011) indicates that they can be considered under a different name.

BEAST version 1.7.4 (Drummond et al., 2012; Drummond et al., 2012) was used to reconstruct phylogenetic relationships among ND2 haplotypes. The best-fit model for each alignment was selected using Akaike's information criterion in Modeltest, version 3.7 (Posada & Crandall, 1998). I ran BEAST for 200,000,000 steps, sampling every 2,000 steps, using a Yule speciation tree prior, a UPGMA starting tree, and a strict molecular

clock with a mutation rate of  $2.9 \times 10^{-8}$  substitutions/site / year for ND2 according to rates previously reported in passerine birds (Lerner et al., 2011). After this analysis, TreeAnnotator, version 1.7.4 (Rambaut & Drummond, 2012) was used to generate a tree file with 25% burn-in and a posterior probability limit of 0.5. Sequences of the nDNA locus, available just for Colombia, were examined using Network (Bandelt et al., 1999) to generate an allele network depicting their relationships.

I acknowledge that the estimates of time trees depend on the selected substitution rate for the loci. For instance, looking broadly for externally calibrated rate estimates of the ND2 rate in birds, one finds variation ranging from 1.94% to 12.3% per my (Arbogast et al., 2006; Benham et al., 2015; Fuchs et al., 2011; Johnson & Weckstein, 2011; Patel et al., 2011; Weir & Schluter, 2008). However, my principal aim is to depict the phylogeographic pattern of both species in northwestern South America and not to detail divergence times among clades. The only temporal issue discussed here is the differentiation between cis-Andean (Orinoquia) and trans-Andean populations for both species to compare it with information on the Andes orogenic formation. Because the substitution rate I used is towards the low end of estimated rates for birds it would lead to ancient dates.

## Results

I gathered new mtDNA sequences (ND2) of 29 individuals of *D. fuliginosa* and *X. minutus* from Colombia, which I combined along with 82 sequences, publically available, from other regions (Appendix 1). mtDNA phylogeographic structure were found in both species across their ranges (Fig. 1). The 20454 nDNA locus, examined only for Colombian samples, presented different alleles on both species, and geographic structure seems to be present in *X. minutus* but not in *D. fuliginosa* (Fig. 1). The phylogenetic trees indicated that there are 6 mtDNA lineages for *X. minutus* and 4 mtDNA lineages for *D. fuliginosa* (Fig. 1).

The 4 *D. fuliginosa* mtDNA lineages exhibited phylogeographic structure (Fig. 1). In addition to the differentiated lineage from eastern South America, a widespread mtDNA lineage was found including the Amazonian individuals from Brazil, Venezuela, Colombia, Ecuador, and Peru. This Amazonian lineage was sister to the clade including 2 sister lineages, one of these includes the Colombian individuals from the Orinoquia and 1 individual from Trinidad and Tobago, while the trans-Andean individuals from Colombia and Panama comprised the other lineage. The Orinoquian individuals (cis-Andean) were sister to the trans-Andean lineage, rather than with the Amazon (cis-Andean) lineage. The network

representation of nDNA alleles (Fig. 1) did not show such structure. However, only the most common allele of the 20454 nDNA locus was shared by individuals from the 3 mtDNA lineages, while the other 6 alleles were exclusive of different mtDNA lineages (Fig. 1). Besides these general patterns in *D. fuliginosa*, it is also notable that the trans-Andean individuals showed geographic differences in their mtDNA haplotypes. For instance, Colombian inter Andean valley's individuals did not share haplotypes with Caribbean individuals, and these Caribbean individuals in spite to be close to Panama individuals harbor a different haplotype (Fig. 1).

The 6 *X. minutus* mtDNA lineages also exhibited phylogeographic structure (Fig. 1). One individual from Paraguay (not depicted in the map in figure 1) and 5 individuals from the Amazon in Brazil (but without locality information) comprise a clade with posterior probability (pp) = 0.66 that is sister to the poorly supported clade (pp = 0.34) including the remaining individuals. One mtDNA lineage including individuals from Venezuela, Brazil, and Guyana appeared as sister (pp = 0.81) to a lineage including individuals from Colombian Amazon. On the other hand, the lineage with individuals from Belize is a sister to a lineage including individuals from Panama, western Ecuador, Colombia (trans-Andean and Orinoquia), and northwestern Venezuela. Colombian individuals from Orinoquia (cis-Andean) are again clustered with trans-Andean individuals and not with the other cis-Andean individuals from the Amazon. This result for *X. minutus* is paralleled by the Network analysis of the nDNA (Fig. 1) that showed that individuals from the Orinoquia (cis-Andean) shared alleles with other Colombian trans-Andean individuals, while individuals from the Colombian Amazon (cis-Andean) not share alleles with the remaining Colombian individuals. As in the case of *D. fuliginosa*, the trans-Andean individuals of *X. minutus* also showed geographic differences in their haplotypes. The Belize haplotypes were well differentiated, while the Ecuador, Panama, and Colombia individuals did not share haplotypes among them. In addition, Colombian individuals from the inter-Andean valleys harbor 1 haplotype that is different from those found in the Caribbean Colombian individuals.

The BEAST analysis (Fig. 1) indicated that divergence of mtDNA lineages in *D. fuliginosa* began approximately 0.5 my (95% HPD between 266,000 and 608,000 years ago), while divergence of lineages in *X. minutus* was older, beginning approximately 1.5 my (95% HPD between 1.17 and 1.9 myA). Haplotypes within each mtDNA lineage of *D. fuliginosa* appear to have coalesced during the last 150,000 years, whereas the mtDNA lineages of *X. minutus* coalesced during the last 370,000 years. Regarding the Colombian haplogroups, the lineage of *D. fuliginosa* in the

Orinoquia diverged from its sister trans-Andean lineage approximately 300,000 years ago, and both of them diverged from the Amazon lineage around 400,000 years ago (Fig. 1). In the case of *X. minutus*, the divergence of

the 2 lineages present in Colombia occurred probably more than 1 million years ago, but the alleles comprising a clade for the Orinoquia (Andean) and trans-Andean samples likely coalesced less than 1 my.

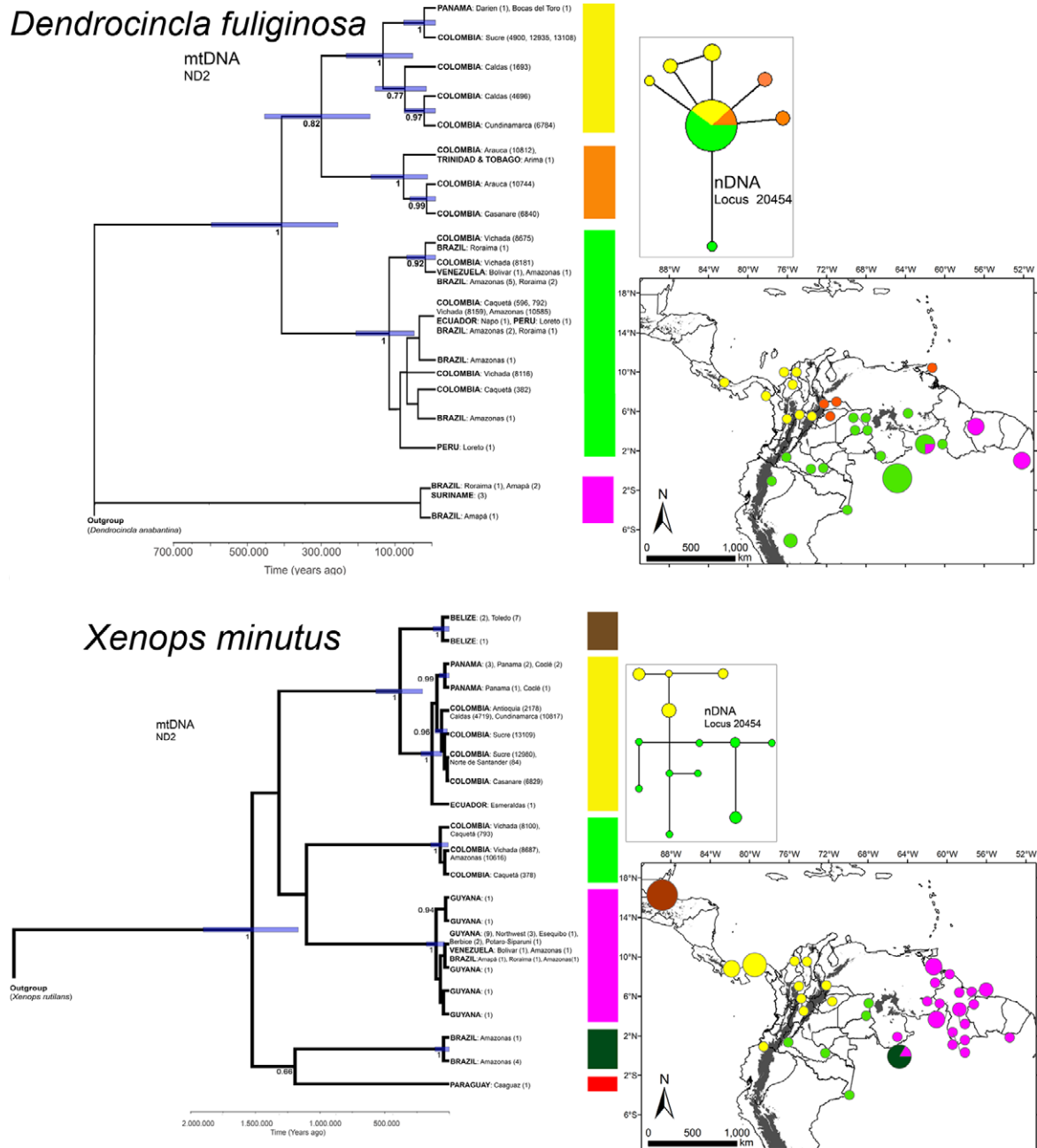


Figure 1. Phylogeography of *D. fuliginosa* and *X. minutus*. Left, phylogenetic reconstruction of the mtDNA (ND2) dataset in BEAST, depicting posterior probabilities (pp) for nodes with values larger than 0.75. The 95% high posterior density calculated for divergence times are presented as error bars for some nodes of interest. Right, and allele network of the nDNA (locus 20454) for Colombian individuals. In the tips of the trees (among brackets) are indicated the IAVH-CT numbers for Colombian samples and the number of sequences used for the other countries. The inset maps depicts the range of each major haplogroup (circles with same color as in the phylogenetic reconstruction and allele network), and elevations above 1,500 m are in dark grey.

## Discussion

Molecular information for *X. minutus* and *D. fuliginosa* was analyzed, and I agree with other authors (e.g., Avendaño et al., 2017; Cadena et al., 2007) in considering the inclusion of samples from Colombia as necessary to draw conclusions about recent biological diversification in the Neotropics, which was the focus of this paper for 2 species of passerine birds. Both species exhibited phylogeographic structure in their whole geographic distribution, suggesting the occurrence of historic processes (i.e., vicariance) separating their populations. Regarding Colombian samples both species show a clear separation of individuals from the Amazon (cis-Andean), while individuals from the Orinoquia (cis-Andean) and the trans-Andean lowlands are more related. These patterns agree with the biogeographic regionalization of the Neotropics which indicates that the Orinoquia and trans-Andean lowlands conform a biogeographic dominion, which is different from the Amazon (Morrone, 2014), but contrast with the idea of the Andes as a barrier for lowland species.

The uplift of the Andes as a process associated with differentiation between Orinoquia (Andean) and trans-Andean populations of *D. fuliginosa* and *X. minutus* can be ruled out because such mountains reached their actual elevation in Colombia 2.7 myA (Gregory-Wodzicki, 2000), while populations of *D. fuliginosa* and *X. minutus* on both sides probably diverged less than 0.5 myA (95% HPD between 450,000 - 175,000 years ago for *D. fuliginosa*, and less than 250,000 years ago for *X. minutus*). However, I do not discard the presence of the Andes as related to genetic differentiation, in the sense that its mountains have facilitated isolation of populations that were connected recently (a possible scenario for *D. fuliginosa*) or have promoted differentiation in the trans-Andean zone followed by dispersal over (or around) these mountains (a possible scenario for *X. minutus*). Another possible scenario for *X. minutus* is that their populations in the Orinoquia and the trans-Andean populations have been connected throughout their history because they are part of the same mtDNA lineage.

Close relationships between Orinoquia and trans-Andean lowlands have been also revealed by biogeographical and ecological analyses of other animal taxa (Lozano-Zambrano & Fernández, 2007; Sigrist & Carvalho, 2009). Similarly, this relationship between cis- and trans-Andean populations has been found in other phylogeographic studies. For instance, in monkey species (Lynch et al., 2015) and another bird (*Chrysomus icterocephalus*, Cadena et al., 2011). Weir & Price (2011) also noted the recent separation of *D. fuliginosa ridgwayi* (trans-Andean) from *D. f. meruloides* (cis-Andean). Several

additional works have found sister relationships between populations in Central America or Choco, and populations in Amazonia (e.g., Marks et al., 2002; Miller et al., 2008; Nyári, 2007; Rheindt et al., 2009), but they did not include Colombian samples that I show here are key to a complete understanding of these lineages' phylogeographic patterns.

Close phylogeographic relationships between cis- and trans-Andean populations are not new for vertebrates (Lynch et al., 2015; Nyári, 2007). However, another result is more novel. I found that the major phylogeographic break for *D. fuliginosa* and *X. minutus* in Colombia is between Orinoquia and Amazonia (both cis-Andean regions), and not among cis- and trans-Andean populations. This phylogeographic break (Amazon/Orinoquia) has been also found in monkeys (*Lagothrix lagotricha*, Botero et al., 2015), and is a noteworthy result, suggesting that ecological differences between Orinoquia and Amazon could be involved in maintaining genetic isolation, which is in line with Brumfield (2012) who considers a secondary role of barriers in the Neotropics in structuring variation that arose elsewhere, and that could be in secondary contact (in this case) in the border between Amazon and Orinoquia. An alternative explanation for this phylogeographic pattern is to consider a major role for the ecological shifts between Orinoquia and Amazonia as the reason for genetic differentiation in these species. Whatever the explanation (either as a zone of division or as a zone of contact); the Amazon/Orinoquia transition must be considered as a necessary factor to explain genetic differentiation in widespread lowland taxa in the Neotropics.

In spite of the large genomic information used by Harvey and Brumfield (2015), which allowed understand several issues of the history of *X. minutus*, the lack of Colombian individuals in their analyses made impossible to appreciate that individuals from Orinoquia (cis-Andean) and from the trans-Andean zone are included in the same lineage. However, Harvey and Brumfield (2015) found evidence of migration from the Amazon into the trans-Andean populations. The close relationship of cis- and trans-Andean populations of birds inhabiting forests suggests that lowlands on both sides of the Andes in northwestern South America have (or recently had) a connection. This observation agrees with the scenario proposed by Haffer (1967), who considered that during glacial periods of the Pleistocene, the climate in northern Colombia was more humid, and then these lowlands were forest-covered much more extensively than they are at present, which provided a broad connection between cis- and trans-Andean lowland forests. This effect was increased by a lower sea level (about 100 m), which promoted the emergence of a large area of land in northern South America (Haffer, 1967; Nores, 2004). For *Ateles*

monkeys, this scenario has been considered to explain their distribution in cis- and trans-Andean zones (Lynch et al., 2015). However, a northern connection between cis- and trans-Andean regions is not the only way supported by analyses of species ranges in lowland species (Cadena et al., 2016). In addition, Avendaño et al. (2013) presented evidence of recent crossings of cis-Andean bird species into the trans-Andean lowlands, apparently promoted by human modifications to the landscape, suggesting that ecological changes could facilitate the interchange of some species between both zones.

Considering only the trans-Andean samples, the differences in their mtDNA haplotypes are noteworthy, particularly these observed between the inter-Andean valleys and the Caribbean Colombian populations that probably occurred during the last 250,000 years. This result parallels the result for *C. icterocephalus* that also shows different haplotypes between the Magdalena valley and the Caribbean lowlands (Cadena et al., 2011), but contrasts with the lack of genetic structure found in the monkey *Ateles hybridus* and other bird species in this same area (Link et al., 2015; Sandoval et al., 2017). Differences found in the 2 species analyzed here could be explained by historic processes of isolation among trans-Andean populations due to climatic fluctuations. For instance, the repeated change of dry and wet climatic periods during the Pleistocene (Haffer, 1967) and fluctuations in sea level in the Caribbean coastal zone (Nores, 2004) could be related to population isolation in trans-Andean lowlands, thus allowing the origin of the genetic patterns observed. Further phylogeographic studies are warranted to depict detailed phylogeographic patterns in this zone and to test the role of these paleoclimatic processes in the genetic differentiation of populations.

It is also noteworthy that trans-Andean samples show genetic differences which contrast with an apparent lack of genetic differences among Amazonian samples. For instance, western Amazonian individuals clustered together, despite that they are widespread and represent localities in 2 or more endemism areas (Cracraft, 1985). Colombian individuals of both species, in this study, from the Napo and Imeri endemism areas shared haplotypes, indicating that these areas are not separable based on the molecular information. For *D. fuliginosa* individuals from Venezuela (Guiana area of endemism) and Peru (Inambari)

harbor haplotypes like the ones found in the Colombian Amazon (Imeri and Napo). These results suggest a more active (and recent) genetic differentiation in the trans-Andean lowlands than in the Amazon.

The Colombian Orinoquia (cis-Andean) and Caribbean (trans-Andean) are 2 gaps in biodiversity knowledge (Arbeláez-Cortés, 2013). The Caribbean and the inter-Andean valleys in Colombia have undergone major anthropogenic changes in their landscapes (Armenteras et al., 2011; Etter et al., 2006), while the Orinoquia is undergoing significant changes in its natural ecosystems (Armenteras et al., 2005; Romero-Ruiz et al., 2012). Therefore, it is urgent to better understand the biodiversity in these zones to have scientific support for its conservation. Further works should test if the close phylogeographic relationship between trans-Andean and Orinoquia (cis-Andean) populations regarding the Amazon (cis-Andean) populations is a generality for birds and other taxa. If such pattern is common, then the genetic differences among populations in this region of the Neotropics will not be explained only by the presence of Andean mountains or large rivers, but also by the ecological shift between ecosystems such as those represented by Amazonia and Orinoquia or by an historical barrier to gene flow between ecosystems that has shifted.

### Acknowledgments

This work was supported by the Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Colombia, under funds allocated to Colecciones Biológicas; and by the Vicerrectoría de Investigación y extensión of Universidad Industrial de Santander, Colombia under grant “Proyecto de investigación capital semilla 2300”. I also thank the family Arbeláez-Cortés and A. G. Navarro-Sigüenza for their support. L. A. Sánchez González, N. Trujillo-Arias, and two anonymous reviewers made valuable comments and corrections that improved this work. A special acknowledgment to the specimen and tissue collectors of the material used in this study. Samples were exported to sequencing overseas under: “Permiso para la exportación de especímenes de la diversidad biológica no listados en los apéndices de la convención CITES número 385 de 2014 de la Autoridad Nacional de Licencias Ambientales, Colombia”.

**Appendix 1. List of individuals of *D. fuliginosa* and *X. minutus* with GenBank accession numbers and locality information for samples and sequences included in this work. Source of the sequences information is indicated.**

Taxon	Collection number	GenBank number: ND2 / 20454	Country	Department or State	County	Locality	Source
<i>D. fuliginosa</i>	STRI TR-DFU1	GU215371	Trinidad and Tobago	Arima		Simla Research Station	Weir et al. (2009)
<i>D. fuliginosa</i>	IAvH-CT 4900, IAvH-A 13106	MN486096 / MN486131	Colombia	Sucre	San Onofre	Corregimiento La Barce, Santuario de Fauna y Flora El Corchal El Mono Hernandez	This study
<i>D. fuliginosa</i>	IAvH-CT 13108, IAvH-A 15248	MN486112 / MN486143	Colombia	Sucre	Toluviejo	Corregimiento El Cañito, Monte de Los Navas	This study
<i>D. fuliginosa</i>	IAvH-CT 12935, IAvH-A 15075	MN486102 / MN486141	Colombia	Sucre	Colosó	Estación Primatologica, Montes de María	This study
<i>D. fuliginosa</i>	IAvH-CT 12997	/ MN486142	Colombia	Sucre			This study
<i>D. fuliginosa</i>	STRI JTW253	GU215373	Panama	Bocas del Toro	Valle de Risco	Not locality information-Valle de Risco	Weir et al. (2009)
<i>D. fuliginosa</i>	STRI JTW744	GU215374	Panama	Darien	Puerto Piña	Not locality information-Puerto Piña	Weir et al. (2009)
<i>D. fuliginosa</i>	IAvH-CT 10744, IAvH-A 14722	MN486109 / MN486139	Colombia	Arauca	Araucuita	Extracción de Arenas Remolinos, Río Arauca	This study
<i>D. fuliginosa</i>	IAvH-CT 10812, IAvH-A 14795	MN486107 / MN486140	Colombia	Arauca	Araucuita	Plataforma Cosecha G	This study
<i>D. fuliginosa</i>	AMNH 11848	JQ445335	Venezuela	Bolivar		Cerro Guaiquinima	Naka et al. (2012)
<i>D. fuliginosa</i>	IAvH-CT 4696, IAvH-A 13282	MN486098 / MN486130	Colombia	Caldas		Vereda La Miel	This study
<i>D. fuliginosa</i>	IAvH-CT 6840, IAvH-A 14175	MN486110 / MN486133	Colombia	Casanare	Pore	Corregimiento Altamira, Vereda Altamira La Esperanza	This study
<i>D. fuliginosa</i>	IAvH-CT 6784, IAvH-A 14146	MN486104 / MN486132	Colombia	Cundinamarca	Puerto Salgar	Not locality information-Puerto Salgar	This study



**Appendix 1.**  
**Continued**

Taxon	Collection number	GenBank number: ND2 / 20454	Country	Department or State	County	Locality	Source
<i>D. fuliginosa</i>	IAvH-CT 8675, IAvH-A 12798	MN486108 / MN486137	Colombia	Vichada	Cumaribo	Corregimiento Santa Rita, Parque Nacional Natural El Tuparro, Bosque asociado al cerro Peinilla	This study
<i>D. fuliginosa</i>	IAvH-CT 1693, IAvH-A 12010	MN486097 / MN486129	Colombia	Caldas	Neira	Vereda El Bohío, Cuenca del Río Tapias, Hacienda Tintina	This study
<i>D. fuliginosa</i>	IAvH-CT 8181, IAvH-A 14400	MN486101 / MN486136	Colombia	Vichada	Cumaribo	Selva de Mataven, Río Orinoco	This study
<i>D. fuliginosa</i>	IAvH-CT 8116, IAvH-A 14334	MN486106 / MN486134	Colombia	Vichada	Cumaribo	Selva de Mataven, Caño Cajaro	This study
<i>D. fuliginosa</i>	IAvH-CT 8159, IAvH-A 14377	MN486103 / MN486135	Colombia	Vichada	Cumaribo	Selva de Mataven, Caño Matavén	This study
<i>D. fuliginosa</i>	LSUMZ B55361	JQ445315	Suriname	Sipaliwini District		Not locality information-Sipaliwini District	Naka et al. (2012)
<i>D. fuliginosa</i>	LSUMZ B55317	JQ445314	Suriname	Sipaliwini District		Not locality information-Sipaliwini District	Naka et al. (2012)
<i>D. fuliginosa</i>	LSUMZ B45787	JQ445316	Suriname			Not locality information-Suriname	Naka et al. (2012)
<i>D. fuliginosa</i>	MPDS 376	JQ445334	Brazil	Roraima	Alto Alegre	Faz. Paraense, Terra Firme e Savana	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A1769	JQ445324	Brazil	Roraima		Not locality information-Roraima	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A1542	JQ445322	Brazil	Roraima		Not locality information-Roraima	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A1537	JQ445318	Brazil	Roraima		Not locality information-Roraima	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A1080	JQ445332	Brazil	Roraima		Not locality information-Roraima	Naka et al. (2012)
<i>D. fuliginosa</i>	AMNH DOT12706	GQ906712	Venezuela	Amazonas		Rio Baria	Claramunt et al. (2010)
<i>D. fuliginosa</i>	IAvH-CT 792, IAvH-A 11394	MN486100 / MN486128	Colombia	Caquetá	San José de Fragua	Corregimiento La Esmeralda,	This study
<i>D. fuliginosa</i>	FMNH 391302	JQ445313	Brazil	Amapá		Not locality information-Amapá	Naka et al. (2012)

**Appendix 1.**  
**Continued**

Taxon	Collection number	GenBank number: ND2 / 20454	Country	Department or State	County	Locality	Source
<i>D. fuliginosa</i>	FMNH FM391298	GU215370	Brazil	Amapá		Not locality information-Amapá	Weir et al. (2009)
<i>D. fuliginosa</i>	FMNH 391303	JQ445317	Brazil	Amapá		Not locality information-Amapá	Naka et al. (2012)
<i>D. fuliginosa</i>	IAvH-CT 382, IAvH-A 11047	MN486099 / MN486126	Colombia	Caquetá		Parque Nacional Natural Serranía de Chiribiquete, Río Mesay	This study
<i>D. fuliginosa</i>	INPA A1940	JQ445330	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A650	JQ445327	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A1230	JQ445333	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A1165	JQ445331	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A694	JQ445328	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A1220	JQ445323	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A2007	JQ445321	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A1596	JQ445320	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>D. fuliginosa</i>	INPA A1938	JQ445319	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>D. fuliginosa</i>	IAvH-CT 596, IAvH-A 11276	MN486105 / MN486127	Colombia	Caquetá		Parque Nacional Natural Serranía de Chiribiquete Río Sararamano, afluente del río Messay	This study
<i>D. fuliginosa</i>	STRI EC-DFU1	GU215372	Ecuador	Napo	Jatun Sacha	Not locality information-Jatun Sacha	Weir et al. (2009)

**Appendix 1.**  
**Continued**

Taxon	Collection number	GenBank number: ND2 / 20454	Country	Department or State	County	Locality	Source
<i>D. fuliginosa</i>	IAvH-CT 10585, IAvH-A 14562	MN486111 / MN486138	Colombia	Amazonas	Leticia	Reserva Forestal Rio Calderon, Estacion Biologica El Zafire	This study
<i>D. fuliginosa</i>	LSUMZ B6895	JQ445325	Peru	Loreto		Not locality information-Loreto	Naka et al. (2012)
<i>D. fuliginosa</i>	LSUMZ B2723	JQ445326	Peru	Loreto		Not locality information-Loreto	Naka et al. (2012)
<i>X. minutus</i>	UAM 24522; ABJ415	FJ175798	Belize	Toledo District		Not locality information- Toledo District	M.J. Miller, 2008 unpublished document
<i>X. minutus</i>	UAM ABJ428	FJ175799	Belize			Not locality information-Belize	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM ABJ622	FJ175800	Belize			Not locality information-Belize	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM ABJ607	FJ175801	Belize			Not locality information-Belize	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM 24355; ABJ294	FJ175802	Belize	Toledo District		Not locality information- Toledo District	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM 24347; ABJ266	FJ175803	Belize	Toledo District		Not locality information- Toledo District	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM 14330; KSW3706	FJ175804	Belize	Toledo District		Not locality information- Toledo District	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM 24348; ABJ270	FJ175805	Belize	Toledo District		Not locality information- Toledo District	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM 24357; ABJ296	FJ175806	Belize	Toledo District		Not locality information- Toledo District	M.J. Miller (2008) unpublished document

**Appendix 1.**  
**Continued**

Taxon	Collection number	GenBank number: ND2 / 20454	Country	Department or State	County	Locality	Source
<i>X. minutus</i>	UAM 24356; ABJ295	FJ175807	Belize	Toledo District		Not locality information-Toledo District	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	IAvH-CT 13109, IAvH-A 15249	MN486118 / MN486154	Colombia	Sucre	Toluviejo	Corregimiento El Cañito, Monte de Los Navas	This study
<i>X. minutus</i>	IAvH-CT 12980, IAvH-A 15120	MN486123 / MN486153	Colombia	Sucre	Colosó	Estación Primatologica, Montes de María	This study
<i>X. minutus</i>	UAM 20495; MJM410	FJ175809	Panama	Panama		Cerro Azul: ANAM Station	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM KSW4392	FJ175810	Panama			Not locality information-Panama	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM 20492; MJM407	FJ175812	Panama			Not locality information-Panama	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM MJM1462	FJ175814	Panama			Not locality information-Panama	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM 22105; MJM675	FJ175815	Panama	Panama		Not locality information-Cerro Azul: ANAM Station	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM 22110	FJ175816	Panama	Panama		Not locality information-Cerro Azul: ANAM Station	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM 20338; MJM244	FJ175808	Panama	Cocle		Molejon, Finca Moreno	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	UAM 20326; MJM232	FJ175811	Panama	Cocle		Molejon, Finca Moreno	M.J. Miller (2008) unpublished document

**Appendix 1.**  
**Continued**

Taxon	Collection number	GenBank number: ND2 / 20454	Country	Department or State	County	Locality	Source
<i>X. minutus</i>	UAM 20350	FJ175813	Panama	Cocle	Molejon, Finca Moreno	Molejon, Finca Moreno	M.J. Miller (2008) unpublished document
<i>X. minutus</i>	USNM 14628	JQ445992	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	AMNH DOT11942	JQ445967	Venezuela	Bolivar		Not locality information-Bolivar	Naka et al. (2012)
<i>X. minutus</i>	USNM 9164	JQ445982	Guyana	Northwest		Not locality information-Northwest	Naka et al. (2012)
<i>X. minutus</i>	USNM 9333	JQ445983	Guyana	Northwest		Not locality information-Northwest	Naka et al. (2012)
<i>X. minutus</i>	IAvH-CT 84, IAvH-A 10842	MN486114 /	Colombia	Norte de Santander	Toledo	Vereda El Diamante Río Negro Parque Nacional Natural Tamá	This study
<i>X. minutus</i>	IAvH-CT 2178	MN486113	Colombia	Antioquia	Amalfi	Vereda Las Animas, Bosque Las Animas, Cuenca de la quebrada Las Animas	This study
<i>X. minutus</i>	USNM 14183	JQ445989	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	USNM 14260	JQ445990	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	USNM 4266	JQ445979	Guyana	Berbice		Not locality information-Berbice	Naka et al. (2012)
<i>X. minutus</i>	USNM 4331	JQ445980	Guyana	Berbice		Not locality information-Berbice	Naka et al. (2012)
<i>X. minutus</i>	IAvH-CT 4719, IAvH-A 13305	MN486115 / MN486146	Colombia	Caldas		Vereda La Miel	This study
<i>X. minutus</i>	IAvH-CT 6829, IAvH-A 14164	MN486117 / MN486147	Colombia	Casanare	Pore	Vereda Altamira, La Esperanza	This study
<i>X. minutus</i>	USNM 5132	JQ445981	Guyana	Essequibo		Not locality information-Essequibo	Naka et al. (2012)
<i>X. minutus</i>	IAvH-CT 8687, IAvH-A 12848	MN486124 / MN486150	Colombia	Vichada	Cumaribo	Corregimineto Santa Rita, Parque Nacional Natural El Tuparro, Bosque de Guaipé	This study

**Appendix 1.**  
**Continued**

Taxon	Collection number	GenBank number: ND2 / 20454	Country	Department or State	County	Locality	Source
<i>X. minutus</i>	USNM 15759	JQ445993	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	USNM 14525	JQ445991	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	LSUMZ B48433	JQ445975	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	LSUMZ B48452	JQ445976	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	LSUMZ B48478	JQ445977	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	UKNHM 1225	JQ445973	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	UKNHM 1276	JQ445974	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	IAvH-CT 8100, IAvH-A 14317	MN486121 / MN486148	Colombia	Vichada	Cumaribo	Selva de Mataven, Caño Cajaro	This study
<i>X. minutus</i>	IAvH-CT 8152, IAvH-A 14370	MN486125 / MN486149	Colombia	Vichada	Cumaribo	Selva de Mataven, Caño Matavén	This study
<i>X. minutus</i>	IAvH-CT 10817, IAvH-A 14208	MN486116 / MN486152	Colombia	Cundinamarca	Anapoima	Club campestre Mesa de Yeguas	This study
<i>X. minutus</i>	ANSP 7407	JQ445968	Guyana	Potaro-Siparuni		Not locality information-Potaro-Siparuni	Naka et al. (2012)
<i>X. minutus</i>	INPA A1709	JQ445972	Brazil	Roraima		Not locality information-Roraima	Naka et al. (2012)
<i>X. minutus</i>	USNM 12223	JQ445987	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	USNM 12772	JQ445988	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	AMNH:DOT8845	JF975328	Venezuela	Amazonas		Not locality information-Amazonas	Derryberry et al. (2011)
<i>X. minutus</i>	FMNH 391346	JQ445969	Brazil	Amapá		Not locality information-Amapá	Naka et al. (2012)
<i>X. minutus</i>	USNM 11810	JQ445986	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	USNM 10412	JQ445984	Guyana			Not locality information-Guyana	Naka et al. (2012)
<i>X. minutus</i>	USNM 10887	JQ445985	Guyana	North West		Not locality information-Northwest	Naka et al. (2012)

**Appendix 1.  
Continued**

Taxon	Collection number	GenBank number: ND2 / 20454	Country	Department or State	County	Locality	Source
<i>X. minutus</i>	IAvH-CT 793, IAvH-A 11395	MN486119 / MN486145	Colombia	Caquetá	San José de Fragua	Corregimiento La Esmeralda	This study
<i>X. minutus</i>	LSUMZ:B11948	JF975329	Ecuador	Esmeraldas	El Placer	Not locality information-El Placer	Derryberry et al. (2011)
<i>X. minutus</i>	IAvH-CT 378, IAvH-A 11043	MN486120 / MN486144	Colombia	Caquetá		Parque Nacional Natural Serranía de Chiribiquete, Río Mesay	This study
<i>X. minutus</i>	AMZ 118 (MPEG 59473)	JQ445964	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>X. minutus</i>	AMZ 119 (MPEG 59474)	JQ445965	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>X. minutus</i>	AMZ 325 (MPEG 59475)	JQ445966	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>X. minutus</i>	INPA A71	JQ445970	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>X. minutus</i>	INPA A1610	JQ445971	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>X. minutus</i>	JAP 662 (MPEG 62739)	JQ445978	Brazil	Amazonas		Not locality information-Amazonas	Naka et al. (2012)
<i>X. minutus</i>	IAvH-CT 10616, IAvH-A 14593	MN486122 / MN486151	Colombia	Amazonas	Leticia	Reserva Forestal Rio Calderon, Estacion Biologica El Zafire	This study
<i>X. minutus</i>	LSUMZ:B25938	JF975330	Paraguay	Caaguaz		Not locality information-Caaguaz	Derryberry et al. (2011)

**References**

- Arbeláez-Cortés, E. (2013). Knowledge of Colombian biodiversity: published and indexed. *Biodiversity and Conservation*, 22, 2875–2906. <https://doi.org/10.1007/s10531-013-0560-y>
- Arbeláez-Cortés, E., Roldán-Piña, D., & Navarro-Sigüenza, A. G. (2014). Multilocus phylogeography and morphology give insights into the recent evolution of a Mexican endemic songbird: *Vireo hypochryseus*. *Journal of Avian Biology*, 45, 253–263. <https://doi.org/10.1111/j.1600-048x.2013.00335.x>
- Arbogast, B. S., Drovetski, S. V., Curry, R. L., Boag, P. T., Seu-tin, G., Grant, P. R. et al. (2006). The origin and diversification of Galapagos mockingbirds. *Evolution*, 60, 370–382. <https://doi.org/10.1554/03-749.1>
- Armenteras, D., Rodríguez, N., Retana, J., & Morales, M. (2011). Understanding deforestation in montane and lowland forests of the Colombian Andes. *Regional Environmental Change*, 11, 693–705. <https://doi.org/10.1007/s10113-010-0200-y>
- Armenteras, D., Romero, M., & Galindo, G. (2005). Vegetation fire in the savannas of the Llanos Orientales of Colombia. *World Resource Review*, 17, 628–647.

- Avendaño, J. E., Arbeláez-Cortés, E., & Cadena, C. D. (2017). On the importance of geographic and taxonomic sampling in phylogeography: A reevaluation of diversification and species limits in a Neotropical thrush (Aves, Turdidae). *Molecular Phylogenetics and Evolution*, *111*, 87–97. <https://doi.org/10.1016/j.ympev.2017.03.020>
- Avendaño, J. E., Cortés-Herrera, J. O., Briceño-Lara, E. R., & Rincón-Guarín, D. A. (2013). Crossing or bypassing the Andes: a commentary on recent range extensions of cis-Andean birds to the West of the Andes of Colombia. *Orinoquia*, *17*, 208–214. <https://doi.org/10.22579/20112629.18>
- Backström, N., Fagerberg, S., & Ellegren, H. (2008). Genomics of natural bird populations: a gene-based set of reference markers evenly spread across the avian genome. *Molecular Ecology*, *17*, 964–980. <https://doi.org/10.1111/j.1365-294x.2007.03551.x>
- Bandelt, H. J., Forster, P., & Röhl, A. (1999). Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution*, *16*, 37–48. <https://doi.org/10.1093/oxfordjournals.molbev.a026036>
- Benham, P. M., Cuervo, A. M., McGuire, J. A., & Witt, C. C. (2015). Biogeography of the Andean metal-tail hummingbirds: contrasting evolutionary histories of tree line and habitat-generalist clades. *Journal of Biogeography*, *42*, 763–777. <https://doi.org/10.1111/jbi.12452>
- Botero, S., Stevenson, P. R., & Di Fiore, A. (2015). A primer on the phylogeography of *Lagotrix lagotricha* (sensu Fooden) in northern South America. *Molecular Phylogenetics and Evolution*, *82*, 511–517. <https://doi.org/10.1016/j.ympev.2014.05.019>
- Brumfield, R. T. (2012). Inferring the origins of lowland Neotropical birds. *Auk*, *129*, 367–376. <https://doi.org/10.1525/auk.2012.129.3.367>
- Cadena, C. D. (2007). Testing the role of interspecific competition in the evolutionary origin of elevational zonation: An example with *Buarremon* brush-finches (Aves, Emberizidae) in the Neotropical mountains. *Evolution*, *61*, 1120–1136. <https://doi.org/10.1111/j.1558-5646.2007.00095.x>
- Cadena, C. D., Gutiérrez-Pinto, N., Dávila, N., & Chesser, R. T. (2011). No population genetic structure in a widespread aquatic songbird from the Neotropics. *Molecular Phylogenetics and Evolution*, *58*, 540–545. <https://doi.org/10.1016/j.ympev.2010.12.014>
- Cadena, C. D., Klicka, J., & Ricklefs, R. E. (2007). Evolutionary differentiation in the Neotropical montane region: Molecular phylogenetics and phylogeography of *Buarremon* brush-finches (Aves, Emberizidae). *Molecular Phylogenetics and Evolution*, *44*, 993–1016. <https://doi.org/10.1016/j.ympev.2006.12.012>
- Cadena, C. D., Pedraza, C. A., & Brumfield, R. T. (2016). Climate, habitat associations and the potential distributions of Neotropical birds: Implications for diversification across the Andes. *Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales*, *40*, 275–287. <https://doi.org/10.18257/raccefyn.280>
- Claramunt, S., Derryberry, E. P., Chesser, R. T., Aleixo, A., & Brumfield, R. T. (2010). Polyphyly of *Campylorhamphus*, and description of a new genus for *C. pucherani* (Dendrocolaptinae). *Auk*, *127*, 430–439. <https://doi.org/10.1525/auk.2009.09022>
- Cracraft, J. (1985). Historical biogeography and patterns of diversification within the South American areas of endemism. In P.A. Buckley, M.S. F., E.S. Morton, R.S. Ridgely & F.G. Buckley (Eds.) *Ornithological Monographs* (pp. 49–84). The American Ornithologist Union. <https://doi.org/10.2307/40168278>
- Chevron, Z. A., Hackett, S. J., & Capparella, A. P. (2005). Complex evolutionary history of a Neotropical lowland forest bird (*Lepidothrix coronata*) and its implications for historical hypotheses of the origin of Neotropical avian diversity. *Molecular Phylogenetics and Evolution*, *36*, 338–357. <https://doi.org/10.1016/j.ympev.2005.01.015>
- Del Hoyo, J., Elliot, A., & Christie, D. A. (2003). *Handbook of the Birds of the World. Broadbills to Tapaculos*. Lynx Edicions, Barcelona.
- Derryberry, E. P., Claramunt, S., Derryberry, G., Chesser, R. T., Cracraft, J., Aleixo, A. et al. (2011). Lineage diversification and morphological evolution in a large-scale continental radiation: The Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution*, *65*, 2973–2986. <https://doi.org/10.1111/j.1558-5646.2011.01374.x>
- Drummond, A. J., Rambaut, A., & Suchard, M. (2012). BEAST v1.7.4 Bayesian Evolutionary Analysis Sampling Trees. *Department of Computer Science University of Auckland, Institute of Evolutionary Biology University of Edinburgh, David Geffen School of Medicine University of California, Los Angeles*, Available at: <http://beast.bio.ed.ac.uk>
- Drummond, A. J., Suchard, M. A., Xie, D., & Rambaut, A. (2012). Bayesian Phylogenetics with BEAUti and the BEAST 1.7. *Molecular Biology and Evolution*, *29*, 1969–1973. <https://doi.org/10.1093/molbev/mss075>
- Etter, A., McAlpine, C., Wilson, K., Phinn, S., & Possingham, H. (2006). Regional patterns of agricultural land use and deforestation in Colombia. *Agriculture, Ecosystems and Environment*, *114*, 369–386. <https://doi.org/10.1016/j.agee.2005.11.013>
- Fernandes, A. M., Wink, M., Sardelli, C. H., Aleixo, A., & Ebach, M. (2014). Multiple speciation across the Andes and throughout Amazonia: the case of the spot-backed antbird species complex (*Hylophylax naevius/Hylophylax naevioides*). *Journal of Biogeography*, *41*, 1094–1104. <https://doi.org/10.1111/jbi.12277>
- Flantua, S. A., van Boxel, J., Hooghiemstra, H., & van Smaalen, J. (2007). Application of GIS and logistic regression to fossil pollen data in modelling present and past spatial distribution of the Colombian savanna. *Climate Dynamics*, *29*, 697–712. <https://doi.org/10.1007/s00382-007-0276-3>
- Fuchs, J., Chen, S., Johnson, J. A., & Mindell, D. P. (2011). Pliocene diversification within the South American Forest falcons (Falconidae: *Micrastur*). *Molecular Phylogenetics*



- and *Evolution*, 60, 398–407. <https://doi.org/10.1016/j.ympv.2011.05.008>
- GeoNames. (2013). GeoNames geographical database, Retrieved January 15, 2013, from: <http://www.geonames.org/>
- Gill, F., & Donsker, D. (2018). IOC World Bird Names v 8.2, Retrieved September 30, 2018, from: <http://www.worldbirdnames.org>
- Google. (2010). Google Earth. <http://earth.google.com/web/>
- Gregory-Wodzicki, K. M. (2000). Uplift history of the Central and Northern Andes: A review. *Geological Society of America Bulletin*, 112, 1091–1105. [https://doi.org/10.1130/0016-7606\(2000\)112<1091:uhotca>2.3.co;2](https://doi.org/10.1130/0016-7606(2000)112<1091:uhotca>2.3.co;2)
- Haffer, J. (1967). Speciation in Colombian forest birds west of the Andes. *American Museum Novitates*, 1–57.
- Hall, T.A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series*, 41, 95–98.
- Harvey, M. G., & Brumfield, R. T. (2015). Genomic variation in a widespread Neotropical bird (*Xenops minutus*) reveals divergence, population expansion, and gene flow. *Molecular Phylogenetics and Evolution*, 83, 305–316. <https://doi.org/10.1016/j.ympv.2014.10.023>
- Johnson, K. P., & Weckstein, J. D. (2011). The Central American land bridge as an engine of diversification in New World doves. *Journal of Biogeography*, 38, 1069–1076. <https://doi.org/10.1111/j.1365-2699.2011.02501.x>
- Lerner, H. R., Meyer, M., James, H. F., Hofreiter, M., & Fleischer, R. C. (2011). Multilocus resolution of phylogeny and timescale in the extant adaptive radiation of Hawaiian Honeycreepers. *Current Biology*, 21, 1838–1844. <https://doi.org/10.1016/j.cub.2011.09.039>
- Librado, P., & Rozas, J. (2009). DNASP v5: a software for comprehensive analysis of DNA polymorphism data. *Bioinformatics*, 25, 1451–1452. <https://doi.org/10.1093/bioinformatics/btp187>
- Link, A., Valencia, L. M., Céspedes, L. N., Duque, L. D., Cadena, C. D., & Fiore, A. D. (2015). Phylogeography of the critically endangered brown spider monkey (*Ateles hybridus*): Testing the riverine barrier hypothesis. *International Journal of Primatology*, 36, 530–547. <https://doi.org/10.1007/s10764-015-9840-6>
- Lozano-Zambrano, F. H., & Fernández, F. (2007). Aproximación al análisis zoogeográfico de las hormigas cazadoras (Hymenoptera: Formicidae) de Colombia. *Boletín del Museo de Entomología de la Universidad del Valle*, 8, 22–31. <https://doi.org/10.2307/3495802>
- Lynch, J. W., Cortés-Ortiz, L., Di Fiore, A., & Boubli, J. P. (2015). Special issue: comparative biogeography of Neotropical primates. *Molecular Phylogenetics and Evolution*, 82, 518–529. <https://doi.org/10.1016/j.ympv.2014.09.027>
- Marks, B. D., Hackett, S. J., & Capparella, A. P. (2002). Historical relationships among Neotropical lowland forest areas of endemism as determined by mitochondrial DNA sequence variation within the Wedge-billed Woodcreeper (Aves: Dendrocolaptidae: *Glyphorhynchus spirurus*). *Molecular Phylogenetics and Evolution*, 24, 153–167. [https://doi.org/10.1016/s1055-7903\(02\)00233-6](https://doi.org/10.1016/s1055-7903(02)00233-6)
- Miller, M. J., Bermingham, E., Klicka, J., Escalante, P., Amaral, F. S. R. d., Weir, J.T. et al. (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: Biological Sciences*, 275, 1133–1142. <https://doi.org/10.1098/rspb.2008.0015>
- Morrone, J. J. (2014). Biogeographical regionalisation of the Neotropical region. *Zootaxa*, 3782, 1–110. <https://doi.org/10.11646/zootaxa.3782.1.1>
- Naka, L. N., Bechtoldt, C. L., Henriques, L. M. P., & Brumfield, R. T. (2012). The role of physical barriers in the location of avian suture zones in the Guiana Shield, northern Amazonia. *The American Naturalist*, 179, E115–E132. <https://doi.org/10.1086/664627>
- Nores, M. (2004). The implications of Tertiary and Quaternary sea level rise events for avian distribution patterns in the lowlands of northern South America. *Global Ecology and Biogeography*, 13, 149–161. <https://doi.org/10.1111/j.1466-882x.2004.00076.x>
- Nyári, Á. S. (2007). Phylogeographic patterns, molecular and vocal differentiation, and species limits in *Schiffornis turdina* (Aves). *Molecular Phylogenetics and Evolution*, 44, 154–164. <https://doi.org/10.1016/j.ympv.2007.02.020>
- Patel, S., Weckstein, J. D., Patané, J. S. L., Bates, J. M., & Aleixo, A. (2011). Temporal and spatial diversification of *Pteroglossus* aracarís (Aves: Ramphastidae) in the neotropics: Constant rate of diversification does not support an increase in radiation during the Pleistocene. *Molecular Phylogenetics and Evolution*, 58, 105–115. <https://doi.org/10.1016/j.ympv.2010.10.016>
- Posada, D., & Crandall, K. A. (1998). Modeltest: testing the model of DNA substitution. *Bioinformatics*, 14, 817–818. <https://doi.org/10.1093/bioinformatics/14.9.817>
- Rambaut, A., & Drummond, A. J. (2012). TreeAnnotator v1.7.4. *Institute of Evolutionary Biology, University of Edinburgh, Department of Computer Science, University of Auckland*, Available as part of the BEAST package at <http://beast.bio.ed.ac.uk/>
- Restall, R., Rodner, C., & Lentino, M. (2006). *Birds of Northern South America: an identification guide*. Yale University Press, New Haven.
- Rheindt, F. E., Christidis, L., Cabanne, G. S., Miyaki, C., & Norman, J. A. (2009). The timing of Neotropical speciation dynamics: A reconstruction of *Myiopagis* flycatcher diversification using phylogenetic and paleogeographic data. *Molecular Phylogenetics and Evolution*, 53, 961–971. <https://doi.org/10.1016/j.ympv.2009.09.001>
- Romero-Ruiz, M. H., Flantua, S. G. A., Tansey, K., & Berrio, J. C. (2012). Landscape transformations in savannas of northern South America: Land use/cover changes since 1987 in the Llanos Orientales of Colombia. *Applied Geography*, 32, 766–776. <https://doi.org/10.1016/j.apgeog.2011.08.010>
- Sandoval, H., J., Gómez, J. P., & Cadena, C. D. (2017). Is the largest river valley west of the Andes a driver of

- diversification in Neotropical lowland birds? *Auk*, 137, 168–180. <https://doi.org/10.1642/auk-16-91.1>
- Schultz, E. D., Burney, C. W., Brumfield, R. T., Polo, E. M., Cracraft, J., & Ribas, C. C. (2017). Systematics and biogeography of the *Automolus infuscatus* complex (Aves; Furnariidae): Cryptic diversity reveals western Amazonia as the origin of a transcontinental radiation. *Molecular Phylogenetics and Evolution*, 107, 503–515. <https://doi.org/10.1016/j.ympev.2016.12.023>
- Sigris, M. S., & Carvalho, C. J. B. d. (2009). Historical relationships among areas of endemism in the tropical South America using Brooks Parsimony Analysis (BPA). *Biota Neotropica*, 9, 79–90. <https://doi.org/10.1590/s1676-06032009000400009>
- Smith, B. T., Harvey, M. G., Faircloth, B. C., Glenn, T. C., & Brumfield, R. T. (2014). Target capture and massively parallel sequencing of ultraconserved elements for comparative studies at shallow evolutionary time scales. *Systematic Biology*, 63, 83–95. <https://doi.org/10.1093/sysbio/syt061>
- 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. <https://doi.org/10.1038/nature13687>
- Sparman, A. (1788). *Museum Carlsonianum, in quo novas et selectas aves, coloribus ad vivum brevique descriptione illustratas, suasu et sumtibus generosissimi possessoris*. Holmiae: Ex Typographia Regia. Biodiversity Heritage Library. <https://doi.org/10.5962/bhl.title.62901>
- Stephens, M., & Donnelly, P. (2003). A comparison of Bayesian methods for haplotype reconstruction from population genotype data. *American Journal of Human Genetics*, 73, 1162–1169. <https://doi.org/10.1086/379378>
- Stephens, M., Smith, N. J., & Donnelly, P. (2001). A new statistical method for haplotype reconstruction from population data. *The American Journal of Human Genetics*, 68, 978–989. <https://doi.org/10.1086/319501>
- Vieillot, L. J. P. (1818). *Nouveau dictionnaire d'Histoire Naturelle appliquée aux arts , à l'agriculture, à l'économie rurale et domestique, à la médecine, etc*. Paris. <https://doi.org/10.5962/bhl.title.51404>
- Weir, J. T., Bermingham, E., & Schluter, D. (2009). The great American biotic interchange in birds. *Proceedings of the National Academy of Sciences*, 106, 21737–21742. <https://doi.org/10.1073/pnas.0903811106>
- Weir, J. T., & Price, M. (2011). Andean uplift promotes lowland speciation through vicariance and dispersal in *Dendrocincla* woodcreepers. *Molecular Ecology*, 20, 4550–4563. <https://doi.org/10.1111/j.1365-294x.2011.05294.x>
- Weir, J. T., & Schluter, D. (2008). Calibrating the avian molecular clock. *Molecular Ecology*, 17, 2321–2328. <https://doi.org/10.1111/j.1365-294x.2008.03742.x>